Aquatic Monocotyledons of North America

Ecology, Life History, and Systematics

Donald H. Les

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This book is dedicated to Elias Landolt (1926–2013), whose incredible contributions to the study of the world's smallest monocotyledons (duckweeds) represent some of the most remarkable taxonomic insights of the past century.

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Introduction

This book is intended to serve as a companion volume to *Aquatic Dicotyledons of North America* (Les, 2017) and follows a similar format by providing a comprehensive overview of the life history, ecology, and systematics of those monocotyledon species designated as obligate wetland indicators (abbreviated throughout the text as OBL) in North America. Following the previous treatment (Les, 2017), aquatic plants are defined as: “indicative taxa capable of perpetuating their life cycles and continuing their existence in still or flowing standing water or upon inundated or non-inundated hydric soils.” Additional clarification should be sought in the more detailed discussion provided in the previous volume (Les, 2017).

The primary focus of this book is to provide information on the indicative taxa, which include those flowering plant species most readily recognized as being adapted to aquatic habitats. As in the companion volume, the species selected for inclusion here meet the criterion of “indicative” by their recognition as OBL wetland indicators in at least some portion of their North American range (Lichvar et al., 2016; USACE, 2016). Consequently, only those species most likely to occur in aquatic and wetland habitats are included. It is important to emphasize that the OBL category can include species that require water to complete an essential part of their life history, even though they might often appear to be growing on dryland following the subsidence of the water table.

This volume follows version 3.3 of the National wetland plant list (<http://rsgisias.crrel.usace.army.mil/NWPL/>), which designates more than 800 monocotyledon species as OBL North American indicators. Of these, 305 species in 97 genera, 34 families, and 11 orders have been included here in exclusion of species belonging to three graminoid families: Cyperaceae, Juncaceae, and Poaceae (see explanation below). Previous versions of the wetland plant list defined the indicator categories quantitatively, using numerical percentages of occurrence in wetlands as delimiters. However, subsequent versions of the list have abandoned that practice in favor of a qualitative assessment, which delimits the various indicator categories as follows:

1. Obligate (OBL): almost always occur in wetlands
2. Facultative wetland (FACW): usually occur in wetlands, but may occur in non-wetlands
3. Facultative (FAC): occur in wetlands and non-wetlands
4. Facultative upland (FACU): usually occur in non-wetlands, but may occur in wetlands
5. Upland (UPL): almost never occur in wetlands

The life history information summarized here for these OBL taxa is intended to facilitate their evaluation as wetland indicators with respect to the categories defined above.

Although this book focuses strictly on aquatic monocotyledonous flowering plants, it is not a taxonomic guide for aquatic

plant species identification but should be regarded as a source of information on their life history, ecology, and systematics. Necessarily, one must first identify a species in order to apply this information effectively, using one of the several available manuals to facilitate species identifications (e.g., those referenced in Les, 2017). The geographical coverage of this book is restricted to North America, which is defined here as comprising the lower 48 United States, Alaska, and Canada. Because many North American aquatics also are found throughout the world, this reference also should be useful elsewhere. Except for the taxonomic outline, the following remarks essentially reiterate those of the companion volume (Les, 2017), but are repeated here for convenience.

The entries in this book are first organized as follows:

Monocotyledons

Monocotyledons I: Early diverging monocotyledons

A group of uncertain phylogenetic position (Acorales)

Alismatid monocotyledons (Alismatidae)

Aroids

Monocotyledons II: Lilioid monocotyledons (“Liliidae”)

Monocotyledons III: Commelinoid monocots (Commelinidae)

The entries then are grouped secondarily by their respective orders (arranged alphabetically), which except for Alismatales and Arales, closely follow the APG IV classification (APG, 2016). A bracketed number follows each ordinal name to indicate the total number of families recognized. A systematic overview (with text citations) follows each order and indicates specifically those families that contain OBL indicator taxa. An overview of each family containing OBL taxa follows sequentially in alphabetical order. Family names are followed by a bracketed estimate of the total number of genera contained. An overview of each family follows (again with cited references) to summarize information on the systematics and economic importance. Each family treatment ends with an alphabetical list of genera that contain OBL species, listing the taxonomic authority for each genus.

Phylogenetic trees describing ordinal and familial relationships are included whenever available. However, it is important to emphasize that the putative relationships indicated by the organization of this book or by the phylogenetic trees included, *all represent hypotheses rather than fact* and that no assurance can be given regarding their accuracy beyond the conclusions advocated by the relevant studies cited.

The main part of the text focuses on genera and species. Each genus name is arranged alphabetically within a family and is followed (in parentheses) by a common name or names in English and French (when available), with the latter separated by a semicolon. Generic treatments follow the same format, listing first the etymology of the name, major synonyms,

and the global and North American distribution and species numbers. Compilation of synonyms was facilitated by consulting *The Plant List* (2013) (www.theplantlist.org/). “In part” is used for synonyms that do not apply exclusively to the taxon. Asterisks designate nonindigenous distributional regions. Next is a list of any species designated as OBL along with any alternative regional rankings (i.e., FACW, FAC, FACU, or UPL) applied to these species. Generic and species names primarily are those accepted by ITIS (www.itis.gov/); otherwise, nomenclatural deviations are explained in the relevant “Systematics” section.

Following that listing is a description of habitat, which indicates salinity (freshwater to marine) and general community type. The latter includes four categories: lacustrine, palustrine, riverine, and oceanic. Lacustrine refers to those species found primarily in the deeper waters of lakes, riverine to those species preferentially occupying watercourses, and palustrine to “wetland” communities, often including those that occur along the shorelines of rivers and lakes. The pH value given next represents the complete range of values (or a qualitative assessment) reported among the individual species or is listed as “unknown” if reports were not found. The entry for “depth” also summarizes the full range of water depth associated with all the OBL species in the genus.

Life-forms are summarized for all the OBL species discussed. Herbs are herbaceous species where the leaves are scattered along an elongate stem (vittate) or extend from a common basal point (rosulate). For herbs, “emergent” refers to those species where substantial vegetative growth (shoot and leaf production) occurs above the water surface; “submersed” plants grow with their shoots and leaves underwater (excluding flowering portions in some cases); “suspended” plants are those whose shoots and leaves remain buoyant just beneath the water surface without any attachment to the substrate; “floating-leaved” plants produce leaves on the surface of water bodies and are rooted in the substrate; all structures of “free-floating” plants float on the water surface and do not attach to the substrate unless stranded in very shallow water or along shorelines. Woody plants grow only as emergents and include trees (strong ascending trunks exceeding 6 m in height) and shrubs (multiply branched, usually less than 6 m in height).

The section on “key morphology” is somewhat non-traditional in that it describes the genus with respect to the salient characteristics summarized only for the OBL species. Consequently, a measurement such as “to 50 cm” indicates that at least one OBL species in the genus is characterized by this value, even though others might be substantially smaller in stature; or potentially, some of the non-OBL members could be larger. Where several discrete ranges occur among the OBL species, they are separated by a comma, e.g. “to 5–10, 50–60 mm.” The values provided indicate the longest axis of a structure, which is not necessarily its length. For monotypic genera or where a single OBL species exists, the description provided is of that species.

The life history section summarizes information for all OBL species in the genus. For duration, the relevant structure

is indicated in parentheses; for fruits, an indication of frequency is indicated parenthetically as well as the presumed vectors associated with the structures involved in local and long-distance dispersal (additional details are provided within the included species treatments).

The imperilment status is summarized for each species using the data reported by NatureServe (www.natureserve.org/). The global [G] rank and regional ranks (where applicable) are listed for each OBL species using standard abbreviations for the US states and Canadian provinces; the latter are underlined for distinction. Taxa that are secure globally will include only the global [G] ranking. Because infraspecific designations are merged with a species name, the same state or province may appear in different categories when subspecies or varieties are given a different imperilment status. The NatureServe website should be consulted to clarify such discrepancies. It is important to realize that the rankings listed reflect the status when each treatment was prepared and always should be verified because they are updated continually to incorporate various taxonomic and ranking changes.

A general ecological overview of each genus is provided, which indicates the frequency of OBL taxa, and summarizes basic common features such as reproductive modes, pollinators, and seed ecology. When a genus is monotypic, information is excluded from this section and is simply summarized under the species treatment.

Each OBL species within the genus is treated successively in alphabetical order. Species names are highlighted in bold and include the names of taxonomic authorities. Habitat types reported in literature accounts or from specimen label descriptions are listed alphabetically. Some designations (e.g., “dunes”) might appear unusual for aquatic plants, but refer to wet areas (pools, swales, etc.) occurring within these landforms. For additional clarification, adjectives for many of the habitat designations are provided in parentheses. For example, an entry of “prairies (mesic, wet)” would indicate that some records simply have described the habitat as “prairies,” whereas others more specifically have cited “mesic prairies” or “wet prairies.” Elevation data have been determined from literature reports or from specimen databases and represent the highest reliably documented values. Thus, a value of “to 3489 m” does not mean that the plants cannot occur above this specific elevation, but only that the designation represents the highest credible value found in the literature and database searches. Evidently anomalous values (due apparently to conversion errors, etc.) have been excluded at the discretion of the author. All available life history information that could be reasonably extracted from literature accounts and specimen database records is summarized. A conscientious effort has been made to locate information pertaining to reproductive ecology, pollination biology, seed germination, dispersal, and other important life history information for each species. When such information is incomplete or essentially absent for a species, a comment usually is made regarding the need for additional research, hopefully as an inspiration to others.

Where specific organisms are mentioned by their common name (e.g., “honeybees” as pollinators), additional taxonomic

information (e.g., “Insecta: Hymenoptera: Apidae: *Apis*”) is provided parenthetically to enable the reader to more specifically identify the intended taxon. Although it might seem obvious and/or redundant to constantly repeat groups like Aves (birds) and Insecta (insects), this convention has been followed for two reasons. First, a designation simply of “insects (Insecta)” indicates that no additional taxonomic information (e.g., order, family, etc.) was available for that particular entry at the time of consultation. Second, the use of this book by non-English speaking readers hopefully will be facilitated by including the scientific names along with the English common names, with which they might be unfamiliar.

To conserve space, none of the information summarized in the species treatments contains any literature citations; however, any literature from which information has been obtained is compiled at the end of each generic treatment under “References.” Admittedly, although more space efficient, this convention does make it somewhat difficult to track down the original source of a specific entry, especially where lengthy reference lists occur.

Comprehensive lists of “Reported associates” are provided for each species, relative to the information available. The names presented here are those accepted in ITIS (www.itis.gov), except for a relatively few instances of disagreement at the author’s discretion. These lists reflect the reported ecological association of any plant genus or species (including non-angiosperms) with the subject species in a variety of resources including published books and papers as well as various data repositories (see Les, 2017 for additional clarification).

Because these lists summarize data throughout the range of a species, they may or may not provide an accurate account of the likely or possible associations at a particular locality, especially for widespread species. Also, there are many factors that influence the inclusion of species in these lists. Records of imperiled taxa often exclude associated species, even when reported on database records, if those records have been “masked” to ensure site confidentiality (which is a widespread convention). Herbarium records for very weedy species often do not mention many associated species because such plants frequently grow in dense monocultures where associated species may not be evident to a collector. Sometimes the associated reports reflect a broader community that includes the habitat of a species, and it often is difficult to distinguish such reports from those where species might be growing closely together in one portion of a habitat. Consequently, these lists should be viewed as identifying those plants most likely to be found in habitats similar to that of the subject species. At the discretion of the author, highly improbable associations have been omitted, but these occurrences represented relatively few of the records evaluated. Unlike the preceding volume, the genus names of associates have not been abbreviated where multiple species occur. Although less space efficient, this convention made it easier to alphabetize the lists and more readily accommodate any necessary nomenclatural changes during the preparation of the text. Listing the full binomial also makes it easier for users of electronic text versions to search for a particular species.

Because infraspecific taxa are not reported, the accuracy of species identities depends entirely on the source from which the data were obtained. In some cases there will be inaccuracies. For instance, if a source cited only “*Xyris caroliniana*” as an associated species, it is impossible to tell whether the author of the record was referring to *Xyris caroliniana* Walter, rather than to an infraspecific taxon such as *X. caroliniana* var. *olneyi* Alph. Wood, which in this case would represent an entirely different species (i.e., *X. smalliana* Nash). Such errors are unavoidable but hopefully represent only a small fraction of those records reported.

A key rationale for including the listing of ecological associates is to provide an alternative means for evaluating the overall wetland indicator status of a particular species. By enumerating and comparing the wetland designations of all the associated species, one can potentially obtain a more accurate perspective of the typical wetland affinity of a single target species. If the associates of a particular OBL species also are typically designated as OBL, then that species itself would serve as a reliable wetland indicator; however, if the associates commonly include species ranked as facultative or upland, then that species would be a poor wetland indicator overall and a re-evaluation of its OBL status might be warranted.

Following the species accounts is a section on their use by wildlife. The species are discussed alphabetically as consistently as possible. Scientific names (at various ranks determined to provide adequate categorization) are provided for all associated organisms mentioned. In addition to published literature accounts, this information also relied on several websites, which are enumerated in the companion volume (Les, 2017).

The economic importance of species in each genus was summarized primarily from literature accounts and information provided by the Native American Ethnobotany website (<http://naeb.brit.org/>). **CAUTION:** *The information regarding food and medicinal uses of plant species provided in this book does not represent an endorsement of their edibility, medical efficacy, or toxicity; but simply reports information that exists in the literature.* Consequently, no wild plant ever should be used for food or medicinal purposes based solely on the information reported here.

The RHS horticultural database (<http://apps.rhs.org.uk/horticulturaldatabase/>) served as a primary source for information on species that are maintained regularly under cultivation. To provide additional information on weeds, the database on herbicide resistant weeds (www.weedscience.org/summary/home.aspx) was consulted.

The systematics section was compiled with the objective of evaluating recent literature on each included genus to provide reasonable syntheses of appropriate classifications, overviews of phylogenetic relationships, cytological information, hybridization, and other systematically pertinent topics. Although infraspecific taxa are not included in the individual OBL species accounts, they are discussed in this section whenever deemed relevant. Phylogenetic trees have been included whenever available and are provided to convey

current (or at least recent) hypotheses regarding evolutionary relationships among the pertinent groups shown. These trees have been simplified without any indication of branch lengths, internal branch support, or other statistics, which usually can be found in the original source that is referenced in the figure caption. Because the simplified trees depicted here may differ in some respects from those presented in the original citation, the original source always should be consulted for a definitive interpretation.

A convention followed throughout the book is to indicate any taxon (at any rank) that contains at least one OBL species to be set in bold type when appearing on a tree diagram. Non-OBL taxa appearing on diagrams typically appear in lighter-shaded (50% gray) type and also display their wetland indicator status where applicable. In many cases, this representation provides a fair estimate of how many independent

origins of the OBL habit have occurred in the group shown (depending on the accuracy of the given phylogenetic tree, of course). It also is important to realize that taxa occurring only outside of North America never will be designated as OBL (because they have not been ranked), even though they may very well represent true aquatic plants.

The “Distribution” section primarily summarizes the geographical distributions of each species in North America and elsewhere, occasionally adding additional important information not covered in other sections.

Lastly, each genus treatment ends with a list of the primary references from which any specific information conveyed in the preceding account was obtained. A number of “general” references (e.g., Sculthorpe, 1967) were consulted throughout the book and are not listed repetitively in each reference section.

The Monocotyledons

The term “monocotyledons” (or “monocots”) refers anatomically to those flowering plants (angiosperms) having a shoot apex that is lateral to a single embryonic seed leaf, which otherwise is known as the cotyledon (Fahn, 1982). The primary root is short-lived in most of the species, resulting in a proliferation of adventitious roots, which often take on a highly fibrous appearance. All of the species lack secondary growth from a vascular cambium, but some (e.g., *Smilax laurifolia*) possess shoots that appear to be “woody” due to a cork cambium and its associated secondary tissues. Most of the species are small herbs, but some (e.g., *Acoelorrhaphe wrightii*) can reach arborescent stature by means of diffuse secondary growth or a secondary thickening meristem (Esau, 1977; Fahn, 1982). The shoot vasculature of monocots varies, but is organized commonly as a series of scattered bundles, which also occur in some early diverging dicotyledon groups.

A trimerous floral perianth was once thought to reliably distinguish between monocots and dicots; however, many dicot families (e.g., Annonaceae, Aristolochiaceae, Berberidaceae, Cabombaceae, Elatinaceae, Haloragaceae, Lauraceae, Lythraceae, Magnoliaceae, Myristicaceae, Papaveraceae, and Polygonaceae) also possess trimerous flowers. Monocots uniformly possess monosulcate pollen, which occurs also in some dicotyledons.

Monocotyledon leaf venation usually is described as “parallel” because of its superficial appearance as prominent, parallel vascular strands. Technically the veins all connect ultimately through smaller lateral veins, rather than ending blindly within the mesophyll as in dicot leaves (Fahn, 1982). Sheathed leaves are common in the group. Although toothed leaf margins are generally uncommon in monocots, a number of aquatic species (e.g., many Hydrocharitaceae) do possess serrate foliage. Compound leaves occur rarely (except for the families Araceae and Arecaceae), and are found in only one OBL monocot (Arecaceae: *Acoelorrhaphe wrightii*). Many monocots possess linear or elongate “grass-like” leaves, which are described as “graminoid” (see below).

Monocotyledons have long been regarded as a monophyletic group and numerous phylogenetic analyses have substantiated that conclusion (Judd et al., 2016). However, their conceptual systematic relationship to dicotyledons has changed considerably over the past decades as a consequence of those same analyses. The long-standing concept of monocots and dicots representing two distinct sister clades was first seriously questioned as the result of a phylogenetic analysis of plastid (*rbcL*) gene sequence data, which resolved the clade as embedded within the monosulcate dicotyledons (Chase et al., 1993). Although most molecular studies have shown similar results, they have relied on highly divergent sequences (e.g., gymnosperms or *Amborella*) as outgroups, the consequences of which are not fully understood.

One problem is that despite its association with various monosulcate dicot families, the monocot clade resolves in different positions among them. In many cases, the topology of the angiosperm clade is such that simply moving the root actually can resolve the monocots and dicots as sister clades. These factors stress a precarious reliance on divergent outgroup sequences to place the angiosperm root properly in phylogenetic analyses. In other cases, the topology rendered obviously is problematic. Notable examples include profile alignments of 18s+26s rDNA data, which resolve the anomalous dicotyledon family Ceratophyllaceae within the monocots as the sister group of Tofieldiaceae (Maia et al., 2014), and *PHYC* data or cpDNA genome sequences, which place Acoraceae among the dicotyledons (Goremykin et al., 2005; Hertweck et al., 2015). As yet, it seems best to accept the monocots as a clade, but one for which a precise phylogenetic placement within the angiosperms remains equivocal.

Plants with grass-like foliage are found throughout the monocots but occur predominately in three families (Cyperaceae, Juncaceae, and Poaceae), which are denoted here as the “graminoid monocots.” Although these families are rich in wetland species (comprising about 65% of all OBL monocots), more than half of their OBL species belong to just

four genera (*Carex*, *Eleocharis*, *Juncus*, and *Rhynchospora*), making it difficult to treat them while avoiding excessively redundant information. Moreover, because of their highly modified structure, the species in these families are notoriously difficult to identify, and therefore, less useful as

wetland indicators to those who are not taxonomic specialists in these groups. Because their inclusion in a book of this nature (which relies on the prior identification of a species) would be of questionable utility, the three graminoid families have been excluded.

1 Monocotyledons I

Early Diverging Monocotyledons

A GROUP OF UNCERTAIN PHYLOGENETIC POSITION (ACORALES)

ORDER 1: ACORALES [1]

1.1. Acoraceae Martinov

Family 1.1. Acoraceae [1]

Because the Acorales contain only the single extant family Acoraceae, the two groups are discussed here simultaneously, with the characteristics of the order being those of the family. Acorales/Acoraceae (as *Acorus*) had been assigned formerly to the family Araceae (Arales). However, morphological and molecular evidence (e.g., Grayum, 1987; Duvall, 1993a) convincingly indicated that *Acorus* should be assigned to its own family (i.e., Acoraceae), a conclusion that later was substantiated by several phylogenetic analyses, which allied the group with other early diverging monocots but in various topological positions (Figure 1.1). Although many authors accept without reservation that Acorales represent the sister group of all monocotyledons, the fundamentally different placement of this clade in different phylogenetic analyses (e.g., Petersen et al., 2016) indicates that the question of its relationship to other monocots is still far from being settled.

Acoraceae contain fewer than six species, all within the genus *Acorus*. The family is distinctive and undeniably monophyletic, although no more than three of the presumed taxa (Ryuk et al., 2014) have yet been analyzed simultaneously in comparative genetic studies. All of the species are aromatic, rhizomatous perennial herbs with equitant, elongate, gladiate leaves. The leaf apex is acute and bent asymmetrically as in the genus *Iris* (Iridaceae), with which it can be confused when found in vegetative condition. The flowers of all species are bisexual, trimerous (six tepals), and arranged densely in a cylindrical spadix, which is associated with a sympodial, spathe-like leaf. The flowers are pollinated either by insects (Insecta) or by wind. The berrylike fruits have thin but leathery pericarps, which are dispersed abiotically by water.

The family is distributed widely throughout the temperate Northern Hemisphere and extends into the higher elevations of tropical Asia; some species have been introduced to the Southern Hemisphere (Thompson, 2000a).

Acorus plants have been used in traditional medicinal practices throughout many parts of the world. Numerous cultivars exist, which are planted as marginal water garden ornamentals.

The OBL North American indicators occur within one genus:

1.1.1. *Acorus* L.

1.1.1. *Acorus*

Ratroot, sweetflag; acore, belle-angélique

Etymology: from the Latin *ācor*, meaning “sour taste”

Synonyms: *Calamus* Garsault [nom. illeg.]

Distribution: **global:** Africa; Asia; North America; **North America:** widespread

Diversity: **global:** 3–6 species; **North America:** 2 species

Indicators (USA): obligate wetland (OBL): *Acorus americanus*, *A. calamus*

Habitat: freshwater; palustrine; **pH:** 5.5–8.6; **depth:** <1 m; **life-form(s):** emergent herb

Key morphology: rhizomes (to 25 cm) branched, aromatic, pinkish, thick; leaves basal, aromatic, equitant, sessile, the blades (to 175 cm) gladiate, flattened medially, the apex acute, bent asymmetrically; inflorescence a dense, cylindrical spadix (to 9 cm), projecting laterally from a sympodial, leaflike bract (to 184 cm); flowers (to 4 mm) numerous (to 652), radial; tepals (to 4 mm) 6; stamens 6; ovary 1, 3-locular; berries (to 6 mm) obpyramidal, the pericarp thin, leathery; seeds (to 4 mm) 1–14, apical, embedded in mucilage

Life history: **duration:** perennial (rhizomes); **asexual reproduction:** rhizomes; **pollination:** insect or wind (uncertain); **sexual condition:** hermaphroditic; **fruit:** leathery berries (absent or common); **local dispersal:** water (rhizome fragments, seeds); **long-distance dispersal:** water (seeds)

Imperilment: **1.** *Acorus americanus* [G5]; SH (DE, MT); S1 (GA, NE, NJ, PA); S2 (BC, NE, OH); S3 (AB, IL, ND, PE); **2.** *A. calamus* [G4]; S1 (CO, MS); S2 (NC); S3 (IA)

Ecology: **general:** All *Acorus* species are obligate wetland plants, which occur only where high substrate moisture levels are maintained. They grow in open meadow-like exposures along with a variety of other graminoid wetland plants. The pollination biology of *Acorus* is uncertain but is assumed to be mediated by insects or wind. Although the triploid taxa are sterile, fairly high fertility can occur in diploids or tetraploids. The spadices of some diploid species emit a large volume of volatile floral substances (e.g., tetrahydrofurans), which are believed to attract insects. In fertile plants, the seeds are morphophysiologically dormant and require a period of cold stratification to induce germination. They are dispersed by water and will lose viability if stored dry for extended periods. The plants reproduce vegetatively by the extension of thick rhizomes, which can fragment; the fragments also are dispersed by water, particularly along watercourses. Due to taxonomic confusion between the following two species (see *Systematics*), it is possible that some of the subsequent

FIGURE 1.1 The groups of early diverging monocotyledons (i.e., Acoraceae, Alismatidae, Araceae, Tofieldiaceae) represent distinct clades; however, their interrelationships remain tenuous as indicated by the varied results obtained in different phylogenetic analyses (A–E). Although many authors have redefined the order “Alismatales” to include Alismatidae, Araceae, and Tofieldiaceae, such a disposition is inconsistent with several of these analyses (e.g., A, B, D). In contrast, the present treatment recognizes Alismatales as one of the two major clades resolved consistently within the alismatid monocots (Alismatidae).

information was assigned incorrectly in the literature consulted; however, care was taken to minimize that possibility.

1.1.1.1. *Acorus americanus* (Raf.) Raf. inhabits bogs, bottomlands, coves, depressions, ditches, fens, floodplains, levees, marshes, meadows, mudflats, prairies, seeps, swales, swamps (in openings), and the margins of lakes, ponds, reservoirs, rivers, streams, and swamps at elevations to 915 m. The plants can tolerate shallow standing water and grow primarily in exposures that receive full sunlight. The best growth occurs in freshwaters, with declining growth rates observed at 25–100 mM NaCl concentrations. Conductivity levels are low to moderate (10–240 $\mu\text{mhos cm}^{-1}$) with low alkalinity (5–115 $\text{mg l}^{-1} \text{CaCO}_3$). Reported substrates span a range of acidity (pH: 5.5–8.6) and include clay, loam, muck, and mud. Experimentally, the plants grow optimally at pH 7.0 but decline substantially at pH levels >8. Flowering occurs from May to September, with fruiting extending into October. Although the precise pollination mechanism is unknown, each spadix can produce from 492 to 652 berries yielding a total of 1,700–2,700 seeds. The seeds are dispersed by water. They can be stored in water (at 1°C–3°C) in which viability will be retained for at least 7 months. The seeds are dormant and require a period of cold stratification and light in order to germinate. Satisfactory germination has been reported for seeds dried at 20°C–25°C, then stratified at 2°C–4°C for 4 weeks, and then incubated under a 25°C/15°C day/night

temperature regime. Under those conditions, the seedlings emerge after 10–30 days. The plants also can be cultivated readily using rhizome cuttings. The plants lack drought tolerance adaptations, but develop drought avoidance characteristics such as fewer stomata having smaller pores, and produce less biomass when growing under water-deprived conditions.

Reported associates: *Acer saccharinum*, *Agalinis purpurea*, *Alisma*, *Alopecurus aequalis*, *Amorpha fruticosa*, *Apocynum cannabinum*, *Arnoglossum plantagineum*, *Asclepias incarnata*, *Betula nigra*, *Bidens laevis*, *Boehmeria cylindrica*, *Bolboschoenus fluviatilis*, *Calamagrostis canadensis*, *Calla palustris*, *Carex aquatilis*, *Carex cristatella*, *Carex haydenii*, *Carex hystericina*, *Carex lacustris*, *Carex pellita*, *Carex stricta*, *Carex utriculata*, *Carex vesicaria*, *Carex vulpinoidea*, *Cephalanthus occidentalis*, *Chelone glabra*, *Cicuta bulbifera*, *Clinopodium glabrum*, *Comarum palustre*, *Cornus amomum*, *Cornus racemosa*, *Crataegus*, *Cyperus strigosus*, *Dasiphora floribunda*, *Deschampsia cespitosa*, *Dulichium arundinaceum*, *Echinochloa crus-galli*, *Eleocharis palustris*, *Equisetum fluviatile*, *Eupatorium perfoliatum*, *Eutrochium maculatum*, *Filipendula rubra*, *Galium obtusum*, *Galium triflorum*, *Gentiana andrewsii*, *Glyceria grandis*, *Glyceria striata*, *Gratiola aurea*, *Helenium autumnale*, *Helianthus grosseserratus*, *Hippuris vulgaris*, *Howellia aquatilis*, *Hypericum kalmianum*, *Hypericum sphaerocarpum*, *Impatiens capensis*, *Iris pseudacorus*, *Iris virginica*, *Juncus dudleyi*, *Juncus nodosus*, *Juncus torreyi*, *Leersia oryzoides*, *Liparis loeselii*, *Lobelia spicata*, *Lycopus americanus*, *Lycopus uniflorus*, *Lysimachia ciliata*, *Lysimachia quadriflora*, *Lysimachia thyrsiflora*, *Lythrum alatum*, *Lythrum salicaria*, *Mimulus ringens*, *Muhlenbergia mexicana*, *Myosotis scorpioides*, *Osmunda regalis*, *Parnassia glauca*, *Pedicularis lanceolata*, *Peltandra virginica*, *Persicaria amphibia*, *Persicaria coccinea*, *Persicaria hydropiperoides*, *Persicaria maculosa*, *Persicaria pensylvanica*, *Persicaria punctata*, *Phalaris arundinacea*, *Phleum*, *Phlox glaberrima*, *Physostegia virginiana*, *Platanthera flava*, *Platanthera leucophaea*, *Populus deltoides*, *Prenanthes racemosa*, *Pycnanthemum virginianum*, *Rumex britannica*, *Sagittaria cuneata*, *Sagittaria latifolia*, *Salix exigua*, *Salix interior*, *Salix nigra*, *Schoenoplectus acutus*, *Schoenoplectus tabernaemontani*, *Scolochloa festucacea*, *Scutellaria galericulata*, *Sium suave*, *Solidago gigantea*, *Solidago ohioensis*, *Solidago riddellii*, *Sparganium emersum*, *Sparganium eurycarpum*, *Spartina pectinata*, *Sphagnum*, *Stachys pilosa*, *Stellaria longifolia*, *Symphyotrichum ericoides*, *Symphyotrichum firmum*, *Symphyotrichum laeve*, *Symphyotrichum novae-angliae*, *Thelypteris palustris*, *Triadenum virginicum*, *Typha angustifolia*, *Typha latifolia*, *Verbena hastata*, *Veronicastrum virginicum*, *Viburnum lentago*, *Zizania aquatica*.

1.1.1.2. *Acorus calamus* L. is a nonindigenous species, which grows in bogs, brooks, canals, depressions, ditches, floodplains, marshes, meadows, pools, prairies, rivulets, roadsides, seeps, sloughs, springs, swales, swamps (openings), and along the margins of lakes, ponds, reservoirs, rivers, and streams at elevations to 1060 m. The plants will tolerate shallow standing water (5–45 cm deep) and primarily occupy exposures of full sunlight. The substrates,

primarily silt (~49%) and sand (~37%), tend to be acidic (pH: <6) but can span a broader range (pH: 5.6–7.2). The nitrogen content of sediments tends to be low (e.g., 3.2 µg l⁻¹), but the organic matter (1–2%) and clay (e.g., 14%) content are relatively high. The substrates are described as alluvium, clay, gravel, humus, loam, muck, mud, and sand. Flowering occurs from May to October (fruiting is not observed in North America). Although sexually sterile, the plants can disperse effectively by vegetative propagules derived from rhizome fragments. These propagules are dispersed by water, wherein they can remain buoyant for at least 6 months and retain an adequate capacity (e.g., 58%) to resprout. Rhizome length has been found to correlate positively with aluminum, calcium, and magnesium levels in the sediment. The rhizomes are tolerant of flooding or drawdown conditions, light or moderate shade, and nitrogen limitation.

Reported associates (North America): *Acer saccharinum*, *Alisma subcordatum*, *Amphicarpa bracteata*, *Angelica atropurpurea*, *Asclepias incarnata*, *Asparagus*, *Boehmeria cylindrica*, *Calamagrostis canadensis*, *Caltha palustris*, *Carex conjuncta*, *Carex crus-corvi*, *Carex frankii*, *Carex grayi*, *Carex jamesii*, *Carex leavenworthii*, *Carex lupulina*, *Carex muskingumensis*, *Carex typhina*, *Celtis occidentalis*, *Cephalanthus occidentalis*, *Chasmanthium latifolium*, *Cladium mariscoides*, *Convolvulus sepium*, *Cyperus*, *Dulichium arundinaceum*, *Equisetum arvense*, *Festuca subverticillata*, *Fraxinus pennsylvanica*, *Fraxinus profunda*, *Glyceria striata*, *Gratiola aurea*, *Hypericum mutilum*, *Hypericum prolificum*, *Impatiens capensis*, *Iodanthus pinnatifidus*, *Iris pseudacorus*, *Juglans*, *Laportea canadensis*, *Leersia oryzoides*, *Leersia virginica*, *Lemna minor*, *Lolium perenne*, *Lycopus virginicus*, *Lysimachia ciliata*, *Lysimachia thyrsiflora*, *Mentha*, *Parthenocissus*, *Pastinaca sativa*, *Persicaria amphibia*, *Persicaria punctata*, *Phalaris arundinacea*, *Phalaris arundinacea*, *Phleum pratense*, *Pilea pumila*, *Poa nemoralis*, *Prunella vulgaris*, *Rhus*, *Robinia pseudoacacia*, *Rosa*, *Rubus occidentalis*, *Rumex*, *Sagittaria latifolia*, *Salix interior*, *Salix nigra*, *Sambucus*, *Sanicula canadensis*, *Scirpus*, *Scutellaria lateriflora*, *Solidago*, *Sparganium eurycarpum*, *Spiraea*, *Symphyotrichum lanceolatum*, *Symphyotrichum lateriflorum*, *Symphyotrichum ontarionis*, *Symplocarpus foetidus*, *Toxicodendron radicans*, *Typha latifolia*, *Ulmus americana*, *Utricularia macrorrhiza*, *Verbena hastata*, *Viola sororia*, *Vitis cinerea*, *Vitis riparia*.

Use by wildlife: *Acorus americanus* and *A. calamus* rhizomes are eaten by muskrats (Mammalia: Cricetidae: *Ondatra zibethicus*) and other mammals. Neither species is particularly valued as a waterfowl food but the seeds of *A. calamus* are eaten by redhead ducks (Aves: Anatidae: *Aythya americana*). The foliage is used as cover by waterfowl. The plants are rated as highly resistant to grazing by deer (Mammalia: Cervidae: *Odocoileus*). The leaves of *A. americanus* are oviposition sites for damselflies (Insecta: Odonata: Aeshnidae: *Aeshna constricta*). *Acorus calamus* is a host to several Fungi (Ascomycota: Glomerellaceae: *Colletotrichum*; Dermateaceae: *Cylindrosporium acori*; Mycosphaerellaceae: *Ramularia aromatica*, *Septocylindrium*, *Sphaerulina acori*;

Phaeosphaeriaceae: *Phaeosphaeria acori*; Basidiomycota: Ceratobasidiaceae: *Rhizoctonia solani*; Doassansiaceae: *Nannfeldtiomyces sparganii*; Pucciniaceae: *Nigredo pyriiformis*, *Uromyces pyriformis*; *U. sparganii*; Oomycota: Pythiaceae: *Pythium*).

Economic importance: food: Consumption of *Acorus* can be dangerous given its potentially toxic properties, and its use as food is not recommended. Deleterious effects can include constipation, diarrhea, digestive disorders, gastroenteritis, and internal bleeding. Some constituents (e.g., β-asarone) are known to induce tumors in laboratory animals. However, the young flower stems and leaf stalks, which emerge in early spring, reportedly are edible in raw form and the candied rhizomes have been made into a confection. Because *A. americanus* lacks the carcinogenic β-asarone and its phenylpropane derivatives, presumably it would be less dangerous to consume; **medicinal:** The medicinal and pharmacological literature on *Acorus* is voluminous. The essential oil of *Acorus* contains over 240 volatile components, including β-asarone, β-farnesene, cis-methylisoeugenol, epishyobunone, geranylacetate, isoshyobunone, methyleugenol, and shyobunone. Concentrations of these substances can differ widely among the taxa; e.g., β-asarone, which occurs at low levels (5%) in *A. calamus* but is absent in *A. americanus*. The plants have been used for centuries to treat numerous ailments worldwide. The rhizomes of *A. americanus* contain α-asarone (similar chemically to the alkaloid mescaline), which is a stimulant at low concentrations but hallucinogenic if ingested in “higher” amounts; β-asarone also is hallucinogenic. Both the essential oil and the asarones are smooth muscle relaxants, having effects similar to those of papaverine (a constituent of opium). The oils also have a wide range of antibacterial and fungicidal properties. *Acorus* species produce lectins, which are mitogenic to human lymphocytes and inhibitory to some cancer cell lines. Many indigenous North American tribes regarded *Acorus* as a medicinal panacea. The plants were particularly important medicinally to the Aboriginal inhabitants of Alberta, Canada. The Chippewa, Hock, Ojibwa, and Potawatomi people used small amounts of the plants to treat colds. The Meskwaki treated burns and sores from boiled rhizome extracts. In other parts of North America the plants have been used as a stimulant and also to treat diabetes, diarrhea, fever, flatulence, heartburn, hyperlipidity, indigestion, liver disorders, pain, rheumatism, stomach upset, and many other disorders; **cultivation:** *Acorus* was first cultivated in Europe during the 16th century and is grown today as an ornamental marginal plant for water gardens. Cultivars of *A. calamus* include ‘Argenteostriatus’, ‘Purpureus’, and ‘Variegatus’; **misc. products:** *Acorus* has long been used for various ceremonial purposes, with remains of the plants recovered from the tomb of King Tutankhamen (dating to the 14th century BC). In modern times, *A. americanus* extracts have been sprayed around camping tents to repel spiders (Arthropoda: Arachnida: Araneae) and snakes (Reptilia: Squamata: Serpentes). Essential oils from the rhizome of *A. calamus* have been used as a household deodorant, as a flavoring for alcoholic beverages (e.g., beer, bitters, gin, vermouth, and wine), as a perfume essence, as a pest repellent,

for ritual oils, and to tan leather. The matted foliage was once used as a floor covering. Exposure to the volatile oils of *A. calamus* causes sterility in male domestic house flies (Insecta: Diptera: Muscidae: *Musca domestica*); **weeds:** *Acorus calamus* can compete with more useful wildlife plants; **nonindigenous species:** The introduction of *Acorus calamus* to North America probably occurred during the mid-18th century.

Systematics: Although the systematic position of *Acorus* remains uncertain, even after the phylogenetic evaluation of a large amount of molecular data (e.g., Figure 1.1), the genus clearly is monophyletic. However, the taxonomy of the genus itself is problematic, with no consensus on the number of species that should be recognized. Molecular phylogenetic analyses have distinguished at least three distinct taxa: *A. calamus*, *A. gramineus* (much smaller in stature), and *A. angustatus* (= *A. tatarinowii*, etc.). The latter possibly is conspecific with *A. americanus* (not included in simultaneous phylogenetic analyses), but this issue has not yet been resolved. The chloroplast genome sequences of *A. americanus* and *A. calamus* in GenBank are virtually identical (>99.9% sequence identity), which indicates that the triploid (or hexaploid) *A. calamus* likely is derived from an ancestor similar to the diploid (or tetraploid) *A. americanus* (or *A. angustatus* if conspecific with the latter). Some of the taxonomic problems are associated with inconsistent cytological observations. The basic chromosome number of *Acorus* has been difficult to determine due to numerous conflicting accounts. It is widely regarded as $x=12$, with the fertile *A. americanus* ($2n=24$) interpreted as diploid and the sterile *A. calamus* ($2n=36$) as a triploid. Tetraploid ($2n=48$) and hexaploid ($2n=72$) races of *A. calamus* also have been reported outside of North America. However, other researchers have found $x=7$ (and an aneuploid derivative $x=9$) as the base numbers in numerous Asian accessions. Several other “anomalous” counts reported (e.g., $2n=54$, 66, 72) could be explained readily by a base number of $x=6$ (rather than 12), which also would accommodate the more widely accepted counts. In that case, *A. americanus* would represent a tetraploid and *A. calamus* a hexaploid. A more definitive cytological assessment of *Acorus* seems necessary in order to reconcile these inconsistencies.

Distribution: *Acorus americanus* is distributed across northern North America; *A. calamus* is widespread throughout the eastern United States and occurs sporadically in the western United States and eastern Canada.

References: Angier, 1974; Azuma & Toyota, 2012; Bains et al., 2005; Baskin & Baskin, 1998; Beal, 1977; Bogner & Mayo, 1998; Calvo-Polanco et al., 2014; Cottam, 1939; Crothers, 2012; Davis et al., 2004; Dolan, 2014; Dozier, 1945; Duvall et al., 1993a; Elmore et al., 2016; Fernald & Kinsey, 1943; Geiger & Banker, 2012; Haines, 2000a; Kindscher & Hurlburt, 1998; Kumar & Singh, 2015; Les & Mehrhoff, 1999; Marles, 2001; Mathur & Saxena, 1975; Morgan, 1980; Morton, 1963; Motley, 1994; Muenscher, 1936a; Nichols, 1999; Packer & Ringius, 1984; Pai & McCarthy, 2005; 2010; Perdomo et al., 2004; Petersen et al., 2016; Romanello et al., 2008; Rudgley, 1999; Sarneel, 2013; Smreciu et al., 2014; 2015; Stevenson et al., 2000; Strong, 2000; Tamura et al., 2004;

Thompson, 2000a; Wang et al., 2001; Wein, 1939; 1940a; 1940b; Wieffering, 1972.

ALISMATID MONOCOTYLEDONS (ALISMATIDAE)

The alismatid monocotyledons consist entirely of aquatic and wetland species, which represent the greatest hydrophyte radiation within the angiosperms. All of the North American members are designated as OBL indicators throughout their ranges. The 11–12 “core” families (a distinction between Cymodoceaceae and Ruppiaceae remains unsettled) comprise a distinct, monophyletic group, which has been recognized at various taxonomic levels (Les & Tippet, 2013; Ross et al., 2016). Although once included in the group, the families Petrosaviaceae and Triuridaceae now are regarded as unrelated (Les & Tippet, 2013).

A long-standing tradition has been to treat this aquatic clade as a subclass (Alismatidae) containing two to four orders (e.g., Takhtajan, 1969; Cronquist, 1981). Older literature refers to the same taxon by the illegitimate ordinal name Helobiae. However, many recent authors (e.g., APG, 2016) have adopted a broader classification circumscribing one large order (Alismatales sensu lato), which contains the alismatid clade along with the former members of Arales (Araceae, Lemnaceae), and Tofieldiaceae. Although the broader concept of Alismatales has been widely followed, several phylogenetic studies (e.g., Figure 1.1A, B, D) do not support that assemblage as monophyletic. Until more consistent and compelling phylogenetic information is available, it seems prudent to restrict the circumscription of alismatids to include only the core families while excluding Araceae, Lemnaceae, and Tofieldiaceae (Les & Tippet, 2013). Full plastid genome sequence analyses (Ross et al., 2016) also indicate that the core alismatids are quite distinct genetically from both Arales and Tofieldiaceae, which also would argue for the distinction of these groups as smaller, ordinal subdivisions. Consequently, the treatment followed here is to recognize the alismatids as a subclass (Alismatidae) containing the twelve core aquatic families (Figure 1.2).

The Alismatidae can be subdivided effectively into two orders. Various molecular phylogenetic analyses (e.g., Les et al., 1993; 1997c; Les & Haynes, 1995; Les & Tippet, 2013; Ross et al., 2016) consistently have resolved two major clades within the group. These clades correspond with distinct (i.e., petaloid vs. tepaloid) floral morphologies (Posluszny et al., 2000) and have been recognized respectively as the orders Alismatales (sensu stricto) and Potamogetonales (Les & Tippet, 2013), which is the convention followed here (Figure 1.2). In this interpretation, the Alismatidae contain 12 families, 57 genera, and about 480 species.

Alismatids are highly diverse, making it difficult to identify consistent synapomorphic traits. Although the group is regarded as representing unspecialized or “primitive” monocots by its inclusion of plants having a combination of polypetalous, hermaphroditic flowers with radial symmetry, apocarpous gynoecia, and numerous stamens and carpels, it also contains many species having derived traits such as

FIGURE 1.2 Phylogenetic relationships of alismatid families as indicated by a likelihood analysis of 83 plastid gene sequences (adapted from Ross et al., 2016). The North American families containing OBL indicators are highlighted in bold (Ruppiaceae are merged with Cymodoceaceae in the present treatment).

unisexuality, syncarpy, epigyny, and the only known flowering plants adapted to life in marine habitats. The subclass also exhibits a broad spectrum of pollination mechanisms incorporating biotic (Insecta) and abiotic (water, wind) vectors as well as self-pollination (Les, 1988; Les et al., 1997a). Representatives of the subclass are found throughout the world.

ORDER 2: ALISMATALES [3]

In molecular phylogenetic analyses, Alismatales consistently comprise a well-defined clade which is sister to the Potamogetonales (Figure 1.2). Referred to commonly as the “petaloid clade,” these species are distinguished from other Alismatidae by having well-differentiated perianths consisting of both a calyx and corolla (Posluszny & Charlton, 1993; Posluszny et al., 2000). Most of the flowers are relatively showy and entomophilous. In some species they are unisexual and arranged in dioecious or monoecious sexual conditions. Until recently, the order segregated *Butomopsis*, *Hydrocleys*, and *Limnocharis* as a fourth family, Limnocharitaceae. Although these three genera associate as a clade, phylogenetic analyses resolve them as being nested in Alismataceae, within which they have been subsumed (Les & Tippery, 2013; Ross et al., 2016).

Alismatales are cosmopolitan in distribution. The order contains three families, all having OBL North American representatives:

- 2.1. **Alismataceae** Ventenat
- 2.2. **Butomaceae** Mirbel
- 2.3. **Hydrocharitaceae** Jussieu

Family 2.1. Alismataceae [17]

The water-plantains (Alismataceae) are herbaceous annuals (rarely) or rhizomatous perennials, which grow in standing water or in wetlands. Their foliage commonly contains laticifers (except *Sagittaria*) and abundant air-space lacunae. The leaves typically are basal and are differentiated into blade and petiole, except when growing

under submersed conditions when they can assume an elongate, graminoid shape (Sculthorpe, 1967; Cronquist, 1981; Judd et al., 2016). The hypogynous flowers are perfect or unisexual, often in whorls, and consist of a well-differentiated perianth of three sepals and three white, pink, or yellowish petals, six–numerous stamens, and an apocarpous gynoecium of three–numerous pistils; the fruits are aggregates of achenes or follicles (Cronquist, 1981; Haynes & Holm-Nielsen, 1994; Haynes et al., 1998a; Judd et al., 2016). Pollination of the nectariferous flowers is facilitated by insects (Insecta: Diptera; Hymenoptera). The fruits are dispersed by water or transported endozoically by waterfowl (Aves: Anatidae).

The family includes three genera (*Butomopsis*, *Hydrocleys*, *Limnocharis*), which formerly were assigned to Butomaceae or were segregated as the family Limnocharitaceae. However, most molecular phylogenetic analyses (e.g., Figure 1.3) resolve these genera as embedded within the clade containing the traditional genera of Alismataceae, where they have been included here. However, conflicting phylogenetic results have been obtained by analyses incorporating morphological characters, which resolve the “Limnocharit” genera as a basal grade of Alismataceae (Lehtonen, 2009).

Members of some genera (e.g., *Echinodorus*, *Hydrocleys*, *Limnocharis*, *Sagittaria*) are grown as ornamental water garden specimens. The underground organs of some species have been used as a source of food or medicine.

Alismataceae have a nearly cosmopolitan distribution. OBL indicators occur in six North American genera:

- 2.1.1. *Alisma* L.
- 2.1.2. *Damasonium* Mill.
- 2.1.3. *Echinodorus* Rich. & Engelm. ex A. Gray
- 2.1.4. *Helanthium* (Benth. & Hook.f.) Engelm. ex J.G.Sm.
- 2.1.5. *Hydrocleys* Rich.
- 2.1.6. *Sagittaria* L.

2.1.1. *Alisma*
Water plantain; plantain d’eau

FIGURE 1.3 Intergeneric relationships in Alismataceae as indicated by a likelihood analysis of 83 plastid gene sequences (adapted from Ross et al., 2016). The North American groups containing OBL indicators are highlighted in bold.

Etymology: an ancient name of unknown meaning but possibly derived from alcea, another Greek name for these plants

Synonyms: none

Distribution: **global:** nearly cosmopolitan; **North America:** widespread

Diversity: **global:** 9 species; **North America:** 4 species

Indicators (USA): obligate wetland (OBL): *Alisma gramineum*, *A. lanceolatum*, *A. subcordatum*, *A. triviale*

Habitat: brackish to freshwater; lacustrine, palustrine, riverine; **pH:** 4.5–9.6; **depth:** <1 m; **life-form(s):** emergent herb, floating-leaved, submersed (rosulate)

Key morphology: plants (to 1 m) arising from a corm-like rhizome (to 3.5 cm) with non-septate roots; leaves basal, the blades (to 35 cm) linear-lanceolate to elliptic or ovate and petiolate (to 55 cm) when emersed or floating, linear (to 100 cm) and sessile when submersed, the margins entire; panicles (to 1 m) spreading, with whorls (to 10) of verticillate cymes containing pedicellate (to 47 mm) flowers; flowers bisexual, radial, cleistogamous (submersed) or chasmogamous (emergent); perianth 3-merous, differentiated into calyx and corolla, petals (to 6.5 mm) pink, purplish, or white; stamens 6–8; gynoecium apocarpous, the pistils (to 28) arranged in a flat ring (to 8 mm); achenes (to 3.1 mm) compressed laterally

Life history: **duration:** perennial (rhizomes); **asexual reproduction:** rhizomes (lateral); **pollination:** insect, self; **sexual condition:** dioecious, hermaphroditic, monoecious; **fruit:** aggregates of achenes or follicles (common); **local dispersal:** seeds (water); **long-distance dispersal:** seeds (birds)

Imperilment: **1.** *Alisma gramineum* [G5]; S1 (CA, MB); S2 (NY, WY); S3 (AB, BC, QC, SK); **2.** *A. lanceolatum* [G4]; **3.** *A. subcordatum* [G5]; S1 (MS, NB, WY); S3 (NC, QC); **4.** *A. triviale* [G5]; S1 (NE, NJ, PA, YT); S2 (IL); S3 (OH, WY)

Ecology: general: *Alisma* is entirely aquatic and all of the North American species are designated as OBL indicators throughout their ranges. The genus is perennial, with some species behaving on occasion as annuals. The flowers contain septal nectaries and are produced in profusion, numbering up

to 1,000 in some plants. They are self-compatible and lack dichogamy, but can be self-pollinating or outcrossed by small insects such as flies (e.g., Insecta: Diptera: Syrphidae) and also by the wind. Submersed, self-pollinating, cleistogamous flowers are produced in some species. The average seed set typically is high, in the range of 88–96%. The seeds are buoyant, dispersed by water, and can remain afloat for extended periods of up to several months. Some seeds reportedly can germinate without treatment but nearly all become physiologically dormant and require a period of cold stratification (e.g., 30–210 days at 2°C) for optimal germination (at 20°C or 25°C/15°C). Germination rates typically are low, usually only 5–10%. Slightly higher rates (to 15%) occur under maximum moisture conditions. The seeds of some species are known to remain viable for more than 10 years and seed banks can develop. Vegetative reproduction can occur by means of lateral offshoots arising from the bulbous rhizome and is more prevalent in plants growing under shaded conditions.

Because of historical taxonomic misunderstandings (see *Systematics*), information can be difficult to associate unambiguously with occurrences of *Alisma subcordatum* and *A. triviale*, which at one time were recognized in North America as subspecies or varieties of *A. plantago-aquatica* (i.e., *A. plantago-aquatica* var. *parviflorum* and *A. plantago-aquatica* var. *americanum*, respectively). It is now quite evident that both *A. subcordatum* and *A. triviale* are distinct from *A. plantago-aquatica* (see *Systematics*) and that the latter does not actually occur in the New World, despite numerous conflicting reports. Consequently, although designated as an OBL North American indicator, *A. plantago-aquatica* has been excluded here.

2.1.1.1. *Alisma gramineum* Lej. grows in shallow to moderately deep (to 1.6 m), fresh to brackish, still to flowing waters of backwashes, beaches, bottoms, canals (dry), channels, depressions, ditches, flats, floodplains, marshes (tidal), mudflats, pools, puddles, roadsides, shores, slopes (to 1%), sloughs, springs, streams, vernal pools, washes, and along the margins

of canals, channels, lakes, playas, ponds, reservoirs, and rivers at elevations to 3180 m. The plants can grow completely submersed (then with ribbon-like foliage and cleistogamous flowers) but also occur often on drying or exposed substrates where ephemeral waters have receded. Their optimal depth has been reported as 50–70 cm. Exposures typically receive full sunlight. The substrates are described as alkaline (e.g., pH: 7.5–9.6; total alkalinity: 48–108 ppm) and include clay, clay loam, clay muck, clay mud, clay silt, gravel, limestone, muck, mucky clay, mud, muddy clay, rock, sand, sandstone, sandy gravel, sandy muck, sandy silt, shales, silty clay, and stones. The flowers of emergent plants are chasmogamous and normally insect pollinated, whereas those of submersed plants are cleistogamous and self-pollinated. Flowering and fruiting occur from June to September. The flowers remain open from 6:30 am to 10:00 pm. Seed set in open-pollinated plants has been estimated at 88%. The achenes are buoyant and dispersed by water, but under continuous agitation, they sink within 128 h. A persistent seed bank develops. Dried seeds (at 15% relative humidity) that are frozen (at -20°C) have remained viable for at least a year. Scarification of the pericarp or stratification is necessary to promote germination. A 60% germination rate has been reported for dried, stored seeds that have been re-exposed to high humidity for 1 day at 21°C , then physically scarified and incubated at 26°C under a 12/12-h photoperiod. High germination rates (56%) have been obtained for seeds that have been cold stratified (e.g., 10 months at 6°C) and then incubated in shallow water under constant (25°C) or fluctuating ($25^{\circ}\text{C}/10^{\circ}\text{C}$) temperatures. Germination rates are reduced nearly by half if the seeds are stratified for a comparable time at 20°C . The best germination rates (94–100%) have been obtained for cold, wet-stored seeds that are pre-treated with bleach and then incubated at 20°C – 30°C . The seedlings have a relatively high vulnerability to winter conditions, and do not fare well unless they initially establish soundly on exposed substrates during the late summer and fall. Because new seedlings are killed by high water conditions, much of the annual reproduction occurs by seed. In subsequent years, the plants must overwinter under water to avoid being killed by frost. Overall, the plants are poorly adapted to changing habitat conditions, although they tolerate constant submergence well. Established stands are known to reduce wave energies, resulting in higher local sedimentation rates. Denser stands can produce 85 culms m^{-2} and achieve a mean biomass of 125 g ash-free dry mass [DM] m^{-2} . **Reported associates:** *Acorus calamus*, *Alisma triviale*, *Allium geyeri*, *Alopecurus aequalis*, *Alopecurus saccatus*, *Artemisia nova*, *Aulosira*, *Bacopa monnieri*, *Beckmannia syzigachne*, *Bidens beckii*, *Bidens laevis*, *Bidens polylepis*, *Bolboschoenus fluviatilis*, *Bolboschoenus maritimus*, *Butomus umbellatus*, *Carex praegracilis*, *Ceratophyllum demersum*, *Chara vulgaris*, *Chenopodium glaucum*, *Chenopodium rubrum*, *Deschampsia danthonioides*, *Distichlis spicata*, *Downingia elegans*, *Elaeagnus angustifolia*, *Elatine*, *Eleocharis acicularis*, *Eleocharis macrostachya*, *Eleocharis palustris*, *Elodea canadensis*, *Elymus*, *Epilobium*, *Eryngium petiolatum*, *Glyceria leptostachya*, *Gnaphalium palustre*,

Gratiola ebracteata, *Grindelia squarrosa*, *Heliotropium*, *Heteranthera dubia*, *Hippuris*, *Hippuris vulgaris*, *Honckenya peploides*, *Hordeum jubatum*, *Hydrocharis morsus-ranae*, *Isoetes howellii*, *Iva axillaris*, *Juncus articulatus*, *Juncus balticus*, *Juncus effusus*, *Juncus tenuis*, *Lemna minor*, *Lemna trisulca*, *Leptochloa fusca*, *Limosella aquatica*, *Myosotis laxa*, *Myosurus minimus*, *Myriophyllum sibiricum*, *Najas flexilis*, *Navarretia intertexta*, *Navarretia squarrosa*, *Nuphar*, *Oryza sativa*, *Oscillatoria*, *Panicum capillare*, *Paspalum distichum*, *Persicaria amphibia*, *Persicaria coccinea*, *Persicaria lapathifolia*, *Persicaria punctata*, *Phalaris arundinacea*, *Plagiobothrys leptocladus*, *Plantago maritima*, *Pluchea odorata*, *Polygonum ramosissimum*, *Polypogon monspeliensis*, *Potamogeton amplifolius*, *Potamogeton berchtoldii*, *Potamogeton friesii*, *Potamogeton pusillus*, *Potamogeton richardsonii*, *Potamogeton zosteriformis*, *Potentilla anserina*, *Puccinellia nuttalliana*, *Ranunculus aquatilis*, *Ranunculus subrigidus*, *Rorippa curvisiliqua*, *Rorippa sinuata*, *Rorippa teres*, *Rumex maritimus*, *Rumex stenophyllus*, *Rumex triangularis*, *Ruppia maritima*, *Sagittaria cuneata*, *Salicornia depressa*, *Salix caroliniana*, *Salix exigua*, *Sarcobatus vermiculatus*, *Schoenoplectus acutus*, *Schoenoplectus pungens*, *Schoenoplectus tabernaemontani*, *Sium suave*, *Sparganium eurycarpum*, *Spergularia*, *Spirodela*, *Stuckenia filiformis*, *Stuckenia pectinata*, *Stuckenia vaginata*, *Triglochin scilloides*, *Typha angustifolia*, *Typha latifolia*, *Vallisneria spiralis*, *Zannichellia palustris*.

2.1.1.2. *Alisma lanceolatum* With. is a nonindigenous species, which grows in shallow standing waters or on exposed substrates in channels (bottoms), depressions, ditches, floodplains, gravel pits, marshes, meadows, mudflats, pools, seeps, streams (intermittent), swamps (drying), washes, and along the margins of lakes, ponds, rivers, and streams at elevations to 1267 m. The plants originate from regions having relatively warmer climate conditions. Exposures range from open sunlight to partial shade. The substrates are circumneutral (pH: 6.5–8.5), tend to be nutrient-rich, and include clay, gravel, mud, sand, and silt. Flowering and fruiting occur from April to August in North America. Fluctuating water conditions appear to promote the flowering response. The flowers remain open from 7:30 am to 7:00 pm and are pollinated by insects (Insecta). Typical seed set in open-pollinated plants has been estimated at 89%. The flat achenes are buoyant and are dispersed by water; however, under continuous agitation, they sink within 96 h. They also are known to be spread by attachment to agricultural machinery. The seeds are dormant when shed and require a period of cold stratification to induce germination. Germination rates often are above 30%. Optimal germination rates (62–75%) have been obtained for seeds that have been cold stratified (e.g., 3–10 months at 6°C) and then incubated in shallow water under constant (15°C , 25°C) or fluctuating ($25^{\circ}\text{C}/10^{\circ}\text{C}$) temperatures. Stratification at higher temperatures (e.g., 20°C) greatly decreases their germination rates. The plants adapt only moderately to changing habitat conditions. However, when conditions are favorable, seed germination is rapid and synchronous, which facilitates colonization and establishment. Seedlings establish more

successfully when they remain emergent or develop under fluctuating water conditions. Higher seedling survival rates occur when growing under submersed conditions (e.g., 40–80 cm depth). The plants have been described both as mycorrhizal (arbuscular) and non-mycorrhizal. **Reported associates (North America):** *Adiantum*, *Alopecurus aequalis*, *Artemisia douglasiana*, *Athyrium*, *Bidens*, *Convolvulus arvensis*, *Cotula coronopifolia*, *Downingia*, *Festuca perennis*, *Gratiola*, *Isolepis carinata*, *Lemna*, *Melilotus indicus*, *Oryza sativa*, *Rubus*, *Rubus ulmifolius*, *Rumex*, *Rumex conglomeratus*, *Salix*, *Salix laevigata*, *Tribulus terrestris*, *Typha latifolia*, *Urtica dioica*, *Veronica*.

2.1.1.3. *Alisma subcordatum* Raf. is found in shallow (e.g., 10–30 cm) standing water or on exposed substrates in alluvial fans, beaches, bogs, bottomlands, bottoms (stream), canals, channels (river), depressions, ditches, flats, floodplains, gravel bars, marshes (ephemeral), meadows, mudflats, oxbows, ponds (intermittent), pools (artificial; ephemeral), prairies (mesic; remnant), puddles, right-of-ways (powerline; railroad), roadsides (springy), sandbars, seeps, shores (marshy), sloughs, springs (outflow), streams (shallow), swamps, thickets (seepy), swales, woodlands, and along the margins of lagoons, lakes, ponds, reservoirs, rivers, streams, swamps, and woodlands at elevations to 1448 m. The plants are heterophyllous, producing floating leaves when grown in standing water (e.g., 25 cm deep) and emergent foliage when growing under shallow conditions (e.g., 2 cm water). Exposures range from fully open conditions to partial shade. The substrates are circumneutral (pH: 6.2–8.4; total alkalinity: 11–290 mg l⁻¹) and are described as alluvium, clay loam muck, cobble, gravel, Hepler silt loam, loamy clay, loamy muck, muck, mud, peat, peaty muck, sand, sandy clay, sandy loam, sandy muck (organic), shale, and silt. Flowering and fruiting occur from May to September. Warming global temperatures have been implicated in a 2 month earlier flowering initiation of some populations during the past two decades. The flowers are self-compatible, but remain open from 11:30 am to 7:30 pm, which enables cross-pollination by insects (see *Use by Wildlife*). Typical seed set in open-pollinated plants has been estimated to approach 90%. Each flower produces from 6 to 18 fruits. The achenes float and are dispersed locally by water, but will sink within 128 hr if the surface is agitated periodically. The seeds are physiologically dormant and require a period of cold stratification (e.g., 210 days at 2°C–5°C) to induce germination (under a 25°C/15°C day/night temperature regime). Successful germination also has been reported for seeds stratified at 5°C for 60 days, and then placed on sand under water. Reported germination rates vary from 0.4% to 35%. The seeds germinate optimally under flooded conditions (up to 62%) but remain dormant under unflooded conditions or when buried. A persistent seed bank can develop and refrigerated achenes have retained 50% viability after 9 years of storage. Adult plants more typically occur in non-flooded sites. Exposed substrates are necessary for the effective establishment of seedlings. The roots reportedly have weak arbuscular mycorrhizal development. **Reported associates:** *Acalypha rhomboidea*, *Acer negundo*, *Acer saccharinum*, *Acorus calamus*,

Agrimonia parviflora, *Agrostis gigantea*, *Agrostis hyemalis*, *Agrostis perennans*, *Agrostis stolonifera*, *Alisma triviale*, *Ambrosia artemisiifolia*, *Ammannia coccinea*, *Ammannia robusta*, *Amorpha fruticosa*, *Apios americana*, *Asclepias incarnata*, *Asclepias syriaca*, *Bacopa rotundifolia*, *Betula nigra*, *Bidens cernuus*, *Bidens connatus*, *Bidens polylepis*, *Bidens tripartitus*, *Boehmeria cylindrica*, *Bolboschoenus fluviatilis*, *Boltonia asteroides*, *Calamagrostis canadensis*, *Campsis radicans*, *Cardamine bulbosa*, *Carex caroliniana*, *Carex conjuncta*, *Carex corrugata*, *Carex cristatella*, *Carex frankii*, *Carex granularis*, *Carex grayi*, *Carex haydenii*, *Carex hyalinolepis*, *Carex lacustris*, *Carex lupulina*, *Carex lurida*, *Carex muskingumensis*, *Carex shortiana*, *Carex stipata*, *Carex stricta*, *Carex tribuloides*, *Carex typhina*, *Cephalanthus occidentalis*, *Chelone glabra*, *Chelone obliqua*, *Chenopodium simplex*, *Cicuta maculata*, *Cladium jamaicense*, *Coleataenia longifolia*, *Conoclinium coelestinum*, *Cornus amomum*, *Cuscuta gronovii*, *Cyperus acuminatus*, *Cyperus bipartitus*, *Cyperus esculentus*, *Cyperus odoratus*, *Cyperus strigosus*, *Dichanthelium clandestinum*, *Dipsacus fullonum*, *Echinochloa crus-galli*, *Echinodorus berteroi*, *Eclipta prostrata*, *Eleocharis acicularis*, *Eleocharis engelmannii*, *Eleocharis erythropoda*, *Eleocharis macrostachya*, *Eleocharis obtusa*, *Eleocharis ovata*, *Eleocharis palustris*, *Eleocharis quadrangulata*, *Epilobium coloratum*, *Equisetum arvense*, *Equisetum fluviatile*, *Erechtites hieracifolius*, *Eupatorium perfoliatum*, *Eupatorium serotinum*, *Eutrochium maculatum*, *Fallopia scandens*, *Fimbristylis autumnalis*, *Fraxinus pennsylvanica*, *Fraxinus profunda*, *Galium obtusum*, *Galium tinctorium*, *Gentiana andrewsii*, *Geum laciniatum*, *Glyceria striata*, *Gratiola aurea*, *Gratiola neglecta*, *Helenium autumnale*, *Helianthus grosseserratus*, *Helianthus mollis*, *Hibiscus moscheutos*, *Holcus lanatus*, *Humbertacalia*, *Hypericum canadense*, *Impatiens capensis*, *Ipomoea lacunosa*, *Iris virginica*, *Juncus acuminatus*, *Juncus effusus*, *Juncus marginatus*, *Juncus tenuis*, *Juncus torreyi*, *Laportea canadensis*, *Leersia lenticularis*, *Leersia oryzoides*, *Leersia virginica*, *Lemna minor*, *Leucospora multifida*, *Lindernia dubia*, *Lobelia siphilitica*, *Ludwigia alternifolia*, *Ludwigia palustris*, *Ludwigia polycarpa*, *Lycopus americanus*, *Lycopus virginicus*, *Lysimachia ciliata*, *Lysimachia nummularia*, *Lysimachia quadriflora*, *Lysimachia terrestris*, *Lythrum alatum*, *Lythrum salicaria*, *Mentha arvensis*, *Mentha x piperita*, *Mimulus ringens*, *Myriophyllum aquaticum*, *Nymphoides peltata*, *Nyssa sylvatica*, *Oenothera pilosella*, *Onoclea sensibilis*, *Panicum dichotomiflorum*, *Panicum virgatum*, *Panicum virgatum*, *Parthenocissus quinquefolia*, *Pedicularis lanceolata*, *Peltandra virginica*, *Penthorum sedoides*, *Persicaria amphibia*, *Persicaria carreyi*, *Persicaria hydropiperoides*, *Persicaria lapathifolia*, *Persicaria pensylvanica*, *Persicaria punctata*, *Persicaria setacea*, *Phalaris arundinacea*, *Phragmites australis*, *Phyla lanceolata*, *Pilea pumila*, *Platanthera peramoena*, *Platanus occidentalis*, *Poa nemoralis*, *Polygonum ramosissimum*, *Pontederia cordata*, *Populus deltoides*, *Potamogeton nodosus*, *Proserpinaca*, *Prunella vulgaris*, *Pycnanthemum virginianum*, *Quercus bicolor*, *Quercus macrocarpa*, *Quercus*

palustris, *Ranunculus hispidus*, *Ranunculus pensylvanicus*, *Rhamnus frangula*, *Rhynchospora capitellata*, *Rosa multiflora*, *Rubus setosus*, *Rudbeckia subtomentosa*, *Rumex obtusifolius*, *Rumex verticillatus*, *Sabatia angularis*, *Saccharum*, *Sagittaria australis*, *Sagittaria latifolia*, *Sagittaria montevidensis*, *Salix discolor*, *Salix interior*, *Salix myricoides*, *Salix nigra*, *Samolus valerandi*, *Saururus cernuus*, *Schoenoplectus hallii*, *Schoenoplectus mucronatus*, *Schoenoplectus pungens*, *Schoenoplectus tabernaemontani*, *Scirpus atrovirens*, *Scirpus cyperinus*, *Scutellaria galericulata*, *Scutellaria lateriflora*, *Sium suave*, *Smilax*, *Solanum dulcamara*, *Solidago riddellii*, *Sparganium americanum*, *Sparganium androcladum*, *Sparganium emersum*, *Sparganium eurycarpum*, *Spartina pectinata*, *Sphagnum*, *Spiraea tomentosa*, *Spirodela polyrhiza*, *Stachys palustris*, *Stellaria longifolia*, *Symphyotrichum lanceolatum*, *Symphyotrichum novi-belgii*, *Symphyotrichum ontarionis*, *Symphyotrichum praealtum*, *Teucrium canadense*, *Thalictrum clavatum*, *Thelypteris palustris*, *Toxicodendron radicans*, *Tridens flavus*, *Typha angustifolia*, *Typha latifolia*, *Verbena hastata*, *Vernonia fasciculata*, *Veronicastrum virginicum*, *Viola sororia*, *Vitis cinerea*, *Vitis riparia*, *Xanthium strumarium*.

2.1.1.4. *Alisma triviale* Pursh occurs in shallow (0.05–1.0 m) fresh to somewhat saline standing waters, or on exposed substrates in backwaters, bays (shallow), bogs, canals, channels (intermittent), ditches (irrigation; roadside), flats (river), floodplains, glades, impoundments, lakes, marshes, meadows, mudflats, oxbows (swampy), ponds (beaver; intermittent; stock), pools (dry; seasonal; vernal), potholes, prairies, puddles, reservoirs (dry), rice fields, roadsides, shores, slopes (to 6%), sloughs, springs, stream beds, swales (drying), swamps, tanks, and along the margins of lagoons, lakes, ponds, pools, reservoirs, rivers (estuaries), and streams at elevations to 2830 m. In experimental manipulations, the optimal water depth ranged from 15 to 20 cm. Exposures can vary from full to partial sunlight. The substrates have been described as acidic or alkaline (pH: 4.5–8.0; total alkalinity: 13.5–47.5 mg l⁻¹) and include adobe, bentonite, clay (Gumbo; Pierre), gravel, loam, loamy clay, logs (decayed), muck (organic), mud, peat, peaty mud, sand, sandy clay loam, sandy loam, silt, silty mud, and stones. Flowering and fruiting extend from June to November. The flowers remain open from 8:00 am to 6:30 pm. Average seed set in open-pollinated plants has been estimated at 91%. The achenes are dispersed by water, and under intermittent agitation, will sink within 96 h. Specific conditions for germination have not been reported, but germination rates have been observed to increase proportionally with water depth. The mean density of germinating seeds can reach 128.2 seeds m⁻². The greatest seedling growth occurs at water depths from 2 to 7 cm. The roots reportedly are colonized by arbuscular mycorrhizae. The plants are known to occur commonly along hedgerows that are adjacent to agricultural fields.

Reported associates: *Acer glabrum*, *Acer negundo*, *Acer saccharinum*, *Achillea millefolium*, *Acmispon wrightii*, *Acorus calamus*, *Agrostis exarata*, *Agrostis scabra*, *Agrostis stolonifera*, *Alisma gramineum*, *Alisma subcordatum*, *Alnus*, *Alopecurus aequalis*, *Alopecurus geniculatus*, *Amaranthus*

powellii, *Amaranthus tuberculatus*, *Ambrosia tomentosa*, *Ammannia*, *Amorpha fruticosa*, *Apocynum cannabinum*, *Arctium minus*, *Aristida oligantha*, *Asclepias incarnata*, *Astragalus humistratus*, *Azolla cristata*, *Baccharis douglasii*, *Baccharis salicifolia*, *Beckmannia syzigachne*, *Bidens aristatus*, *Bidens beckii*, *Bidens cernuus*, *Bidens connatus*, *Bidens frondosus*, *Bidens trichospermus*, *Bistorta bistortoides*, *Bolboschoenus fluviatilis*, *Bolboschoenus maritimus*, *Bolboschoenus robustus*, *Boltonia asteroides*, *Bouteloua curtipendula*, *Brassica*, *Brickellia californica*, *Bromus inermis*, *Bromus tectorum*, *Calamagrostis canadensis*, *Callitriche heterophylla*, *Callitriche palustris*, *Capsella bursa-pastoris*, *Carex annectens*, *Carex aquatilis*, *Carex athrostachya*, *Carex bebbii*, *Carex brevior*, *Carex buxbaumii*, *Carex canescens*, *Carex comosa*, *Carex cristatella*, *Carex densa*, *Carex frankii*, *Carex lasiocarpa*, *Carex leptalea*, *Carex lupuliformis*, *Carex lyngbyei*, *Carex meadii*, *Carex muskingumensis*, *Carex normalis*, *Carex occidentalis*, *Carex pellita*, *Carex praegracilis*, *Carex retrorsa*, *Carex scoparia*, *Carex siccata*, *Carex simulata*, *Carex stipata*, *Carex utriculata*, *Carex vesicaria*, *Carex xayouettei*, *Castilleja angustifolia*, *Ceanothus fendleri*, *Ceratophyllum demersum*, *Chara*, *Chelone glabra*, *Chenopodium*, *Cicuta bulbifera*, *Cicuta maculata*, *Cirsium arvense*, *Cirsium undulatum*, *Cirsium vulgare*, *Cirsium wheeleri*, *Clintonia*, *Conium maculatum*, *Convolvulus*, *Coreopsis*, *Cornus amomum*, *Cornus drummondii*, *Cornus sericea*, *Crypsis vaginiflora*, *Cuscuta glomerata*, *Cyperus difformis*, *Cyperus eragrostis*, *Cyperus strigosus*, *Damasonium californicum*, *Decodon verticillatus*, *Deschampsia elongata*, *Dichanthelium oligosanthos*, *Distichlis spicata*, *Downingia laeta*, *Dracocephalum parviflorum*, *Echinochloa crus-galli*, *Echinodorus berteroi*, *Echinodorus cordifolius*, *Eclipta prostrata*, *Elatine californica*, *Elatine chilensis*, *Elatine rubella*, *Eleocharis acicularis*, *Eleocharis engelmannii*, *Eleocharis erythropoda*, *Eleocharis macrostachya*, *Eleocharis montana*, *Eleocharis ovata*, *Eleocharis palustris*, *Eleocharis parishii*, *Eleocharis rostellata*, *Eleocharis tenuis*, *Eleocharis wolfii*, *Eloдея canadensis*, *Elymus elymoides*, *Epilobium campestre*, *Epilobium ciliatum*, *Epilobium torreyi*, *Equisetum arvense*, *Equisetum fluviatile*, *Equisetum laevigatum*, *Eragrostis pectinacea*, *Erigeron divergens*, *Erigeron speciosus*, *Erigeron strigosus*, *Eriogonum racemosum*, *Eryngium articulatum*, *Eupatorium perfoliatum*, *Euphorbia marginata*, *Eustoma exaltatum*, *Euthamia occidentalis*, *Eutrochium maculatum*, *Fallopia convolvulus*, *Fallugia paradoxa*, *Festuca arizonica*, *Fimbristylis spadicea*, *Flaveria campestris*, *Forestiera pubescens*, *Fraxinus pennsylvanica*, *Galium aparine*, *Galium trifidum*, *Geranium caespitosum*, *Geranium richardsonii*, *Geum laciniatum*, *Geum macrophyllum*, *Glyceria borealis*, *Glyceria elata*, *Glyceria grandis*, *Glyceria septentrionalis*, *Glyceria striata*, *Glycyrrhiza lepidota*, *Gnaphalium exilifolium*, *Gnaphalium uliginosum*, *Gratiola neglecta*, *Grindelia squarrosa*, *Hackelia floribunda*, *Helianthus annuus*, *Helianthus grosseserratus*, *Helianthus maximiliani*, *Heteranthera*, *Hippuris vulgaris*, *Hordeum jubatum*, *Hymenoxys hoopesii*, *Hymenoxys subintegra*, *Hypericum*

anagalloides, *Impatiens capensis*, *Impatiens pallida*, *Iris missouriensis*, *Isoetes*, *Juncus acuminatus*, *Juncus articulatus*, *Juncus balticus*, *Juncus bufonius*, *Juncus effusus*, *Juncus ensifolius*, *Juncus interior*, *Juncus oxymeris*, *Juncus patens*, *Juncus torreyi*, *Juncus xiphioides*, *Juniperus monosperma*, *Juniperus osteosperma*, *Juniperus scopulorum*, *Lactuca seriola*, *Landoltia punctata*, *Lappula occidentalis*, *Leersia lenticularis*, *Leersia oryzoides*, *Leersia virginica*, *Lemna minor*, *Liatris lancifolia*, *Lilaeopsis*, *Limosella acaulis*, *Lindernia dubia*, *Lobelia cardinalis*, *Lobelia siphilitica*, *Ludwigia palustris*, *Ludwigia peploides*, *Lupinus argenteus*, *Lupinus kingii*, *Lycopus americanus*, *Lycopus asper*, *Lycopus uniflorus*, *Lysimachia terrestris*, *Lythrum alatum*, *Lythrum hyssopifolia*, *Lythrum salicaria*, *Madia*, *Marsilea mollis*, *Marsilea vestita*, *Medicago lupulina*, *Medicago sativa*, *Melilotus albus*, *Melilotus officinalis*, *Mentha arvensis*, *Mentha x piperita*, *Mikania scandens*, *Mimulus guttatus*, *Mimulus ringens*, *Muhlenbergia frondosa*, *Muhlenbergia wrightii*, *Myosotis laxa*, *Myosurus*, *Myriophyllum pinnatum*, *Myriophyllum sibiricum*, *Najas flexilis*, *Nasturtium*, *Navarretia intertexta*, *Nuphar polysepala*, *Oenothera rhombipetala*, *Onoclea sensibilis*, *Orthocarpus luteus*, *Ottelia alismoides*, *Panicum virgatum*, *Parthenocissus quinquefolia*, *Pascopyrum smithii*, *Paspalum distichum*, *Peltandra virginica*, *Pennisetum glaucum*, *Penstemon barbatus*, *Penstemon linarioides*, *Penthorum sedoides*, *Persicaria amphibia*, *Persicaria coccinea*, *Persicaria coccinea*, *Persicaria hydropiper*, *Persicaria hydropiperoides*, *Persicaria lapathifolia*, *Persicaria maculosa*, *Persicaria pennsylvanica*, *Persicaria punctata*, *Phalaris arundinacea*, *Phleum pratense*, *Phragmites australis*, *Phyla lanceolata*, *Phyla nodiflora*, *Picea mariana*, *Pinus ponderosa*, *Plagiobothrys*, *Plantago*, *Platanus occidentalis*, *Poa arida*, *Poa nemoralis*, *Poa pratensis*, *Polygonum aviculare*, *Polygonum douglasii*, *Polypogon monspeliensis*, *Pontederia cordata*, *Populus angustifolia*, *Populus deltoides*, *Populus tremuloides*, *Porterella carnosula*, *Portulaca oleracea*, *Potamogeton amplifolius*, *Potamogeton berchtoldii*, *Potamogeton diversifolius*, *Potamogeton foliosus*, *Potamogeton gramineus*, *Potamogeton natans*, *Potamogeton nodosus*, *Potamogeton pusillus*, *Potamogeton richardsonii*, *Potamogeton zosteriformis*, *Potentilla crinita*, *Potentilla gracilis*, *Potentilla hippiana*, *Potentilla norvegica*, *Prunella*, *Prunus virginiana*, *Pseudocymopterus montanus*, *Pseudognaphalium luteoalbum*, *Quercus bicolor*, *Quercus gambelii*, *Quercus grisea*, *Ranunculus aquatilis*, *Ranunculus cymbalaria*, *Ranunculus trichophyllus*, *Rhus aromatica*, *Ribes cereum*, *Robinia neomexicana*, *Rorippa curvipes*, *Rorippa islandica*, *Rorippa sphaerocarpa*, *Rosa arkansana*, *Rosa woodsii*, *Rotala*, *Rumex crispus*, *Rumex maritimus*, *Rumex salicifolius*, *Rumex triangulivalvis*, *Sagittaria cuneata*, *Sagittaria latifolia*, *Sagittaria montevidensis*, *Salix amygdaloides*, *Salix exigua*, *Salix gooddingii*, *Salix nigra*, *Salix interior*, *Sambucus nigra*, *Schizachyrium scoparium*, *Schoenoplectus acutus*, *Schoenoplectus pungens*, *Schoenoplectus tabernaemontani*, *Schoenoplectus triquetus*, *Scirpus atrovirens*, *Scirpus cyperinus*, *Scirpus lineatus*, *Scirpus microcarpus*, *Scrophularia parviflora*, *Scutellaria*

lateriflora, *Senecio spartioides*, *Senecio wootonii*, *Setaria parviflora*, *Setaria viridis*, *Sidalcea*, *Sisyrinchium angustifolium*, *Sium suave*, *Solanum dulcamara*, *Solidago missouriensis*, *Sparganium angustifolium*, *Sparganium emersum*, *Spartina pectinata*, *Sphenoclea zeylanica*, *Sphenopholis obtusata*, *Spiraea*, *Spiranthes cernua*, *Spiranthes diluvialis*, *Spirodela polyrhiza*, *Sporobolus compositus*, *Stachys palustris*, *Stachys pilosa*, *Stuckenia pectinata*, *Suaeda calceoliformis*, *Symphoricarpos*, *Symphyotrichum ericoides*, *Symphyotrichum lanceolatum*, *Symphyotrichum lateriflorum*, *Symphyotrichum subulatum*, *Taraxacum officinale*, *Thalictrum fendleri*, *Thermopsis*, *Torreyochloa pallida*, *Toxicodendron radicans*, *Tragopogon*, *Triglochin scilloides*, *Typha angustifolia*, *Typha latifolia*, *Urtica dioica*, *Utricularia*, *Verbascum thapsus*, *Verbena bracteata*, *Verbena hastata*, *Verbena urticifolia*, *Vernonia fasciculata*, *Veronica anagallis-aquatica*, *Veronica peregrina*, *Veronica serpyllifolia*, *Vicia cracca*, *Viola sororia*, *Vitis riparia*, *Wolffia brasiliensis*, *Wolffia columbiana*, *Xanthium strumarium*, *Zannichellia palustris*.

Use by wildlife: The achenes of *Alisma gramineum* are eaten by various ducks (Aves: Anatidae: *Anas*), including baldpates (*A. americana*), blue-winged teal (*A. discors*), gadwells (*A. strepera*), and shovelers (*A. clypeata*). *Alisma subcordatum* is grazed by Canada geese (Aves: Anatidae: *Branta canadensis*) and European ambersnails (Gastropoda: Succineidae: *Succinea putris*). Its flowers are visited (and likely pollinated) by flies (Insecta: Diptera) and occasionally by skippers (Insecta: Lepidoptera: Hesperidae: *Ancyloxypha numitor*). *Alisma triviale* is a host to moth larvae (Lepidoptera: Noctuidae: *Hypena madefactalis*) and spittlebugs (Insecta: Hemiptera: Cercopidae). The roots are host to slime molds (Fungi: Myxomycota: Plasmodiophoraceae: *Ligniera junci*). The plants serve as an oviposition substrate for aster leafhoppers (Insecta: Hemiptera: Cicadellidae: *Macrostelus fascifrons*). The achenes are eaten by blue-winged teal (Aves: Anatidae: *Anas discors*) and mallard ducks (*Anas platyrhynchos*). In North America, *Alisma* plants (species uncertain) are host to several Fungi (Ascomycota: Mycosphaerellaceae: *Cercospora alismatis*, *C. callae*; Basidiomycota: Doassansiaceae: *Doassansia alismatis*; Blastocladiomycota: *Cladochytrium alismatis*).

Economic importance: food: After washing and drying, the bulblike leaf bases of *Alisma* plants were eaten by the Calmucks; however, some sources suggest that the foliage (especially when bruised) can be poisonous or cause skin irritation; **medicinal:** Some *Alisma* species contain protostane triterpenoids, which exhibit antiparasitic activity against *Plasmodium falciparum*, a causative agent of malaria. *Alisma gramineum* has been used to treat gastrointestinal disorders, skin diseases, and to treat abrasions and cuts in parts of Asia. *Alisma subcordatum* was used by the Cherokee to treat gastrointestinal disorders and skin ailments. The Iroquois used *A. triviale* to treat kidney ailments and tuberculosis; **cultivation:** Various *Alisma* species are planted occasionally as ornamental plants in water gardens or along river gardens; **misc. products:** *Alisma gramineum* has been used as a natural

insect repellent. Seeds of *A. subcordatum* have been included in mixes used for wetland restoration programs. *Alisma triviale* has been planted in free water surface constructed wetlands; **weeds:** *Alisma lanceolatum* and *A. triviale* have been reported as rice field weeds in western North America. Strains resistant to bensulfuron-methyl herbicides have been reported in *A. lanceolatum*; **nonindigenous species:** *Alisma lanceolatum* likely was introduced to California and Oregon from Eurasia by means of contaminated rice stock. *Alisma plantago-aquatica* has been characterized as nonindigenous to North America; however, no verifiable records of this species are known to occur in the region.

Systematics: Various analyses of DNA sequence data (e.g., Figures 1.3 and 1.4) confirm that *Alisma* is monophyletic and indicate that it is related most closely to *Baldellia*. Analysis of nrITS sequence data (Figure 1.4) effectively distinguishes *A. gramineum* and *A. lanceolatum* from the majority of species but fails to resolve relationships among *A. plantago-aquatica*, *A. subcordatum*, and *A. triviale*, which indicates their relatively recent divergence. However, all three taxa are clearly separable using RAPDs markers. Although North American specimens of *A. subcordatum* and *A. triviale* were long treated taxonomically as variants of the Old World diploid species *A. plantago-aquatica*, many morphological, chromosomal, and genetic isolating distinctions eventually became evident. Even though these taxa are similar morphologically, no crosses have succeeded despite numerous reciprocal attempts involving *A. plantago-aquatica* × *A. subcordatum*, *A. plantago-aquatica* or *A. subcordatum* × *A. triviale*, which indicates that all three species are well isolated genetically. In contrast, some successful crosses (i.e., those resulting in seed set) have been obtained involving either *A. lanceolatum* or *A. gramineum* × *A. plantago-aquatica*, and *A. lanceolatum* × *A. gramineum*, which exhibit more distant interrelationships. The basic chromosome number of *Alisma* is $x=7$. *Alisma*

gramineum and *A. subcordatum* ($2n=14$) are diploids; *A. lanceolatum* ($2n=26, 28$) and *A. triviale* ($2n=28$) are tetraploids. The two cytotypes of *A. lanceolatum* are well isolated genetically. No spontaneous interspecific *Alisma* hybrids have been reported in North America. There have been no successful intergeneric hybrids resulting from crossing attempts involving *Alisma*, *Baldellia*, and *Luronium*.

Distribution: *Alisma gramineum* and *A. triviale* occur throughout central North America and *A. subcordatum* is widespread in the eastern United States. The nonindigenous *A. lanceolatum* is restricted to California and Oregon.

References: Adams et al., 2011; Andersson et al., 2000; Baldwin, Jr. & Speese, 1955; Barrett & Seaman, 1980; Baskin & Baskin, 1998; Beas et al., 2013; Bergeron & Pellerin, 2014; Björkqvist, 1967; 1968; Boutin et al., 2002; Burgess, 1970; Calha et al., 1998; Conover & Pelikan, 2010; Countryman, 1968; Duke, 2000; Fernald, 1946; Fernald & Kinsey, 1943; Grau & Leonard, 1978; Haynes & Holm-Nielsen, 1994; Haynes & Hellquist, 2000a; Haynes et al., 1998a; Hellquist & Crow, 1981; Hendricks, 1957; Hopkins, 1969; Hroudová et al., 2004; Hudon, 1997; Johnson, 1999; Kaul, 1978; 1985; Keith, 1961; Kellogg et al., 2003; Knight, 1965; Kratzer, 2014; Les & Tippery, 2013; Lieneman, 1929; Lovell, 1899; McIntyre & Newnham, 1988; Mollik et al., 2010; Moravcová et al., 2001; Parker et al., 1969; Pogan, 1963; Putman, 1953; Ransom & Oelke, 1983; Rhoades, 1962; Rogers, 1983; Ryser et al., 2011; Scott, 2014; Seabloom et al., 1998; Smith, 1953; Swanson & Bartonek, 1970; Todorova et al., 2013; Tucker et al., 2015; Ungar, 1964; Vermaat et al., 2000; Vymaza, 2013; Wagner & Oplinger, 2017; Wang & Qiu, 2006; Way, 1982; Weiher et al., 2003; Yatskievych & Raveill, 2001; Zákavsky & Hroudová, 1998.

2.1.2. Damasonium

Fringed water plantain

Etymology: an ancient name of unknown derivation, but possibly commemorating Damasos, a Trojan soldier of the Iliad

Synonyms: *Actinocarpus*; *Machaerocarpus*

Distribution: **global:** Australia; Europe; North America; **North America:** western

Diversity: **global:** 5 species; **North America:** 1 species

Indicators (USA): **obligate wetland (OBL):** *Damasonium californicum*

Habitat: freshwater; lacustrine, palustrine, riverine; **pH:** alkaline; **depth:** <1 m; **life-form(s):** emergent or floating-leaved herb

Key morphology: foliage arising from a corm; the leaves erect, blades undeveloped or lanceolate to ovate (to 9 cm), the margins entire, petioles (to 15 cm) triangular in section; inflorescence an erect raceme (rarely a panicle), the flowers (to 22 mm) bisexual, trimerous, apocarpous, pedicellate (to 65 mm), in whorls (to 9); sepals (to 5 mm) persistent, somewhat hoodlike; petals (to 10 mm) white with basal yellow spot, rarely pink, their apex erose; stamens 6; pistils (to 15) in a ring, spreading or radiating in a star-like pattern; follicles (to 5.5 mm) laterally compressed, beaked (to 6 mm), dehiscing basally, sometimes indehiscent and achene-like

FIGURE 1.4 Phylogenetic relationships of *Alisma* derived from analysis of nrITS sequence data (adapted from Jacobson & Hedrén, 2007). The North American species categorized as OBL indicators are highlighted in bold. Confirmed ploidy levels for the *Alisma* species are shown in parentheses.

Life history: duration: annual (seeds) or perennial (corms); **asexual reproduction:** corm buds; **pollination:** insect or self; **sexual condition:** hermaphroditic; **fruit:** aggregates (follicles) (common); **local dispersal:** mud, water; **long-distance dispersal:** mud, water

Imperilment: 1. *Damasonium californicum* [G4]; S1 (WA); S2 (ID)

Ecology: general: All *Damasonium* species occur in wetlands. The plants are perennial or annual, but all North American representatives are perennial. All of the species are self-compatible, with most being highly autogamous or even cleistogamous. The North American plants are outcrossing, which is associated with protandry, higher pollen quantities (i.e., greater pollen:ovule ratios), and fewer but heavier seeds than the inbreeding Australian or European species, which are homogamous, produce less pollen, and have lighter seeds. The seeds are dispersed in mud or by water. Vegetative reproduction occurs in two species by the production of corm buds.

2.1.2.1. *Damasonium californicum* Torr. occurs in shallow waters (e.g., 15–61 cm deep) or on exposed substrates associated with bottoms (pool; stream), canals (drying), depressions, ditches (roadside), flats, floodplains, marshes, meadows, mudflats (drying), playas, ponds, pools, prairies, rice fields, roadsides, seeps, shores, sloughs (roadside; vernal), streams (flowing), swales, vernal pools, and along the margins of lakes, ponds, reservoirs, and streams (intermittent) at elevations to 2057 m. Although typically emergent, the plants will develop floating leaves when growing in deeper water. The habitats occur in open exposures that receive full sunlight. The substrates are alkaline and include adobe, alluvium, clay, loamy clay, muck, mud, rock (basaltic), sand, sandy silt, serpentine, silty clay, silty mud, stony Tuscan loam, and Tuscan mudflow. Flowering and fruiting occur from May to September, often after standing waters recede. Plants grown in cultivation have flowered from April to June. The variance in flower production is substantial, but averages about 47 flowers/plant. The flowers are strongly protandrous, have the highest pollen:ovule ratios (1,000–1,200:1) in the genus, and are assumed to be highly outcrossed, presumably by insects (Insecta). The male phase occurs from 9 to 14 hr after the onset of flowering, with pollen often accumulating near the base of the petals. The female phase initiates on the second day (27–32 hr after the onset of flowering), as the styles spread radially to expose the stigmas. The petals remain open throughout anthesis. Although the flowers are highly self-compatible, their protandry prevents spontaneous self-pollination. The seeds (averaging 1.42 mg) are dispersed by water or in mud that becomes attached to animal vectors. **Reported associates:** *Alisma*, *Allium*, *Arnica chamissonis*, *Artemisia cana*, *Artemisia tridentata*, *Arthrocnemum subterminale*, *Callitriche hermaphroditica*, *Carex praegracilis*, *Comarum palustre*, *Crypsis schoenoides*, *Cynodon dactylon*, *Distichlis spicata*, *Downingia bacigalupii*, *Downingia concolor*, *Downingia insignis*, *Downingia ornatissima*, *Downingia yina*, *Eleocharis macrostachya*, *Eleocharis palustris*, *Epilobium campestre*, *Epilobium cleistogamum*, *Eryngium alismifolium*, *Eryngium aristulatum*, *Eryngium castrense*, *Frankenia salina*, *Hippuris vulgaris*,

Hydrocotyle ranunculoides, *Isoetes howellii*, *Juncus arcticus*, *Juncus balticus*, *Juncus nevadensis*, *Lasthenia conjugens*, *Lasthenia glaberrima*, *Limosella*, *Lythrum hyssopifolia*, *Marsilea vestita*, *Muhlenbergia richardsonis*, *Myriophyllum sibiricum*, *Navarretia leucocephala*, *Nuphar polysepala*, *Orcuttia tenuis*, *Pascopyrum smithii*, *Phyla*, *Plagiobothrys leptocladus*, *Plagiobothrys mollis*, *Plagiobothrys scouleri*, *Plagiobothrys stipitatus*, *Plantago elongata*, *Pleuropogon*, *Porterella carnosula*, *Potamogeton amplifolius*, *Potamogeton gramineus*, *Psilocarphus brevissimus*, *Ranunculus aquatilis*, *Rosa*, *Rumex*, *Sagittaria cuneata*, *Sparganium*, *Triglochin scilloides*, *Typha latifolia*, *Utricularia macrorhiza*, *Xanthium strumarium*, *Zannichellia palustris*.

Use by wildlife: The seeds of *Damasonium californicum* are eaten by waterfowl (Aves: Anatidae). The plants are a host of nematodes (Nematoda: Hoplolaimidae: *Pratylenchus morettoii*).

Economic importance: food: no reported uses; **medicinal:** no reported uses; **cultivation:** not in cultivation; **misc. products:** none; **weeds:** none; **nonindigenous species:** none.

Systematics: In molecular phylogenetic analyses (e.g., Figure 1.3), *Damasonium* resolves as the sister group to a clade containing *Alisma* and *Baldellia*. Although the genus appears to be monophyletic, a comprehensive phylogenetic survey has yet to be conducted for the group. The basic chromosome number of *Damasonium* is $x=7$. Counts are unavailable for *D. californicum*.

Distribution: *Damasonium californicum* occurs in the western United States.

References: Cook, 1996; Haynes & Hellquist, 2000a; Kaul, 1976; Les & Tippery, 2013; Martin & Uhler, 1951; Michel et al., 1986; Ramaley, 1919; Ross et al., 2016; Turner et al., 2012; Vuille, 1987.

2.1.3. Echinodorus

Burhead, swordplant; plante-épée

Etymology: from the Greek *echinos doro* (“spiny spear”) in reference to the spiny fruiting heads and sword-like leaves

Synonyms: *Alisma* (in part); *Sagittaria* (in part)

Distribution: global: New World; **North America:** southern

Diversity: global: 28 species; **North America:** 3 species

Indicators (USA): obligate wetland (OBL): *Echinodorus berteroi*, *E. cordifolius*, *E. grandiflorus*

Habitat: freshwater; lacustrine, palustrine, riverine; **pH:** 4.8–7.4; **depth:** 0–2 m; **life-form(s):** emergent herb, floating-leaved, submersed (rosulate)

Key morphology: shoots herbaceous, rosulate, rhizomatous; leaves all basal, the blades (to 32 cm) emersed or submersed, lanceolate, ovate, or elliptic, and marked by translucent lines or dots, the base attenuate, cordate, or truncate, the margins entire, often undulating, the petioles (to 115 cm) triangular (rarely roundish) or ridged; inflorescence (to 131 cm) an erect or decumbent (then arching and proliferating) raceme or erect panicle, the flowers (1.1–4 cm) in 1–9 whorls, bisexual, pedicellate (to 7.5 cm), trimerous; sepals (to 21-veined) erect, recurved, or spreading; petals (to 15 mm) white, clawed or sessile; stamens numerous (to 22), the anthers versatile; pistils

numerous (to 250), arranged spirally in a head; achenes (to 2.5 mm) oblanceolate, 3–5-ribbed, beaked (to 1.3 mm), sometimes flattened

Life history: duration: annual (fruits/seeds); perennial (rhizomes); **asexual reproduction:** rhizomes; **pollination:** insect, self; **sexual condition:** hermaphroditic; **fruit:** aggregates (achenes) (common); **local dispersal:** rhizomes, achenes (water, wind); **long-distance dispersal:** achenes (waterfowl)

Imperilment: 1. *Echinodorus berteroi* [G5]; SX (IN); S1 (AZ, TN, UT); S2 (AR, KY, OH); 2. *E. cordifolius* [G5]; SX (DC); S1 (IN, MD); S2 (KS); S3 (IL, NC, VA); 3. *E. grandiflorus* [GNR]

Ecology: general: All *Echinodorus* species characteristically are aquatic, growing either in standing waters or on moist substrates at sites where the waters have receded. The three North American species are designated as OBL indicators throughout their distributional ranges. Although fairly showy, the flowers of most species appear to be strongly self-compatible, which allows for self-pollination to occur. Otherwise they are believed to be pollinated by insects (Insecta). The plants most often are perennial but reportedly can behave as annuals in more temperate areas. The seeds generally germinate well at high temperatures (25°C–30°C) and any dormancy usually can be broken by incubating them in a 50°C water bath for 10 min, followed by warm incubation at 30°C–35°C until germination occurs. They are buoyant and are dispersed locally by water or wind, or to greater distances via epizootic transport by waterfowl (Aves: Anatidae) or other animal vectors. Most of the species are rhizomatous. When submersed, some taxa develop proliferous inflorescences, which produce vegetative propagules (bulbils) or adventitious plantlets. Because of their popularity as aquarium specimens, many of the species present a risk of becoming nonindigenous introductions via their escape from cultivation.

2.1.3.1. *Echinodorus berteroi* (Spreng.) Fassett is an amphibious annual or perennial, which grows in standing waters (e.g., 7–180 cm deep) or on exposed substrates of beaches, canals, depressions, dikes, ditches (roadside), flats, floodplains, lake beds (dried), marshes, meadows, mudflats, playas, ponds (stock), pools, rice fields, river bottoms, riverbeds (drying), roadsides, sandbars, seeps, shores (drying), silt bars, sloughs (vernal), stream beds (dry), swamps, tire ruts, washes, and along the margins of borrow pits, gravel pits, lakes (drying), ponds, reservoirs, and streams at elevations to 2080 m. The plants occur typically in small, temporary water bodies. In deeper waters (and under short photoperiods) the plants remain sterile and produce elongate, ribbon-like leaves. Water temperatures from 18°C to 27°C are considered optimal. Habitat exposures range from full sun to partial shade. The substrates are characterized as alkaline or saline and include alluvium, clay, clay loam, gravel, humus, loamy clay, muck, mud, Riverwash, sand (coarse), sandstone, sandy gravel, sandy loam, sandy muck, silt, silty clay, and stones. Flowering and fruiting extend from April to October. The flowers are self-compatible and have high seed set, presumably as a consequence of self-pollination. The achenes often remain attached to the receptacle when mature, even after the inflorescences

senesce. When shed, they float for prolonged periods and also can be dispersed by their attachment to fur, feathers, or in mud that clings to a potential animal vector. The achenes require no pretreatment and germinate readily at 25°C–30°C. In North America, the plants usually perennate and disperse locally by means of rhizomes; however, they reportedly behave as annuals when growing at more temperate latitudes. **Reported associates:** *Acer negundo*, *Acer saccharinum*, *Alisma subcordatum*, *Alisma triviale*, *Amaranthus tuberculatus*, *Ambrosia psilostachya*, *Ammannia coccinea*, *Ammannia robusta*, *Artemisia californica*, *Atriplex serenana*, *Azolla filiculoides*, *Baccharis salicifolia*, *Baccharis sarothroides*, *Baccharis sergiloides*, *Bassia hyssopifolia*, *Bergia texana*, *Bidens con-natus*, *Bidens frondosus*, *Bidens tripartitus*, *Bolboschoenus fluviatilis*, *Brassica nigra*, *Brickellia californica*, *Celtis laevigata*, *Cenchrus setaceus*, *Cephalanthus occidentalis*, *Ceratophyllum demersum*, *Chaenactis glabriuscula*, *Chara*, *Cirsium vulgare*, *Coleataenia longifolia*, *Conoclinium coelestinum*, *Conyza canadensis*, *Cressa truxillensis*, *Crypsis schoenoides*, *Crypsis vaginiflora*, *Cylindropuntia prolifera*, *Cynodon dactylon*, *Cyperus acuminatus*, *Cyperus eragrostis*, *Cyperus erythrorhizos*, *Cyperus esculentus*, *Cyperus squarrosus*, *Cyperus strigosus*, *Datura wrightii*, *Digitaria sanguinalis*, *Echinochloa crus-galli*, *Echinochloa muricata*, *Eclipta prostrata*, *Eleocharis acicularis*, *Eleocharis macrostachya*, *Eleocharis obtusa*, *Eleocharis palustris*, *Epilobium ciliatum*, *Epilobium densiflorum*, *Epilobium torreyi*, *Eragrostis hypnoides*, *Eriogonum fasciculatum*, *Ferocactus viridescens*, *Frankenia salina*, *Fraxinus*, *Gratiola neglecta*, *Helianthus annuus*, *Heliotropium*, *Heteranthera limosa*, *Hordeum murinum*, *Ibicella lutea*, *Iva axillaris*, *Juglans*, *Lasthenia glaberrima*, *Leersia oryzoides*, *Lemna gibba*, *Leptochloa fusca*, *Lindernia dubia*, *Ludwigia palustris*, *Ludwigia peploides*, *Ludwigia polycarpa*, *Lythrum hyssopifolia*, *Malvella leprosa*, *Marsilea vestita*, *Mimulus cardinalis*, *Najas*, *Nasturtium officinale*, *Navarretia fossalis*, *Oryza sativa*, *Panicum capillare*, *Panicum dichotomiflorum*, *Paspalum dilatatum*, *Paspalum distichum*, *Paspalum pubiflorum*, *Penthorum sedoides*, *Persicaria coccinea*, *Persicaria lapathifolia*, *Phalaris arundinacea*, *Phyla lanceolata*, *Phyla nodiflora*, *Plagiobothrys leptocladus*, *Plagiobothrys undulatus*, *Plantago major*, *Platanus racemosa*, *Pluchea odorata*, *Polypogon monspeliensis*, *Pontederia cordata*, *Populus fremontii*, *Potamogeton nodosus*, *Pseudognaphalium luteoalbum*, *Quercus berberidifolia*, *Raphanus sativus*, *Rotala ramosior*, *Rumex persicarioides*, *Rumex pulcher*, *Sagittaria graminea*, *Sagittaria latifolia*, *Sagittaria montevidensis*, *Salix gooddingii*, *Salix laevigata*, *Schinus molle*, *Schoenoplectus acutus*, *Schoenoplectus californicus*, *Schoenoplectus hallii*, *Schoenoplectus mucronatus*, *Schoenoplectus tabernaemontani*, *Sphenoclea zeylanica*, *Stuckenia pectinata*, *Tamarisk*, *Trichocoronis wrightii*, *Typha angustifolia*, *Typha domingensis*, *Typha latifolia*, *Veronica anagallis-aquatica*, *Veronica peregrina*, *Xanthium strumarium*, *Zannichellia palustris*.

2.1.3.2. *Echinodorus cordifolius* (L.) Griseb. is a perennial, which grows in shallow (e.g., 1–20 cm depth), tidal or non-tidal waters or on exposed substrates of backwaters,

bayous, bottomlands, depressions, ditches (roadside), floodplains, marshes, meadows, mudflats, oxbows, ponds (depression), pools, prairies, rice fields (abandoned), roadsides, shores (seepy), sloughs, springs, streams, swales, swamps, and along the margins of canals, Carolina bays, channels, lakes, ponds, reservoirs, and rivers at elevations to 500 m. The plants frequently occur as emergents in drawdown areas but will develop submersed leaves when growing under photoperiods of less than 12 h. All the leaves will die back when temperatures fall below 10°C. Site exposures range from full sunlight to partial shade. The substrates (pH: 5.8–7.4) are described as calcareous and include alluvium (clayey), clay, clay mud, humus, loam, muck, mucky Dowling clay, mud, sand, sandy loam (Cecil), sandy silt, silt, silty loam, and silty sand. Flowering occurs under long-day conditions from May to October; fruiting has been observed from July to October. Low seed set typically has been reported, which might indicate a greater requirement for pollinator visitation (and increased outcrossing). A seed bank can develop with recovery densities of germinating seeds ranging from 0.7 (non-flooded sites) to 1.4 (flooded sites) seeds m⁻². The arching inflorescences proliferate by producing adventitious plantlets, which can function as vegetative propagules. Vegetative reproduction also occurs by means of rhizomes. The plants have been micropropagated successfully (from rhizomes) using a combination of 24.6 µM *N*-isopentenyladenine and 2.68 µM naphthalene acetic acid. **Reported associates:** *Acer saccharinum*, *Ammannia coccinea*, *Ampelopsis arborescens*, *Asclepias perennis*, *Bacopa*, *Bergia texana*, *Boehmeria cylindrica*, *Bolboschoenus fluviatilis*, *Campsis radicans*, *Carex comosa*, *Carex crus-corvi*, *Carex longii*, *Carex lupulina*, *Carpinus caroliniana*, *Celtis laevigata*, *Cephalanthus occidentalis*, *Chamaecrista fasciculata*, *Chasmanthium latifolium*, *Cornus foemina*, *Cynoscadium digitatum*, *Cyperus pseudovegetus*, *Cyperus squarrosus*, *Diospyros virginiana*, *Echinochloa colona*, *Elaeagnus umbellata*, *Elatine californica*, *Eragrostis hypnoides*, *Eupatorium*, *Forestiera acuminata*, *Hibiscus*, *Hydrolea uniflora*, *Ipomoea hederacea*, *Iris tridentata*, *Juncus effusus*, *Leersia oryzoides*, *Lemna*, *Leptochloa fusca*, *Leptochloa panicoides*, *Leucospora*, *Lindernia dubia*, *Liquidambar styraciflua*, *Lobelia cardinalis*, *Ludwigia alternifolia*, *Ludwigia peploides*, *Ludwigia repens*, *Marsilea vestita*, *Micranthemum umbrosum*, *Mimulus alatus*, *Najas flexilis*, *Nelumbo lutea*, *Nuphar*, *Nyssa biflora*, *Persicaria hydropiperoides*, *Phylla lanceolata*, *Phylla nodiflora*, *Pilea*, *Pinus taeda*, *Planera aquatica*, *Pluchea camphorata*, *Populus heterophylla*, *Quercus lyrata*, *Quercus nigra*, *Quercus palustris*, *Quercus shumardii*, *Rhynchospora corniculata*, *Rotala ramosior*, *Sabal minor*, *Sabatia calycina*, *Sagittaria latifolia*, *Sagittaria platyphylla*, *Salix caroliniana*, *Salix nigra*, *Sarracenia flava*, *Saururus cernuus*, *Schoenoplectus tabernaemontani*, *Scirpus cyperinus*, *Scleria*, *Senna marilandica*, *Sium*, *Sparganium americanum*, *Taxodium distichum*, *Torilis*, *Toxicodendron radicans*, *Triadica sebifera*, *Tridens flavus*, *Typha latifolia*, *Ulmus alata*, *Ulmus rubra*, *Utricularia gibba*, *Vitis*, *Xanthium strumarium*, *Zannichellia palustris*.

2.1.3.3. *Echinodorus grandiflorus* (Cham. & Schltdl.) Micheli is a nonindigenous perennial, which occurs in swamps at elevations to 10 m. The plants can tolerate a fairly wide range of acidity (pH: 4.8–7.4) and in North America, occur on sand substrates. Flowering (North America) occurs from summer through the fall. In its native range, flowering occurs in the mornings of the rainy season and lasts about 8 hr in duration. The plants are self-compatible but attract various pollinating bees (Insecta: Hymenoptera: Andrenidae; Anthophoridae; Apidae; Colletidae; Halictidae). Seed set can range from 0.2% to 73% but typically is low; it is substantially higher in open-pollinated plants than in selfed individuals. The unscarified seeds germinate moderately (18–35%) when incubated under continuous illumination at 25°C–30°C, but not under continuous darkness. Scarified seeds (the seed coat slit near the site of embryo emergence) germinate well (98–99%) under constant illumination or in darkness. The inflorescences are proliferous and produce numerous vegetative plantlets. Vegetative reproduction also occurs by means of rhizomes. **Reported associates (North America):** *Acer rubrum*, *Colocasia esculenta*, *Juncus effusus*, *Magnolia virginiana*, *Mikania scandens*, *Myrica cerifera*, *Nyssa biflora*, *Osmunda regalis*, *Osmundastrum cinnamomeum*, *Persea palustris*, *Persicaria punctata*, *Pinus elliottii*, *Rhynchospora miliacea*, *Sabal minor*, *Saururus cernuus*, *Smilax walteri*, *Taxodium distichum*, *Thelypteris palustris*, *Woodwardia areolata*.

Use by wildlife: The achenes of several *Echinodorus* species are eaten occasionally by waterfowl (e.g., Aves: Anatidae: *Anas platyrhynchos*), which have been suggested as potential long-distance dispersal agents. The achenes of *E. berteroi* are eaten by cinnamon teal (Aves: Anatidae: *Anas cyanoptera*). *Echinodorus berteroi* is used frequently as a nesting site of coots (Aves: Rallidae: *Fulica americana*, *F. caribaea*). *Echinodorus berteroi* and *E. cordifolius* are the hosts of sac Fungi (Ascomycota: Mycosphaerellaceae: *Cercospora echinodori*). *Echinodorus cordifolius* is a larval host plant of moths (Insecta: Lepidoptera: Crambidae: *Synclita occidentalis*); it also is fed upon by weevils (Insecta: Coleoptera: Curculionidae: *Listronotus echinodori*).

Economic importance: food: *Echinodorus cordifolius* plants can contain up to 81.6% digestible dry matter and 17.2% protein; however, they have not been used as a human food; **medicinal:** Root decoctions of *E. berteroi* have been used as a folk remedy for epilepsy and have been found to exhibit neuroleptic and antiepileptic activity. Aqueous extracts of *E. grandiflorus* have been shown to exhibit potent vasodilator activity and also may be a potential therapeutic agent for asthma; ethanolic extracts from the plants are antihypertensive. Foliar alcoholic extracts of *E. grandiflorus* are rich in diterpenes and flavonoids, which have been linked to their effectiveness in treating inflammatory conditions; **cultivation:** Several *Echinodorus* species are cultivated widely as ornamental aquarium plants, including *E. berteroi*, *E. cordifolius*, and *E. grandiflorus*. Cultivars of *E. cordifolius* include ‘Marble Queen’, ‘Oriental’, and ‘Ozelot Green’; **misc. products:** *Echinodorus cordifolius* has been recommended as a

potentially effective phytoremedial agent for the removal of azo dyes, ethylene glycol, and phosphorous from contaminated wastewater; **weeds:** *Echinodorus berteroi* is a weed of California rice fields; **nonindigenous species:** *Echinodorus grandiflorus* was introduced to Florida as an escape from cultivation, sometime before 1981.

Systematics: *Echinodorus* resolves as a clade after the removal of species assigned previously to subgenus *Helanthium*, which have been transferred to the genera *Albidella* and *Helanthium*. Its sister group is not certain, but has included combinations of various genera (*Alisma*, *Astonia*, *Baldellia*, *Helanthium*, *Sagittaria*, and *Wiesneria*) depending on the analysis and data sets analyzed. Originally named as a distinct species, *E. floridanus* does not appear to differ from *E. grandiflorus* (Figure 1.5), and it has been treated here as a synonym of the latter (along with the transfer of its OBL indicator status to *E. grandiflorus*). Phylogenetic analyses have indicated that the formerly proposed sectional divisions of *Echinodorus* are not entirely monophyletic. However, the assignment of *E. cordifolius* and *E. grandiflorus* to the same section (sect. *Cordifolii*) and *E. berteroi* to a different section (sect. *Berteroi*) is consistent with the results of phylogenetic analyses, which resolve *E. berteroi* as a distinct group and unite *E. cordifolius* and *E. grandiflorus* within the same clade (Figure 1.5). The basic chromosome number of *Echinodorus* is $x=11$. All counted species in the genus, including *E. berteroi*, *E. cordifolius*, and *E. grandiflorus*, are uniformly diploid ($2n=22$). Hybridization is known to occur commonly among species in cultivation; however, no accounts of natural hybridization involving *Echinodorus* have been reported in North America. Putative intergeneric hybrids involving *Alisma* and *Echinodorus* have been called $\times$ *Alismodorus* H.R.Wehrh.

Distribution: *Echinodorus berteroi* occurs across southern North America, with *E. cordifolius* restricted to the southeastern United States; both species extend into South America. The nonindigenous *E. grandiflorus* currently occurs only in Florida, but is native to South America.

References: Beal, 1977; Boyd & McGinty, 1981; Braun et al., 2014; Brugiolo et al., 2011; Buznego & Pérez-Saad, 2006; Cook, 1996; Correll & Correll, 1975; de Faria Garcia et al., 2010; Dissanayake et al., 2007; DiTomaso & Healy, 2003; Fassett, 1955; 1957; Gordón, 1997; Harms & Grodowitz, 2009; Haynes & Burkhalter, 1998; Haynes & Hellquist, 2000a; Haynes & Holm-Nielsen, 1994; Hohman & Ankney, 1994; Kasselmann, 2001; Knobloch, 1972; Lehtonen, 2009a; Lehtonen & Myllys, 2008; Lessa et al., 2008; McAtee, 1918; McNair & Cramer-Burke, 2006; Middleton, 2009; Mühlberg, 1982; Munz & Johnston, 1922; Noonpui & Thiravetyan, 2011; Rataj, 1975; 2004; Reese & Lubinski, 1983; Teamkao & Thiravetyan, 2010; Tibiriça et al., 2007; Torit et al., 2012; Tucker et al., 2015; Usinger, 1956; Vieira & de Souza Lima, 1997.

2.1.4. *Helanthium*

Marsh flower, mudbabies

Etymology: from the Greek *helos anthos* (“marsh flower”) in reference to the habitat

Synonyms: *Alisma* (in part); *Echinodorus* (in part); *Helanthium*

Distribution: global: New World; **North America:** eastern United States

Diversity: global: 3 species; **North America:** 1 species

Indicators (USA): obligate wetland (OBL): *Helanthium tenellum*

Habitat: freshwater; freshwater (tidal); palustrine; **pH:** 6.1–7.6; **depth:** <1 m; **life-form(s):** emergent or submersed (rosulate) herbs

Key morphology: foliage (to 6 cm) arising from rosettes, connected by fine pseudostolons; submersed leaves (to 10 cm) sessile and linear, emerged leaves with ridged petioles (to 9.5 cm), the blades (to 7.4 cm) narrowly lanceolate to ovate; umbels or racemes (to 8 cm) pedunculate (to 4 cm), with 1–2 whorls of 4–16 flowers; flowers (to 10 mm) pedicellate (to 3 cm), trimerous, radial; petals (to 4 mm) clawed, white; stamens 9; gynoecium apocarpous (to 20 pistils); fruit a headlike aggregate of flattened achenes (to 1.5 mm) with lateral beaks (to 0.2 mm)

Life history: duration: annual (fruits/seeds); **asexual reproduction:** pseudostolons; **pollination:** unknown; **sexual condition:** hermaphroditic; **fruit:** aggregates (achenes) (common); **local dispersal:** achenes (water?), pseudostolons; **long-distance dispersal:** achenes (animals)

Imperilment: 1. *Helanthium tenellum* [G5]; SX (DE, NY); SH (LA, MA, NC); S1 (CT, IL, KS, MI, MS, VA); S2 (SC)

Ecology: general: All *Helanthium* species occur in wetlands and are amphibious plants capable of growing under emerged or submersed conditions. Their reproductive biology and seed ecology have not been described in any detail and require further study.

2.1.4.1. *Helanthium tenellum* Britt. is an annual, which inhabits shallow waters (up to at least 50 cm depth) or colonizes exposed substrates in borrow pits, canals, depressions, ditches, flats, meadows, pools (gum; swamp), prairies, sinkholes, swales, and along the margins of small lakes (depression), ponds (depression; drying; limesink depression; sink hole; temporary; swale), rivers, and streams at elevations to 591 m. Although most often found on wet, exposed substrates, the plants also grow well when fully submersed. Exposures typically receive full sunlight, but also include partially shaded conditions. Occurrences span a pH range from 6.1 to 7.6, but the plants thrive in weakly acidic waters of soft to medium hardness at temperatures from 18°C to 28°C (but up to 33°C). The substrates typically are acidic and include clay, Cowarts (typic hapludults), loam, muck (organic), mud (exposed), peat, peaty sand, Plummer (grossarenic pale-aquults), Rutlege (typic humaquepts), sand, sandy peat, and silty loam. Flowering occurs only when the inflorescences are emerged. Flowering and fruiting extend from March to September. The pollination biology of this species has not been described, but seed set tends to be high as in most annuals. In its South American range, this species can dominate the seed bank, comprising more than 24% of the total germinating propagules. The mechanism of seed dispersal also has not been elucidated but likely involves water over short distances

FIGURE 1.5 Interspecific relationships in *Echinodorus* as indicated by phylogenetic analysis of combined morphological and DNA sequence data (adapted from Lehtonen & Myllys, 2008). The OBL North American wetland indicators (in bold) represent diverse origins in the genus. These results do not distinguish *E. floridanus* and *E. grandiflorus* (the latter name has been retained in the present treatment); the currently defined subspecific divisions of *E. cordifolius* also are untenable.

and attachment to various animal vectors over greater distances. The plants can be connected by delicate “pseudostolons,” i.e., sterilized inflorescences from which vegetative buds can develop. Although unusual for an annual species, this means of vegetative reproduction can quickly result in the development of large, dense “cushions” of plants during the growing season. **Reported associates:** *Alisma triviale*, *Bidens cernuus*, *Bidens connatus*, *Bidens frondosus*, *Bidens*

vulgatus, *Boehmeria cylindrica*, *Bolboschoenus fluviatilis*, *Callitriche heterophylla*, *Cardamine pensylvanica*, *Carex barrattii*, *Carex lasiocarpa*, *Carex lurida*, *Cephalanthus occidentalis*, *Chelone glabra*, *Coleataenia longifolia*, *Cyperus dentatus*, *Cyperus diandrus*, *Cyperus esculentus*, *Cyperus haspan*, *Cyperus strigosus*, *Echinochloa crus-galli*, *Eleocharis acicularis*, *Eleocharis melanocarpa*, *Eleocharis obtusa*, *Eleocharis ovata*, *Eleocharis palustris*, *Fimbristylis*

vahlilii, *Gratiola aurea*, *Helenium virginicum*, *Heteranthera limosa*, *Hypericum mutilum*, *Hyptis alata*, *Isoetes virginica*, *Juncus acuminatus*, *Leersia oryzoides*, *Lindernia dubia*, *Lipocarpa maculata*, *Lipocarpa micrantha*, *Ludwigia palustris*, *Lycopus uniflorus*, *Lysimachia terrestris*, *Lythrum salicaria*, *Mayaca fluviatilis*, *Mentha arvensis*, *Nelumbo lutea*, *Nuphar variegata*, *Nymphaea odorata*, *Oldenlandia boscii*, *Oldenlandia uniflora*, *Panicum hemitomon*, *Panicum verrucosum*, *Penthorum sedoides*, *Persicaria hydropiperoides*, *Persicaria lapathifolia*, *Persicaria longiseta*, *Persicaria maculosa*, *Persicaria pensylvanica*, *Phalaris arundinacea*, *Physostegia leptophylla*, *Pilea pumila*, *Polypremum procumbens*, *Pontederia cordata*, *Proserpinaca palustris*, *Rhexia virginica*, *Rorippa palustris*, *Rotala ramosior*, *Rotala ramosior*, *Sagittaria graminea*, *Sagittaria latifolia*, *Schoenoplectus erectus*, *Schoenoplectus hallii*, *Schoenoplectus smithii*, *Scirpus cyperinus*, *Scutellaria lateriflora*, *Serenoa repens*, *Solanum dulcamara*, *Sparganium americanum*, *Sphagnum*, *Stachys hyssopifolia*, *Symphyotrichum lateriflorum*, *Taxodium*, *Typha latifolia*, *Xanthium strumarium*, *Xyris jupicai*.

Use by wildlife: none reported.

Economic importance: food: not reported as edible; **medicinal:** *Helanthium tenellum* has been used in South America in preparing treatments for headaches, rheumatism, and syphilis; **cultivation:** *Helanthium tenellum* is grown as an aquarium plant; **misc. products:** none; **weeds:** none; **nonindigenous species:** none.

Systematics: Once treated as a section or subgenus of *Echinodorus*, *Helanthium* has more recently been recognized as a distinct genus in accordance with results of phylogenetic analyses. The species assigned to *Helanthium* group consistently as a clade, which resolves as the sister group of *Echinodorus* in several studies, including analyses of complete cpDNA gene sequences (Figure 1.3); however, other studies indicate *Ranalisma* as a possible sister group (Figure 1.6). Phylogenetic analyses of the three consistently recognized species using combined molecular and morphological data resolve *H. tenellum* as the sister to the remainder of the genus (Figure 1.6). Some authors have recognized as many as 10 species in the genus, indicating that a more comprehensive taxonomic evaluation is necessary. The base

FIGURE 1.6 Phylogenetic relationships in *Helanthium* as indicated by analysis of combined molecular and morphological data (adapted from Lehtonen & Myllys, 2008). These results resolve the OBL *H. tenellum* (in bold) as the sister to the remainder of the genus. They also indicate the possibility of a fourth species, which had been identified provisionally as *H. bolivianum*, but does not associate with that species.

chromosome number of *Helanthium* is $x=11$. *Helanthium tenellum* has diploid and triploid cytotypes ($2n=22, 33$). The triploids have meiotic abnormalities and reduced pollen stainability (~50%) with respect to the diploids (normal meiosis and 100% pollen stainability). Chromosomal (C-banding) analyses indicate that the triploids are of autopolyploid origin.

Distribution: *Helanthium tenellum* occurs sporadically throughout the eastern United States.

References: Bercu, 2015; Brooks & Wardrop, 2013; Charlton, 1979; Chester & Palmer-Ball, 2011; Chester & Souza, 1984; Costa, 2004; Haynes & Hellquist, 2000a; Haynes & Holm-Nielsen, 1994; Kasselman, 2003; Lehtonen, 2007; 2009; Lehtonen & Myllys, 2008; Les & Tippery, 2013; Pagotto et al., 2011; Rataj, 2004.

2.1.5. Hydrocleys

Waterpoppy

Etymology: probably from the Greek *hydro keleuthos* (“leaving a water path”), in reference to the stepping-stone-like pattern displayed on the water by the floating leaves

Synonyms: *Hydrocleis*; *Ostenia*; *Vespuccia*

Distribution: global: New World; **North America:** southern United States

Diversity: global: 5 species; **North America:** 1 species

Indicators (USA): obligate wetland (OBL): *Hydrocleys nymphoides*

Habitat: freshwater; lacustrine, palustrine; **pH:** 5.5–6.0;

depth: 0–2 m; **life-form(s):** floating-leaved

Key morphology: plants (to 50 cm) stoloniferous (to 45 cm); leaves submersed (sessile and phyllodial) or floating, then the petioles long (to 40 cm), septate, sheathing (to 8.5 cm), the blades (to 11.9 cm) ovate to orbiculate, the base rounded or cordate; inflorescence (to 6 flowers) umbellate, proliferous, the peduncle (to 30 cm) septate; flowers (to 6.5 cm) pedicellate (to 17.5 cm); petals (to 4.1 cm) spreading, yellow to white, yellow at base; stamens (to 25) and outer staminodes (to 20+) numerous; gynoecium apocarpous, pistils (5–8; to 10 mm) attenuate to an inwardly curved style; follicles (to 14.5 mm) beaked (to 5.5 mm), dehiscent adaxially; seeds (to 50+) small (~1 mm), with glandular trichomes (to 0.15 mm)

Life history: duration: perennial (stolons); **asexual reproduction:** stolons; **pollination:** insect; **sexual condition:** hermaphroditic; **fruit:** aggregates of follicles (common); **local dispersal:** seeds (water), stolons, vegetative plantlets (water); **long-distance dispersal:** seeds (water, waterfowl?)

Imperilment: 1. *Hydrocleys nymphoides* [G5]

Ecology: general: All *Hydrocleys* species are floating-leaved hydrophytes (also producing submersed foliage), which occupy relatively shallow lentic or standing waters. Although normally rooted in the muddy substrate, the plants can dislodge and assume a free-floating habit. They produce floating inflorescences with showy flowers that are pollinated primarily by bees (Insecta: Hymenoptera: Apidae; Colletidae) or flies (Insecta: Diptera), which are attracted to their bright perianths by volatile methoxylated aromatics (e.g., *p*-methylanisole). Unlike many monocots, the perianth is not shed, but becomes extremely soft when water-soaked,

eventually withering. Flowering can extend year-round in the native South American range. The sterility of some nonindigenous populations indicates the possibility of self-compatibility in the genus, but that prospect has not been investigated. The seeds are dispersed by water and possibly to greater distances by attachment to the plumage of waterfowl (Aves: Anatidae). There are no known specific germination requirements. The inflorescences of some species proliferate and produce vegetative buds, which produce adventitious roots and can develop into new plantlets as the peduncles arch over and contact the substrate.

2.1.5.1. *Hydrocleys nymphoides* (Humb. & Bonpl. ex Willd.)

Buch. is a nonindigenous perennial, which grows in ditches, pools (shallow), and along the margins of lakes at elevations to 70 m. It can tolerate depths to 2 m, but thrives in shallower waters from 20 to 45 cm. Exposures can range from fully open to strongly shaded sites. Waters in the native South American habitats are acidic (pH: 5.5–6.0), soft, and can range from 6°C to 24°C; the native substrates include loam and sandy gravel. Flowering (North America) has been observed in July, but the pollination biology has not been studied in this nonindigenous region. In their native South American range, the flowers are visited by flies (Insecta: Diptera) and bees (Insecta: Hymenoptera: Apidae: *Geotrigona argentina*) and the pollen is found in various honey samples, which indicates that the plants normally are entomophilous. Plants introduced to Australia completely fail to set seed. The inflorescence often proliferates into leaves or stolons, which are capable of vegetative reproduction (the primary reproductive mode at least in nonindigenous populations). Detached, floating vegetative plantlets can facilitate late seasonal dispersal. Unlike many indigenous species, the photosynthetic surface area (and biomass accumulation) increases proportionally with nutrient levels, which facilitates their invasion into new territories. The plants are non-mycorrhizal. **Reported associates (North America):** *Acmella repens*, *Alternanthera philoxeroides*, *Cyperus flavicomus*, *Diodia virginiana*, *Eleocharis obtusa*, *Hydrocotyle verticillata*, *Kyllinga brevifolia*, *Sagittaria platyphylla*.

Use by wildlife: In the Pantanal of Brazil, *Hydrocleys nymphoides* is consumed frequently by marsh deer (Mammalia: Cervidae: *Blastocerus dichotomus*). The plants are known hosts of powdery mildew (Fungi: Ascomycota: Erysiphaceae: *Erysiphe*).

Economic importance: food: *Hydrocleys nymphoides* supposedly is edible, but no specific uses have been reported; **medicinal:** Extracts of *Hydrocleys nymphoides* have exhibited antimicrobial activity against pathogenic bovine mastitis microbes; **cultivation:** *Hydrocleys nymphoides* is a popular ornamental plant for aquariums and garden ponds; **misc. products:** none; **weeds:** *Hydrocleys nymphoides* is a “vigorously controlled” weed in New Zealand; **nonindigenous species:** *Hydrocleys nymphoides* is nonindigenous to North America, having escaped from cultivation sometime during the 20th century. The plants were introduced to Hawaii before 1938. They also have become naturalized in Australia, Japan, Korea, New Zealand, and Taiwan.

Systematics: *Hydrocleys* formerly was placed in the Butomaceae or Limnocharitaceae until several phylogenetic analyses consistently indicated that the group was nested within Alismataceae. However, the sister group of *Hydrocleys* remains somewhat uncertain, with either *Butomopsis* or *Butomopsis* + *Limnocharis* resolving in that position depending on the specific data set analyzed. A closer relationship between *Butomopsis* and *Hydrocleys* is indicated by their highly similar chromosome morphology and symmetry; chromosomally, they are both interpreted as relatively primitive elements compared to *Limnocharis*. Interspecific relationships in *Hydrocleys* have been investigated to some degree using morphological phylogenetic analyses, which indicate that the group is monophyletic. However, those analyses are incongruent with respect to the relationships depicted when using different outgroups (i.e., *Butomopsis* vs. *Limnocharis*), which is problematic given the uncertain sister-group relationships (see above). *Hydrocleys nymphoides* resolves either as the sister species of *H. martii* or *H. matogrossensis* in the morphological cladograms. A phylogenetic evaluation of the genus using molecular data potentially would be helpful in resolving the interspecific relationships and also might help to clarify the sister group of *Hydrocleys*. The chromosomal base number is $x=7$ or $x=8$. *Hydrocleys nymphoides* ($2n=16$; $x=8$) is a diploid, with a triploid cytotype ($2n=24$) also reported. The diploid *H. modesta* ($2n=14$; $x=7$) differs by having a pair of telocentric chromosomes and a pair of acrocentric chromosomes replaced by a pair of metacentric chromosomes as a result of Robertsonian fission or fusion. No natural hybrids involving *H. nymphoides* have been reported.

Distribution: The nonindigenous *Hydrocleys nymphoides* reportedly is naturalized in Florida, Louisiana, and Texas.

References: Aston & Jacobs, 1980; Boxell, 2014; Carvalho et al., 2014; Clayton, 1996; Cook et al., 1997; Edgerton, 2014; Fagúndez & Caccavari, 2006; Forni-Martins & Calligaris, 2002; Haynes, 2004; Haynes & Holm-Nielsen, 1992; Haynes et al., 1998b; Kadono, 2004; Kasselmann, 2003; Kenton, 1981; Les & Tippery, 2013; MacRoberts & MacRoberts, 2010; McKenzie & Lovell, 1992; Nesom, 2009; Ross et al., 2016; Rossi et al., 2011; Shin et al., 2012; Tomas & Salis, 2000; Vossler et al., 2010; Wang & Qiu, 2006; Wester, 1992; Wu et al., 2010.

2.1.6. *Sagittaria*

Arrowhead, wapato; flèche d'eau, sagittaire

Etymology: derived from the Latin *sagitta* (“arrow”), in reference to the arrow-like leaves of some species

Synonyms: *Alisma* (in part); *Echinodorus* (in part); *Lophiocarpus* (later homonym); *Lophotocarpus*

Distribution: global: Eurasia; Western hemisphere; **North America:** widespread

Diversity: global: 40 species; **North America:** 26 species

Indicators (USA): obligate wetland (OBL): *Sagittaria ambigua*, *S. australis*, *S. brevirostra*, *S. calycina*, *S. cristata*, *S. cuneata*, *S. demersa*, *S. engelmanniana*, *S. fasciculata*, *S. filiformis*, *S. graminea*, *S. guayanensis*, *S. isoetiformis*, *S. kurziana*, *S. lancifolia*, *S. latifolia*, *S. longiloba*, *S. macrocarpa*,

S. montevidensis, *S. papillosa*, *S. platyphylla*, *S. rigida*, *S. sanfordii*, *S. secundifolia*, *S. subulata*, *S. teres*

Habitat: brackish, freshwater; freshwater (tidal); lacustrine, palustrine, riverine; **pH:** 4.4–9.2; **depth:** 0–2 m; **life-form(s):** emergent, floating-leaved, or submersed (rosulate) herbs

Key morphology: rosettes emersed, floating-leaved, or submersed, with stolons or rhizomes (sometimes producing tubers), the roots septate; leaves (when submersed) phyllodial (to 7–70 cm; to 250 cm in some species), leaves (when emersed or floating) with blades cordate, elliptic, hastate, lance-elliptic, lanceolate, linear, linear-lanceolate, linear-oblongate, linear-ovate, ovate, sagittate, spatulate (to 2.5–35 cm), margins entire, petioles (to 4–100 cm) circular or triangular; inflorescences (to 4–72 cm) erect, floating, or emergent racemes or panicles, the flowers (to 0.8–4.0 cm) sessile (rarely) or stalked (to 1.0–6.5 cm), in whorls (to 4–17); flowers bisexual (rarely) or unisexual and in andromonoecious (rarely; normally pistillate flowers with a ring of stamens), dioecious (rarely), or monoecious (distally male) arrangements, perianth trimerous; sepals recurved or erect; petals white (rarely with a purplish spot); stamens numerous (to 30); gynoecium apocarpous, pistils numerous (to 1,500+), spirally arranged; fruit an aggregate head (to 0.5–3.0 cm) of achenes (to 1.5–4.0 mm); achenes compressed, abaxial keel and/or abaxial/lateral wings absent or present, with an erect or lateral beak (to 0.2–2.1 mm; to 17 mm in one species)

Life history: **duration:** annual (fruits/seeds); perennial (corms, rhizomes, stolons); **asexual reproduction:** rhizomes, stolons, tubers; **pollination:** insect; **sexual condition:** dioecious, monoecious; **fruit:** aggregates (achenes) (common); **local dispersal:** fish, water (achenes); **long-distance dispersal:** birds (achenes)

Imperilment: 1. *Sagittaria ambigua* [G2]; S1 (AR, MO); S2 (KS); 2. *S. australis* [G5]; S1 (DC, IL, NJ); S2 (IN); 3. *S. brevirostra* [G5]; SH (MN, VA); S1 (TN); S2 (CO); S3 (IL); 4. *S. calycina* [G5]; SH (DC, NH); S1 (CO, DE, MA, NC, PA, QC, VA, WI, WV); S2 (MD, NB, NJ, NY, OR, WV); S3 (CT, DE, IL, ME, NJ); 5. *S. cristata* [G4]; S3 (ON); 6. *S. cuneata* [G5]; S1 (CT, NH, NJ, OH, OK, PA); S2 (MA, YT); S3 (IA, WY); 7. *S. demersa* [G2/G4]; 8. *S. engelmanniana* [G5]; SH (VA); S1 (WV); S2 (DE, MD, NC); 9. *S. fasciculata* [G2]; S2 (NC, SC); 10. *S. filiformis* [G4/G5]; SX (PA); SH (NC, NJ); S2 (ME); 11. *S. graminea* [G5]; S1 (AZ, CO, KY, NC, OH, PE, SC, TN); S2 (DE, KS, NC, NE, RI); S3 (GA, IA, IL, NC, NE, VA); 12. *S. guayanensis* [G5]; 13. *S. isoetiformis* [G4]; S1 (MS); S2 (AL, NC); S3 (SC); 14. *S. kurziana* [G4]; S1 (MS); 15. *S. lancifolia* [G5]; S1 (DE); S3 (NC); 16. *S. latifolia* [G5]; S1 (AZ, NE, WY); S2 (AB, NC); S3 (DE, OH); 17. *S. longiloba* [G5]; S1 (AZ, NE); 18. *S. macrocarpa* [G5T2]; S2 (NC); 19. *S. montevidensis* [G5]; 20. *S. papillosa* [G5]; 21. *S. platyphylla* [G5]; S1 (GA, KS, KY, MO, NC, OH, WV); S2 (TN); 22. *S. rigida* [G5]; SX (DC); SH (AR, DE, NH, PE); S1 (ID, KS, KY, MD, VA, TN); S2 (ME, MB, MA, OH); S3 (NE, QC, VT); 23. *S. sanfordii* [G3]; S3 (CA); 24. *S. secundifolia* [G1]; S1 (AL, GA); 25. *S. subulata* [G4]; SH (RI); S1 (MA); S2 (DE, NC, NJ); S3 (CT, NY, PA, VA); 26. *S. teres* [G3]; S1 (NH, NJ, NY, RI); S3 (MA)

Ecology: general: *Sagittaria* is entirely aquatic, with all 26 North American species designated as OBL indicators throughout their ranges. Although not recognized in the National list, *S. calycina* and *S. macrocarpa* have been reinstated here as distinct species and are included as OBL indicators (see *Systematics*). Three species (*S. chapmanii*, *S. spathulata*, *S. weatherbiana*) retain OBL rankings on the National Wetland list, but are excluded here on taxonomic grounds (see *Systematics*). Information attributed to these taxa has been included with the species to which they currently are assigned. Most of the species are perennials (from coarser rhizomes or finer stolons) but a few behave as annuals. The stolons often are terminated by tubers, which some refer to as corms. The plants grow as submersed, floating-leaved, and emergent life-forms, with the various species producing leaves that range from narrow, submersed phyllodes to emergent broad-bladed structures. The flowers almost always are unisexual (sometimes the pistillate appearing to be bisexual by the presence of sterile stamens), rarely perfect, and are arranged in andromonoecious (having some perfect flowers), dioecious, or monoecious sexual conditions; sexual conditions sometimes are mixed within a species. Monoecious individuals have the staminate flowers situated above the pistillate flowers. They are self-compatible (i.e., capable of geitonogamy) but most of the flowers produce nectar and display a showy corolla of prominent white petals, which serves to attract various bees, beetles, butterflies, flies, and wasps (Insecta: Coleoptera; Diptera; Hymenoptera; Lepidoptera) as potential pollinators. Seed production generally tends to be high in both monoecious and dioecious populations. Seed germination requirements are poorly understood for many species and can be complex. Varied reports indicate germination in water without any pretreatment, germination following a five- to seven-month cold treatment, germination requiring warm stratification, and germination under constant or fluctuating incubation temperatures. Physical scarification (by puncture of the integument) is known to increase germination rates in some species. Seeds originating from dioecious plants can produce germination inhibitors, which require stratification and/or scarification to overcome. Usually, the seeds are consumed only occasionally by waterfowl (Aves: Anatidae); however, locally they can be important components of their meals, with several hundred achenes being consumed during a feeding period. The mature achenes will float (for up to 2 months) and are dispersed by water. In some species they are eaten by fish (e.g., Osteichthyes: Teleostei: *Cyprinus carpio*) and are excreted in viable state, which facilitates their transport within water bodies. They also are transported over longer distances by their external attachment to or consumption and subsequent egestion by birds (e.g., Aves: Anatidae; Charadriidae). Vegetative reproduction can occur in most species by the proliferation of stolons (the thicker structures categorized as rhizomes) and associated tubers. This is a taxonomically difficult group and a good number of literature accounts (even those authored by experts) often involve misidentifications or improper species assignments.

2.1.6.1. *Sagittaria ambigua* J.G. Sm. is a perennial, which inhabits shallow waters or wet exposed sites in depressions, ditches, gravel pits, mudflats, ponds (shallow), pools, prairies, roadsides, sloughs, swamps, and along the margins or shores of lakes, ponds, and streams at elevations to 230 m. The plants are common along shores where water levels fluctuate and have been characterized as pioneer species of shallow pond bottoms. The substrates often are described as mud. Flowering occurs from April to September. There is no information on the reproductive biology or seed ecology of this species. Seed dispersal likely occurs primarily by water. **Reported associates:** *Alisma subcordatum*, *Ammannia auriculata*, *Callitriche heterophylla*, *Cephalanthus occidentalis*, *Echinochloa crus-galli*, *Eclipta prostrata*, *Eleocharis engelmannii*, *Eleocharis macrostachya*, *Eleocharis obtusa*, *Fimbristylis autumnalis*, *Gratiola virginiana*, *Helenium flexuosum*, *Hydrolea ovata*, *Juncus brachycarpus*, *Juncus torreyi*, *Ludwigia alternifolia*, *Ludwigia glandulosa*, *Ludwigia palustris*, *Nelumbo lutea*, *Persicaria pensylvanica*, *Rhexia mariana*, *Rotala ramossior*, *Sagittaria brevirostra*, *Sagittaria calycina*, *Sagittaria latifolia*, *Samolus ebracteatus*, *Schoenoplectus pungens*, *Schoenoplectus tabernaemontani*, *Typha latifolia*, *Verbena hastata*.

2.1.6.2. *Sagittaria australis* (J.G. Sm.) Small is a perennial, inhabits exposed sediments or shallow waters (e.g., 15 cm depth) within bottomlands (alluvial; dry; creek), channels (river), depressions, ditches (banks), floating mats, floodplains, marshes, meadows (alluvial), oxbows, ponds (spring-fed; vernal), slopes (to 40%), sloughs, streams (lentic), swales, swamps, and along the margins of lakes, ponds, reservoirs, streams, and swamps at elevations to 488 m. The plants can tolerate exposures ranging from fully open to shaded conditions. The substrates are consistently circumneutral (pH: 6.0–7.6) and include Cecil clay loam, Cecil sandy loam, Congaree silt loam, dredge material, gravel, mud, and sand. Flowering and fruiting in this monoecious species extend from July to October. The flowers are pollinated by generalist bees (see *Use by wildlife*). Seeds collected from late August through early October, and stored moist or in water, have germinated well on saturated media (23% to 52%) within 10–11 weeks after planting. The breeding system is not well correlated with subsequent seed germination, with higher, lower, and equal rates reported for inbred vs. outcrossed seeds. **Reported associates:** *Acer floridanum*, *Acer negundo*, *Acer rubrum*, *Acorus calamus*, *Alisma subcordatum*, *Arundinaria tecta*, *Bacopa*, *Betula nigra*, *Bidens frondosus*, *Bidens tripartitus*, *Boltonia*, *Calamagrostis canadensis*, *Carex alata*, *Carex lurida*, *Carex vulpinoidea*, *Cicuta maculata*, *Commelina virginica*, *Conoclinium coelestinum*, *Cyperus flavescens*, *Cyperus squarrosus*, *Cyperus strigosus*, *Eleocharis ovata*, *Epilobium coloratum*, *Fraxinus pennsylvanica*, *Geum canadense*, *Glyceria striata*, *Hydrocotyle verticillata*, *Hypericum mutilum*, *Ipomoea lacunosa*, *Isoetes engelmannii*, *Juncus effusus*, *Kosteletzkya*, *Leersia oryzoides*, *Leersia virginica*, *Leptochloa*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Lobelia*, *Ludwigia alternifolia*, *Lycopus virginicus*, *Microstegium vimineum*, *Mimulus alatus*, *Murdannia keisak*,

Nitella, *Nuphar advena*, *Nymphaea odorata*, *Nyssa*, *Oxypolis rigidior*, *Panicum*, *Peltandra virginica*, *Persicaria amphibia*, *Persicaria longiseta*, *Persicaria setacea*, *Potamogeton*, *Ptilimnium costatum*, *Quercus*, *Rhexia virginica*, *Rosa palustris*, *Rumex conglomeratus*, *Sagittaria calycina*, *Sagittaria latifolia*, *Sagittaria platyphylla*, *Salix caroliniana*, *Salix nigra*, *Samolus valerandi*, *Saururus cernuus*, *Scirpus cyperrinus*, *Sesbania*, *Sparganium americanum*, *Sphenoclea zeylanica*, *Taxodium distichum*, *Typha latifolia*.

2.1.6.3. *Sagittaria brevirostra* Mackenzie & Bush is a perennial, which occurs on exposed substrates or in shallow waters (to 60 cm deep) of alluvial fans, bottomlands, canals, channels (ravine), ditches (dredged; roadside), floodplains, gravel pits, lakebeds, marshes, meadows, mud bars, mudflats, oxbows, ponds (dessicated; sand), prairies, ravines (dried), seeps, shores, slopes (to 5%), sloughs, springs, swamps (dried), and along the margins of lakes, ponds, rivers, streams, and swamps at elevations to 1539 m. Exposures from open sunlight to shade are tolerated. The substrates are described as clay loam, clay mud, loamy clay, loam muck, mud, rock, sand, sandy loam (Bolivar), and silt. The plants exhibit a highly plastic morphology. Smaller leaves develop when growing in dry and deep-water conditions than those when growing in shallow water. In deep waters, the leaves are quite narrow. These monoecious plants flower and fruit from June to October. Plants growing in deep waters are sterile. The individuals are self-compatible, allowing for either geitonogamous or xenogamous pollination to occur. The pollinators consist of numerous types of small insects (Insecta). Inflorescence size varies but does not influence seed set, which typically is high in all female flowers. Inflorescences are larger and produce more flowers under wet vs. dry conditions. Male flowers outnumber females in either dry or wet conditions, but sex ratios are more highly male biased in plants growing under dry conditions. Details on seed germination are unavailable. The achenes are dispersed by water. **Reported associates:** *Acalypha rhomboidea*, *Acer negundo*, *Acer saccharinum*, *Agalinis purpurea*, *Alisma subcordatum*, *Ambrosia*, *Ammannia coccinea*, *Ammannia robusta*, *Asclepias incarnata*, *Azolla*, *Bacopa rotundifolia*, *Betula nigra*, *Boehmeria cylindrica*, *Bolboschoenus fluvialis*, *Calamagrostis canadensis*, *Callitriche heterophylla*, *Campanula americana*, *Campanula aparinoides*, *Campsis radicans*, *Carex caroliniana*, *Carex cristatella*, *Carex frankii*, *Carex grayi*, *Carex muskingumensis*, *Carex stipata*, *Carex stricta*, *Carex tribuloides*, *Carex typhina*, *Carex vesicaria*, *Carya laciniosa*, *Cephalanthus occidentalis*, *Cicuta*, *Coleataenia longifolia*, *Cornus amomum*, *Cornus drummondii*, *Cornus racemosa*, *Doellingeria umbellata*, *Echinochloa crus-galli*, *Eleocharis erythropoda*, *Eleocharis macrostachya*, *Eleocharis obtusa*, *Eleocharis ovata*, *Epilobium leptophyllum*, *Equisetum*, *Eupatorium perfoliatum*, *Fraxinus pennsylvanica*, *Galium tinctorium*, *Gleditsia aquatica*, *Glyceria septentrionalis*, *Gratiola virginiana*, *Helenium autumnale*, *Helianthus hirsutus*, *Heteranthera limosa*, *Heteranthera rotundifolia*, *Hibiscus laevis*, *Hypericum mutilum*, *Ilex decidua*, *Ilex vomitoria*, *Impatiens capensis*, *Ipomoea lacunosa*, *Iris virginica*, *Juncus canadensis*,

Juncus dudleyi, *Juncus effusus*, *Juncus torreyi*, *Justicia americana*, *Laportea canadensis*, *Leersia oryzoides*, *Lemna minor*, *Lindernia dubia*, *Lobelia cardinalis*, *Ludwigia alternifolia*, *Ludwigia palustris*, *Ludwigia peploides*, *Ludwigia polycarpa*, *Lycopus americanus*, *Lycopus rubellus*, *Lycopus virginicus*, *Lysimachia ciliata*, *Lysimachia quadriflora*, *Lythrum*, *Marsilea vestita*, *Mentha arvensis*, *Mimulus ringens*, *Myrica cerifera*, *Nymphaea odorata*, *Onoclea sensibilis*, *Panicum virgatum*, *Peltandra virginica*, *Penthorum sedoides*, *Persicaria amphibia*, *Persicaria bicornis*, *Persicaria coccinea*, *Persicaria hydropiperoides*, *Persicaria pensylvanica*, *Persicaria punctata*, *Phalaris arundinacea*, *Phragmites australis*, *Phyla*, *Pinus taeda*, *Platanus occidentalis*, *Polygonum ramosissimum*, *Populus deltoides*, *Potamogeton nodosus*, *Potamogeton pusillus*, *Proserpinaca pectinata*, *Pycnanthemum virginianum*, *Quercus macrocarpa*, *Quercus palustris*, *Ranunculus flabellaris*, *Rhynchospora*, *Rorippa aquatica*, *Rorippa palustris*, *Rumex altissimus*, *Rumex crispus*, *Rumex stenophyllus*, *Sagittaria ambigua*, *Sagittaria calycina*, *Sagittaria graminea*, *Sagittaria latifolia*, *Sagittaria rigida*, *Salix amygdaloides*, *Salix exigua*, *Salix interior*, *Salix myricoides*, *Salix nigra*, *Schoenoplectus heterochaetus*, *Scirpus atrovirens*, *Scirpus cyperinus*, *Scutellaria lateriflora*, *Sium suave*, *Solidago nemoralis*, *Solidago ulmifolia*, *Spiraea tomentosa*, *Stachys palustris*, *Symphyotrichum ontarionis*, *Symphyotrichum patens*, *Teucrium canadense*, *Thelypteris palustris*, *Triadenum fraseri*, *Tridens flavus*, *Typha latifolia*, *Verbena hastata*, *Vitis cinerea*, *Wolffia brasiliensis*.

2.1.6.4. *Sagittaria calycina* Engelm. is an annual, which inhabits shallow (<100 cm), tidal or non-tidal, brackish to freshwater sites including canals, depressions, ditches (irrigation), estuaries, floodplains, gravel bars, marshes, meadows, mudflats (lake; river), ponds (artificial; catchment; sand), pools, ravines (dried), rice fields, roadsides, saltmarshes, sandbars, seeps, shores, sinkholes, sloughs, swales, swamps, and the margins of lakes (artificial; small), ponds, reservoirs, rivers, and stock tanks at elevations to 1829 m. Although the plants can grow either emersed or submersed, they regularly appear as emergents on mudflats and at other sites with open exposures where standing waters have receded. The substrates are described as alkaline (e.g., pH: 8.5) or calcareous, and include alluvium, ballast (railroad), clay, clay loam (over limestone), loam, muck, mud, sand, sandy gravel, silt, silty loam (Humphrey's Cherty), and silty sand. Flowering occurs from June to October, with developing fruits observed by late June. Individuals are described as being andromonoecious, i.e., bearing perfect and staminate flowers. However, the perfect flowers are described as possessing either functional stamens or staminodes, depending on the source consulted. Whether these flowers retain any capacity for autogamy should be clarified, especially given the annual habit of the plants. The pollination biology of this species has not been described in any detail; however, the fruits are known to mature within a few weeks following anthesis. Mature plants can reach densities of 20–30 plants m⁻² and are known to produce up to 2,000 achenes per inflorescence with up to 32 inflorescences per plant, yielding an average of 20,000 achenes per plant. Other

estimates indicate achene yields of 73 cubic cm m⁻², or by mass, an average of 400 kg ha⁻¹. As the fruiting peduncles become prostrate along the substrate, the pedicels recurve to push the fruiting heads into the mud. Consequently, many seeds are planted near the maternal plant. However, the achenes also are buoyant and can remain afloat for up to 2 weeks. They can be dispersed locally by water, and potentially are transported over greater distances by waterfowl (Aves: Anatidae). The achenes remain viable in the seed bank where they retain 54% viability after 1 year and 45% viability after 3 years. The seeds will germinate at temperatures below 10°C, but much higher rates are observed above 11°C (optimal germination occurs at 12°C–24°C). **Reported associates:** *Abutilon theophrasti*, *Acalypha gracilens*, *Acalypha rhomboidea*, *Acer negundo*, *Acer saccharinum*, *Agrimonia parviflora*, *Alisma subcordatum*, *Amaranthus*, *Ammannia coccinea*, *Andropogon virginicus*, *Apocynum cannabinum*, *Bergia texana*, *Betula nigra*, *Bidens aristosus*, *Bidens bidentoides*, *Bidens con-natus*, *Bidens frondosus*, *Bidens tripartitus*, *Boehmeria cylindrica*, *Bolboschoenus novae-angliae*, *Carex hyalinol-epis*, *Celtis*, *Cephalanthus occidentalis*, *Chamaecrista fas-ciculata*, *Chasmanthium latifolium*, *Coleataenia longifolia*, *Conoclinium coelestinum*, *Conyza canadensis*, *Cyperus acu-minatus*, *Cyperus bipartitus*, *Cyperus erythrorhizos*, *Cyperus esculentus*, *Cyperus flavescens*, *Cyperus odoratus*, *Cyperus squarrosus*, *Cyperus strigosus*, *Dichanthelium clandesti-num*, *Dichanthelium dichotomum*, *Digitaria ischaemum*, *Diodella teres*, *Diodia virginiana*, *Dioscorea*, *Dysphania ambrosioides*, *Echinochloa muricata*, *Echinodorus berteroi*, *Eclipta prostrata*, *Eleocharis acicularis*, *Eleocharis ambig-ens*, *Eleocharis diandra*, *Eleocharis erythropoda*, *Eleocharis macrostachya*, *Eleocharis obtusa*, *Eleocharis ovata*, *Eleocharis parvula*, *Eleusine indica*, *Eragrostis hypnoides*, *Eragrostis pectinacea*, *Erigeron annuus*, *Erigeron philadel-phicus*, *Erigeron strigosus*, *Eriocaulon parkeri*, *Eupatorium perfoliatum*, *Eupatorium serotinum*, *Euphorbia maculata*, *Euphorbia nutans*, *Fimbristylis autumnalis*, *Fragaria vir-giniana*, *Galium triflorum*, *Gamochaeta purpurea*, *Hedeoma hispida*, *Helenium flexuosum*, *Heteranthera limosa*, *Heteranthera reniformis*, *Hypericum mutilum*, *Hypericum punctatum*, *Impatiens capensis*, *Isoetes riparia*, *Juncus acu-minatus*, *Juncus diffusissimus*, *Juncus effusus*, *Juncus tenuis*, *Justicia americana*, *Kummerowia stipulacea*, *Kummerowia striata*, *Kyllinga brevifolia*, *Kyllinga pumila*, *Leersia ory-zoides*, *Leersia virginica*, *Leptochloa fusca*, *Lespedeza pro-cumbens*, *Lespedeza thunbergii*, *Leucanthemum vulgare*, *Lilaeopsis chinensis*, *Lindernia dubia*, *Lobelia cardina-lis*, *Lobelia inflata*, *Lobelia siphilitica*, *Ludwigia palustris*, *Ludwigia peploides*, *Lycopus americanus*, *Lycopus rubel-lus*, *Microstegium vimineum*, *Mimulus alatus*, *Mimulus ringens*, *Mollugo verticillata*, *Nuphar advena*, *Panicum dichotomiflorum*, *Panicum philadelphicum*, *Paronychia fas-tigiata*, *Paspalum*, *Peltandra virginica*, *Penthorum sedoi-des*, *Persicaria hydropiper*, *Persicaria hydropiperoides*, *Persicaria lapathifolia*, *Persicaria maculosa*, *Persicaria pensylvanica*, *Persicaria posumbu*, *Persicaria punctata*, *Persicaria sagittata*, *Persicaria virginiana*, *Phlox bifida*,

Phytolacca americana, *Plantago lanceolata*, *Plantago rugelii*, *Pluchea camphorata*, *Pluchea odorata*, *Pontederia cordata*, *Potentilla norvegica*, *Potentilla simplex*, *Prunella vulgaris*, *Ptelea*, *Quercus bicolor*, *Ranunculus*, *Rhexia mariana*, *Rorippa palustris*, *Rorippa sylvestris*, *Rotala ramosior*, *Rumex crispus*, *Rumex obtusifolius*, *Sagittaria ambigua*, *Sagittaria australis*, *Sagittaria brevirostra*, *Sagittaria graminea*, *Sagittaria latifolia*, *Sagittaria longiloba*, *Sagittaria platyphylla*, *Sagittaria subulata*, *Salix*, *Samolus valerandi*, *Schoenoplectus hallii*, *Schoenoplectus pungens*, *Schoenoplectus smithii*, *Scirpus polyphyllus*, *Scutellaria lateriflora*, *Senna marilandica*, *Setaria viridis*, *Sida spinosa*, *Solanum carolinense*, *Solidago canadensis*, *Sonchus asper*, *Sparganium americanum*, *Spartina alterniflora*, *Spartina cynosuroides*, *Symphyotrichum lanceolatum*, *Symphyotrichum ontarionis*, *Symphyotrichum pilosum*, *Symphyotrichum racemosum*, *Tradescantia bracteata*, *Trifolium repens*, *Tussilago farfara*, *Typha angustifolia*, *Typha latifolia*, *Urochloa platyphylla*, *Verbascum thapsus*, *Verbena hastata*, *Verbena urticifolia*, *Verbesina alternifolia*, *Vernonia gigantea*, *Vitis*, *Xanthium strumarium*, *Zizania aquatica*.

2.1.6.5. *Sagittaria cristata* Engelm. is an annual or a perennial, which inhabits shallow to moderately deep waters (to 2 m) in lakes, rivers, sloughs, and along the margins of lakes, ponds, and swamps at elevations to 1000 m. The habitats are categorized as hard water (pH: 7.0–8.6; total alkalinity >40 ppm; e.g., 54.0 mg l⁻¹; sulfates <50 ppm). The sediments (means: organic matter: 1.5%; pH: 5.5; Ca: 10/50 µg g⁻¹; K: 5/7.3 µg g⁻¹; Mg: 5/14.8 µg g⁻¹; P: 5/8.4 µg g⁻¹) are described as muck and sand. This is one of the more aquatic species in the genus, found normally in deeper standing water and less often on exposed shorelines. The foliage has relative low ratios of C:P (400), C:N (16), and N:P (20). The plants are monoecious, with flowering and fruiting observed from July to September. Additional details on the reproductive biology or seed ecology of this species are lacking. **Reported associates:** *Bidens beckii*, *Brasenia schreberi*, *Ceratophyllum demersum*, *Chara*, *Drepanocladus*, *Dulichium arundinaceum*, *Elatine minima*, *Eleocharis acicularis*, *Elodea canadensis*, *Eriocaulon aquaticum*, *Heteranthera dubia*, *Isoetes echinospora*, *Juncus pelocarpus*, *Lemna minor*, *Lemna trisulca*, *Lobelia dortmanna*, *Myriophyllum sibiricum*, *Myriophyllum tenellum*, *Najas flexilis*, *Najas guadalupensis*, *Nitella*, *Nuphar advena*, *Nuphar variegata*, *Nymphaea odorata*, *Persicaria amphibia*, *Potamogeton amplifolius*, *Potamogeton foliosus*, *Potamogeton gramineus*, *Potamogeton illinoensis*, *Potamogeton natans*, *Potamogeton praelongus*, *Potamogeton pusillus*, *Potamogeton richardsonii*, *Potamogeton robbinsii*, *Potamogeton strictifolius*, *Potamogeton zosteriformis*, *Ranunculus flammula*, *Ruppia maritima*, *Schoenoplectus acutus*, *Schoenoplectus subterminalis*, *Sparganium americanum*, *Sparganium angustifolium*, *Sparganium eurycarpum*, *Sparganium fluctuans*, *Stuckenia filiformis*, *Stuckenia pectinata*, *Utricularia cornuta*, *Utricularia macrorhiza*, *Utricularia minor*, *Utricularia resupinata*, *Vallisneria americana*.

2.1.6.6. *Sagittaria cuneata* Sheldon is a perennial, which inhabits still or slow-moving standing waters (to 1.2 m deep) or exposed substrates within backwaters, beaches, bogs, borrow pits, canals (irrigation), depressions, ditches (roadside), draws, fens, flats, lake beds (dry), marshes, meadows, mudflats, ponds (intermittent; montane; retention; spring-fed; stock), pools (culvert; dried; roadside), potholes, riverbeds, rivers, roadsides (disturbed; gravelly), slopes (to 6%), sloughs, streambeds, swales, swamps, and along the margins or receding shores of channels, lakes, ponds, potholes, reservoirs, rivers, and streams at elevations to 3048 m. The plants are highly polymorphic, producing linear or sagittate emergent foliage when growing in shallow sites but developing phyllodial submersed or cordate/sagittate floating leaves in deeper water. Exposures can range from full sun to shade. The surrounding waters can vary widely in terms of alkalinity (from 5 to 628 mg l⁻¹ CaCO₃) but tend to be moderately alkaline to calcareous (e.g., pH: 6.8–8.9; $\bar{x}$ = 7.4; total hardness: 184 mg l⁻¹; Ca: 2.7 mg l⁻¹; Mg 0.8 mg l⁻¹). The substrates are described as acidic (e.g., pH: 5.5–7.0) or brackish and include alluvium, clay (black; Pierre), clay loam (Shingle-Samday; Worthenton), clay silt, gravel, gravelly sand, gumbo, loam (black; organic), muck (alkaline; black), mud (alluvial; desiccated), peat, rock, sand, sandy clay, sandy loam, sandy ooze, Shingle-Haverdard series, silt, silty clay, silty loam, silty muck, silty sand, and Worfka-Shingle-Samday series. Flowering occurs from April to September, with fruiting extending into October. Individuals are monoecious but self-compatible, theoretically enabling geitonogamous pollination to occur; however, the reproductive ecology of this species has not been characterized in any detail. Outcrossing presumably is carried out by bees (Insecta: Hymenoptera) and flies (Insecta: Diptera). A plant typically produces six flowers, which can yield about 5,150 seeds, each weighing about 0.235 mg. A seed bank develops. The highest experimental germination rates occurred for seeds buried at less than 1 cm (3-week stratification at 10°C; they were then placed under ambient greenhouse conditions: 15°C–30°C; 14–16 hr light). The seeds are dispersed by water and perhaps to greater distances by their adherence to various animals. **Reported associates:** *Acer negundo*, *Acer saccharinum*, *Agrostis gigantea*, *Alisma subcordatum*, *Alisma triviale*, *Alopecurus aequalis*, *Amaranthus*, *Anagallis minima*, *Angelica atropurpurea*, *Arnica chamissonis*, *Artemisia frigida*, *Artemisia nova*, *Artemisia tridentata*, *Asclepias incarnata*, *Bacopa rotundifolia*, *Beckmannia syzigachne*, *Berula erecta*, *Bidens cernuus*, *Boehmeria cylindrica*, *Bouteloua gracilis*, *Calla*, *Callitriche hermaphroditica*, *Callitriche palustris*, *Carex aquatilis*, *Carex arcta*, *Carex athrostachya*, *Carex comosa*, *Carex cristatella*, *Carex emoryi*, *Carex lasiocarpa*, *Carex molesta*, *Carex nebrascensis*, *Carex rostrata*, *Carex stipata*, *Carex utriculata*, *Carex utriculata*, *Carex vesicaria*, *Carex vulpinoidea*, *Cephalanthus occidentalis*, *Ceratophyllum demersum*, *Ceratophyllum echinatum*, *Chara*, *Chenopodium glaucum*, *Cicuta bulbifera*, *Comarum palustre*, *Convolvulus arvensis*, *Cornus amomum*, *Cyperus bipartitus*, *Cyperus odoratus*, *Damasonium californicum*, *Deschampsia cespitosa*, *Downingia bella*, *Downingia*

yina, *Dulichium arundinaceum*, *Echinochloa crus-galli*, *Elaeagnus angustifolia*, *Elatine heterandra*, *Eleocharis acicularis*, *Eleocharis erythropoda*, *Eleocharis macrostachya*, *Eleocharis palustris*, *Eleocharis quinqueflora*, *Elodea canadensis*, *Equisetum fluviatile*, *Eupatorium perfoliatum*, *Fimbristylis autumnalis*, *Glyceria borealis*, *Glyceria grandis*, *Glyceria septentrionalis*, *Glyceria striata*, *Gnaphalium palustre*, *Gratiola heterosepala*, *Gratiola neglecta*, *Gutierrezia sarothrae*, *Helenium*, *Hippuris vulgaris*, *Hordeum jubatum*, *Iris virginica*, *Isoetes bolanderi*, *Juncus alpinoarticulatus*, *Juncus balticus*, *Juncus effusus*, *Juncus nodosus*, *Juncus torreyi*, *Leersia oryzoides*, *Lemna minor*, *Lepidium virginicum*, *Limosella*, *Lindernia dubia*, *Ludwigia palustris*, *Lycopus americanus*, *Lycopus asper*, *Lycopus uniflorus*, *Lysimachia nummularia*, *Lythrum salicaria*, *Madia glomerata*, *Marsilea vestita*, *Melilotus officinalis*, *Mentha arvensis*, *Mimulus primuloides*, *Mimulus ringens*, *Myriophyllum sibiricum*, *Myriophyllum spicatum*, *Najas flexilis*, *Najas marina*, *Nuphar polysepala*, *Nuphar variegata*, *Peltandra virginica*, *Persicaria amphibia*, *Persicaria coccinea*, *Persicaria hydropiper*, *Persicaria hydropiperoides*, *Persicaria maculosa*, *Persicaria punctata*, *Phalaris arundinacea*, *Phleum pratense*, *Phragmites australis*, *Physostegia virginiana*, *Pilea pumila*, *Poa nemoralis*, *Poa pratensis*, *Polypogon monspeliensis*, *Populus angustifolia*, *Populus balsamifera*, *Populus deltoides*, *Porterella carnosula*, *Potamogeton berchtoldii*, *Potamogeton diversifolius*, *Potamogeton epiphydrus*, *Potamogeton foliosus*, *Potamogeton gramineus*, *Potamogeton illinoensis*, *Potamogeton natans*, *Potamogeton pusillus*, *Potamogeton richardsonii*, *Potamogeton zosteriformis*, *Potentilla gracilis*, *Ranunculus aquatilis*, *Ranunculus pensylvanicus*, *Ranunculus sceleratus*, *Rhamnus cathartica*, *Rhaponticum repens*, *Rorippa islandica*, *Rorippa palustris*, *Rosa multiflora*, *Rosa setigera*, *Rotala ramosior*, *Rudbeckia laciniata*, *Rumex altissimus*, *Rumex salicifolius*, *Rumex verticillatus*, *Sagittaria latifolia*, *Salix amygdaloides*, *Salix exigua*, *Salix interior*, *Salix lasiandra*, *Salix nigra*, *Sambucus nigra*, *Schedonorus arundinaceus*, *Schoenoplectus acutus*, *Schoenoplectus pungens*, *Schoenoplectus tabernaemontani*, *Scirpus atrovirens*, *Scutellaria lateriflora*, *Sium suave*, *Solanum dulcamara*, *Solidago altissima*, *Solidago gigantea*, *Sparganium angustifolium*, *Sparganium emersum*, *Sparganium eurycarpum*, *Spartina pectinata*, *Sphagnum*, *Spirodela polyrhiza*, *Stuckenia filiformis*, *Stuckenia pectinata*, *Tamarix ramosissima*, *Thalictrum dasycarpum*, *Trifolium*, *Triglochin scilloides*, *Typha angustifolia*, *Typha latifolia*, *Typha xglaucha*, *Ulmus americana*, *Urtica dioica*, *Vallisneria americana*, *Verbesina alternifolia*, *Vitis riparia*, *Zannichellia palustris*.

2.1.6.7. ***Sagittaria demersa* J.G. Sm.** is an annual, which occurs in standing waters (0.2–1.2 m), or (more rarely) is stranded on the exposed substrates of lakes, pools, and streams at elevations from 1500 to 2082 m. The plants produce phyllodial leaves, which are submersed or are floating. In Mexico, this species occurs in montane, clean, medium-hard to soft waters (pH: 6.0–7.2; CaCO₃: 48.0–88.0 mg l⁻¹). The sediments contain average levels of nitrogen, total phosphorus,

and organic matter, and are described as clay, clayey sand, and sandy sandstone. Further life history information is unavailable for this species, particularly for the few North American occurrences. The plants apparently are intolerant of pollution and readily succumb to eutrophication and other human disturbances. **Reported associates:** none.

2.1.6.8. ***Sagittaria engelmanniana* J.G. Sm.** is a perennial, which inhabits shallow waters (e.g., 30 cm deep) of alluvial fans, backwaters, beaches, bogs (peat), bottoms (exposed; stream), Carolina bays, channels (drainage), depressions, ditches, fens, floodplains, lakes, marshes, oxbows, pocosins (streamside), ponds (dried), reservoirs, shores, sloughs, swales, swamps, woodlands, and the margins of lakes, ponds, rivers, and streams at elevations to 127 m. The sites typically occur in open exposures with waters that characteristically are acidic (pH: 5.6–6.3). The substrates are described as muck, mucky peat, mud, peat, sand, and silty sand. The plants are monoecious and are in flower from June to September with fruiting extending into October. Individuals are self-compatible, which allows for geitonogamous pollination to occur (but to what extent has not been determined). The usual pollinators presumably are insects (Insecta). Other life history details are lacking for this species. **Reported associates:** *Acer rubrum*, *Agrostis hyemalis*, *Alnus maritima*, *Alnus serrulata*, *Andropogon glomeratus*, *Andropogon virginicus*, *Apios americana*, *Aronia arbutifolia*, *Bartonia paniculata*, *Bartonia virginica*, *Bidens frondosus*, *Bidens mitis*, *Bidens trichospermus*, *Burmannia capitata*, *Calamagrostis canadensis*, *Callitriche heterophylla*, *Carex albolutescens*, *Carex atlantica*, *Carex bullata*, *Carex canescens*, *Carex exilis*, *Carex lasiocarpa*, *Carex striata*, *Cephalanthus occidentalis*, *Chamaecyparis thyoides*, *Chamaedaphne calyculata*, *Cladium mariscoides*, *Clethra alnifolia*, *Coleataenia longifolia*, *Cuscuta*, *Cyperus dentatus*, *Cyperus squarrosus*, *Cyrilla racemiflora*, *Dichanthelium acuminatum*, *Dichanthelium dichotomum*, *Dichanthelium ensifolium*, *Dichanthelium scabriusculum*, *Drosera intermedia*, *Drosera rotundifolia*, *Dulichium arundinaceum*, *Eleocharis acicularis*, *Eleocharis equisetoides*, *Eleocharis flavescens*, *Eleocharis robbinsii*, *Eleocharis tenuis*, *Eleocharis tuberculosa*, *Eriocaulon aquaticum*, *Eriocaulon compressum*, *Eriocaulon decangulare*, *Eriophorum virginicum*, *Eubotrys racemosa*, *Eupatorium perfoliatum*, *Eupatorium pilosum*, *Eupatorium resinosum*, *Eupatorium xpinatifidum*, *Euthamia graminifolia*, *Eutrochium dubium*, *Fuirena squarrosa*, *Galium tinctorium*, *Gaylussacia dumosa*, *Glyceria obtusa*, *Gratiola aurea*, *Hydrocotyle verticillata*, *Hypericum canadense*, *Hypericum densiflorum*, *Hypericum denticulatum*, *Hypericum mutilum*, *Ilex glabra*, *Iris versicolor*, *Itea virginica*, *Juncus canadensis*, *Juncus effusus*, *Juncus militaris*, *Juncus pelocarpus*, *Juncus trigonocarpus*, *Kalmia angustifolia*, *Kalmia buxifolia*, *Lachnanthes caroliniana*, *Leersia oryzoides*, *Lindernia dubia*, *Lobelia canbyi*, *Lobelia elongata*, *Lobelia nuttallii*, *Ludwigia palustris*, *Ludwigia sphaerocarpa*, *Lycopus amplexans*, *Lycopus uniflorus*, *Lycopus virginicus*, *Lyonia ligustrina*, *Lyonia mariana*, *Lysimachia terrestris*, *Magnolia virginiana*, *Micranthemum*

umbrosum, *Microstegium vimineum*, *Mikania scandens*, *Muhlenbergia uniflora*, *Murdannia keisak*, *Nuphar variegata*, *Nymphaea odorata*, *Nymphoides aquatica*, *Nyssa sylvatica*, *Oclemena nemoralis*, *Orontium aquaticum*, *Osmunda regalis*, *Osmundastrum cinnamomeum*, *Oxypolis rigidior*, *Panicum hemitomon*, *Panicum verrucosum*, *Panicum virgatum*, *Peltandra virginica*, *Persicaria hydropiperoides*, *Pinus rigida*, *Pogonia ophioglossoides*, *Polygala cruciata*, *Polygala ramosa*, *Pontederia cordata*, *Potamogeton confervoides*, *Potamogeton oakesianus*, *Rhexia mariana*, *Rhexia nashii*, *Rhexia virginica*, *Rhododendron viscosum*, *Rhynchospora alba*, *Rhynchospora capitellata*, *Rhynchospora chalarocephala*, *Rhynchospora fusca*, *Rhynchospora microcephala*, *Rubus hispidus*, *Sabatia difformis*, *Sagittaria latifolia*, *Sagittaria macrocarpa*, *Sarracenia purpurea*, *Sassafras albidum*, *Schizachyrium scoparium*, *Schoenoplectus subterminalis*, *Scirpus cyperinus*, *Smilax glauca*, *Smilax herbacea*, *Smilax laurifolia*, *Smilax rotundifolia*, *Smilax walteri*, *Sparganium americanum*, *Sphagnum*, *Spiraea tomentosa*, *Spiranthes cernua*, *Symphyotrichum dumosum*, *Symphyotrichum novi-belgii*, *Taxodium*, *Toxicodendron radicans*, *Triadenum virginicum*, *Triadenum walteri*, *Utricularia cornuta*, *Utricularia gibba*, *Utricularia juncea*, *Utricularia striata*, *Vaccinium corymbosum*, *Vaccinium macrocarpon*, *Viburnum nudum*, *Viola lanceolata*, *Woodwardia areolata*, *Woodwardia virginica*, *Xyris difformis*, *Xyris fimbriata*, *Zizania aquatica*.

2.1.6.9. *Sagittaria fasciculata* E.O. Beal is a short-lived perennial (usually <2 years), which grows in shallow (<5 cm deep), freshwater alluvial floodplains, seeps, or streams, at elevations to 1000 m. The plants require cool, clean waters with continuous flow, moderate levels of dissolved oxygen (3–7 mg l⁻¹), and low conductivities (20–50 µS). They are intolerant of droughts, floods, and other hydrological fluctuations. The exposures become well shaded by late summer. The substrates are acidic (e.g., pH: 4.8–6.8) and have been described as hydrated muck–sand suspension, sandbars, or sandy mucks with a high organic matter content (6.5–10%) and high Mg content (108.6 µg g⁻¹). Ecological details for this rare species are difficult to compile, due in part to the redaction of information from electronic database records. Flowering occurs from May to July, with fruiting extending into August. The reproductive ecology of this species has not been elucidated. Genetic analyses using ISSR markers have indicated some genetic differentiation among watersheds but little differentiation within watersheds. The plants reproduce vegetatively by stolons (also referred to as rhizomes), which are produced in greater prevalence when flow rates or shading conditions are altered. The plants are of conservation concern, with their status interpreted as “declining.” Their threats include alterations of hydrological conditions, shading by competitive vegetation, and trampling. **Reported associates:** *Carex*, *Decumaria barbara*, *Glyceria striata*, *Gratiola virginiana*, *Murdannia keisak*.

2.1.6.10. *Sagittaria filiformis* J.G. Sm. is a perennial, which inhabits still or flowing, shallow (0.01–1.8 m deep), tidal or non-tidal waters in canals (drainage), depressions, ditches,

lakes, marshes, pits (borrow; phosphate), ponds (artificial; karst; seasonal), pools, sloughs, streams (blackwater), swamps, and the shores of lakes at elevations to 100 m. The shoots are heterophyllous, developing linear submersed leaves and ovate floating leaves. Exposures range from open to shaded conditions. The plants supposedly inhabit more lotic sites in the north of their distribution and more lentic waters in the southern portion of their range. The waters are somewhat alkaline (e.g., pH: 7.1; alkalinity: 35.0 mg l⁻¹). The sediments have been described as muck, mud, and sand. Flowering and fruiting occur from January to October. Some of the lower scape verticels are proliferous, capable of producing roots, phyllodial leaves, and flowering pedicels from the bract axils. The pollination biology is unknown. The seed germination requirements also have not been determined; however, a persistent seed bank does develop. Vegetative reproduction occurs by the expansion of stolons (also referred to as rhizomes). **Reported associates:** *Acer rubrum*, *Alternanthera philoxeroides*, *Ampelopsis arborea*, *Azolla filiculoides*, *Bacopa caroliniana*, *Bidens discoideus*, *Boltonia diffusa*, *Brasenia schreberi*, *Carya cordiformis*, *Cephalanthus occidentalis*, *Ceratophyllum muricatum*, *Clethra alnifolia*, *Crotalaria spectabilis*, *Cynodon dactylon*, *Cyperus erythrorhizos*, *Echinodorus*, *Eclipta prostrata*, *Eleocharis baldwinii*, *Eubotrys racemosa*, *Eupatorium capillifolium*, *Fimbristylis autumnalis*, *Fraxinus*, *Hibiscus moscheutos*, *Hydrilla verticillata*, *Hydrocotyle ranunculoides*, *Hydrocotyle verticillata*, *Ilex myrtifolia*, *Juncus diffusissimus*, *Juncus effusus*, *Landoltia punctata*, *Leersia hexandra*, *Lemna valdiviana*, *Limnobium spongia*, *Lindernia dubia*, *Liquidambar styraciflua*, *Ludwigia*, *Lycopus*, *Lyonia lucida*, *Myrica cerifera*, *Myriophyllum aquaticum*, *Myriophyllum pinnatum*, *Nelumbo lutea*, *Nitella translucens*, *Nymphaea odorata*, *Nymphoides cordata*, *Nyssa biflora*, *Nyssa sylvatica*, *Panicum dichotomiflorum*, *Panicum hemitomon*, *Paspalum urvillei*, *Peltandra virginica*, *Persea palustris*, *Persicaria hydropiperoides*, *Persicaria punctata*, *Pinus taeda*, *Pistia stratiotes*, *Pontederia cordata*, *Proserpinaca palustris*, *Quercus phellos*, *Rhynchospora glomerata*, *Rhynchospora macrostachya*, *Rhynchospora microcephala*, *Rotala ramosior*, *Rumex verticillatus*, *Saccharum*, *Sagittaria graminea*, *Sagittaria latifolia*, *Saururus cernuus*, *Scirpus cyperinus*, *Smilax rotundifolia*, *Spirodela*, *Taxodium distichum*, *Thalia*, *Typha domingensis*, *Typha latifolia*, *Utricularia gibba*, *Utricularia purpurea*.

2.1.6.11. *Sagittaria graminea* Michx. is a perennial, which grows in shallow to moderately deep waters (30–180 cm; average: 60 cm depth) in bogs, borrow pits, Carolina bays, cypress domes, depressions, ditches (drainage), flats, flatwoods, floodplains, gravel pits, hammocks, lakebeds, marshes, meadows, mudflats, pinelands, pocosins, pools (savannah), ponds (railroad; roadside; sand; sinkhole; stock), prairies, rice fields, roadsides, seeps, sloughs (dried), swales, swamps (blackwater; dried; river), and along the margins or shores of canals, lakes, ponds, rivers, and streams at elevations to 789 m. The waters are broadly circumneutral (pH: 5.7–8.4; $\bar{x}$ = 7.0) with low conductivity (<200 µmhos cm⁻¹) and low total alkalinity (<112 mg l⁻¹ CaCO₃; $\bar{x}$ = 18.7 mg l⁻¹).

The substrates are more acidic (pH: 4.4–7.7). Exposures can range from open (full sunlight) to deep shade. The substrates have been characterized as clay, clay loam, gravelly alluvium, loam, loamy sand (Ocilla), muck, mucky loam, mud (over dolomite), peat, peaty mud, Placid (typic humaquepts), psammaquents (Basinger; St. Johns), sand (organic), sandy clay loam, sandy muck, sandy peat, silt, silty loam, silty muck, and silty sandy loam. The leaf morphology varies substantially from phyllodial to broad-bladed; however, experimental transplant studies indicate only minor plasticity due to water level variation, and that plants having different leaf types are genetically distinct and adapted differentially to the specific habitats in which they are found. Flowering and fruiting occur from March to December. Submersed plants remain sterile (unless under very high irradiance and shallow conditions), with flowering generally requiring the emergence of non-phyllodial leaves from the water. Flowering (usually initiating from 5:00 to 6:00 am) can occur under daily photoperiods ranging from 7 to 15 hr of light. The plants are monoecious. A greater proportion of male flowers is produced under high phosphorus and low nitrogen conditions; under opposite conditions (low phosphorus, high nitrogen), more female flowers, and subsequently more seeds, are produced. All flowers (and seeds) increase in number when both nutrients are elevated. Individuals are self-compatible (but protogynous within an inflorescence) and require insects (Insecta) in order to achieve successful pollination and fruit set. Female and male floral phases overlap less in smaller populations than in larger populations. Once deposited, pollen must remain undisturbed for a period of 3 hr in order to achieve fertilization. Seed set is highly reduced (by nearly 90%) in plants subjected to tidal activity, which is attributed to inviability or washing away of the pollen when exposed to water. Higher fruit set occurs in populations with male-biased floral sex ratios. The fruits ripen and disperse within 50 days. Seeds have germinated following 5 days of cold stratification, when subjected to a 30°C/15°C day/night temperature regime. Isozyme analyses (13 loci) of the typical subspecies indicated that a single multilocus genotype characterized 97% of the accessions surveyed, which indicates extremely low levels of genetic variation in the species (see *Systematics*). Vegetative reproduction is well developed. High phosphorous levels yield larger corms, whereas high nitrogen levels yield smaller corms but more numerous and longer stolons (also characterized as coarse rhizomes), which produce tubers. In late fall, tuber biomass of mudflat plants (124 g m⁻²) can greatly exceed that of pond dwelling plants (44 g m⁻²). Dispersal occurs by means of the achenes or tubers, which typically are transported by water, especially during flood conditions. **Reported associates:** *Acer rubrum*, *Acer saccharinum*, *Aletris lutea*, *Alisma subcordatum*, *Alternanthera philoxeroides*, *Amaranthus*, *Amsonia rigida*, *Andropogon*, *Asclepias incarnata*, *Asclepias perennis*, *Azolla cristata*, *Bacopa rotundifolia*, *Bidens cernuus*, *Bidens frondosus*, *Boehmeria cylindrica*, *Bolboschoenus fluviatilis*, *Brasenia schreberi*, *Calamagrostis canadensis*, *Callitriche heterophylla*, *Carex gigantea*, *Carex haydenii*, *Carex scoparia*, *Carex striata*, *Carex tribuloides*,

Carex vesicaria, *Carex vulpinoidea*, *Centella asiatica*, *Cephalanthus occidentalis*, *Ceratophyllum demersum*, *Chara*, *Cladium jamaicense*, *Commelina*, *Cuscuta gronovii*, *Cyperus haspan*, *Cyperus squarrosus*, *Cyrilla racemiflora*, *Didiplis diandra*, *Digitaria serotina*, *Diodella teres*, *Diospyros virginiana*, *Drosera capillaris*, *Dulichium arundinaceum*, *Elatine minima*, *Eleocharis acicularis*, *Eleocharis baldwinii*, *Eleocharis equisetoides*, *Eleocharis microcarpa*, *Eleocharis palustris*, *Eleocharis quadrangulata*, *Elodea canadensis*, *Equisetum fluviatile*, *Eriocaulon compressum*, *Eupatorium perfoliatum*, *Eupatorium serotinum*, *Fimbristylis autumnalis*, *Fraxinus caroliniana*, *Fraxinus profunda*, *Fuirena*, *Glossostigma cleistanthum*, *Glyceria septentrionalis*, *Glyceria striata*, *Gratiola aurea*, *Gratiola brevifolia*, *Gratiola virginiana*, *Helanthium tenellum*, *Helenium flexuosum*, *Helenium pinnatifidum*, *Heteranthera limosa*, *Heteranthera reniformis*, *Heteranthera rotundifolia*, *Hordeum jubatum*, *Hydrocotyle*, *Hymenocallis crassifolia*, *Hypericum fasciculatum*, *Hypericum mutilum*, *Ilex*, *Iris virginica*, *Isoetes lacustris*, *Juncus acuminatus*, *Juncus effusus*, *Juncus megacephalus*, *Juncus repens*, *Lachnanthes caroliniana*, *Larix laricina*, *Lemna minor*, *Lindernia grandiflora*, *Lindernia monticola*, *Liquidambar styraciflua*, *Ludwigia lanceolata*, *Ludwigia polycarpa*, *Lycopodiella appressa*, *Lysimachia nummularia*, *Magnolia grandiflora*, *Marsilea vestita*, *Mayaca fluviatilis*, *Myrica cerifera*, *Myriophyllum pinnatum*, *Myriophyllum spicatum*, *Myriophyllum tenellum*, *Najas flexilis*, *Najas guadalupensis*, *Nitella*, *Nuphar microphylla*, *Nuphar polysepala*, *Nuphar variegata*, *Nymphaea odorata*, *Nyssa aquatica*, *Nyssa biflora*, *Nyssa ogeche*, *Osmunda regalis*, *Panicum hemitomon*, *Paspalum praecox*, *Persea borbonia*, *Persicaria amphibia*, *Persicaria bicornis*, *Persicaria coccinea*, *Persicaria hirsuta*, *Persicaria hydropiperoides*, *Persicaria lapathifolia*, *Persicaria pensylvanica*, *Persicaria punctata*, *Phalaris arundinacea*, *Phyla lanceolata*, *Picea mariana*, *Pinus echinata*, *Pinus elliotii*, *Pinus palustris*, *Pinus taeda*, *Pluchea baccharis*, *Pluchea foetida*, *Polygala lutea*, *Polypremum procumbens*, *Pontederia cordata*, *Potamogeton amplifolius*, *Potamogeton foliosus*, *Potamogeton gramineus*, *Potamogeton nodosus*, *Potamogeton pusillus*, *Potamogeton richardsonii*, *Potamogeton robbinsii*, *Potamogeton zosteriformis*, *Proserpinaca pectinata*, *Quercus laurifolia*, *Quercus nigra*, *Quercus virginiana*, *Ranunculus flabellaris*, *Ranunculus laxicaulis*, *Ranunculus longirostris*, *Rhexia aristosa*, *Rhexia nashii*, *Rhynchospora chalarocephala*, *Rhynchospora inundata*, *Rhynchospora macra*, *Rhynchospora macrostachya*, *Rhynchospora tracyi*, *Rorippa aquatica*, *Rorippa palustris*, *Rubus*, *Rumex altissimus*, *Rumex crispus*, *Rumex stenophyllus*, *Sabal minor*, *Sabal palmetto*, *Sabatia*, *Sagittaria brevirostra*, *Sagittaria calycina*, *Sagittaria filiformis*, *Sagittaria lancifolia*, *Sagittaria latifolia*, *Sagittaria papillosa*, *Sagittaria rigida*, *Sagittaria subulata*, *Sagittaria teres*, *Salix amygdaloides*, *Salix nigra*, *Samolus valerandi*, *Saururus cernuus*, *Schoenoplectus acutus*, *Schoenoplectus heterochaetus*, *Schoenoplectus pungens*, *Schoenoplectus tabernaemontani*, *Scirpus cyperinus*, *Scirpus pendulus*, *Scutellaria lateriflora*, *Serenoa reprens*, *Sium*

suave, *Smilax*, *Solanum carolinense*, *Solidago gigantea*, *Sparganium eurycarpum*, *Spartina cynosuroides*, *Sphagnum*, *Spirodela polyrrhiza*, *Symphyotrichum novae-angliae*, *Taxodium distichum*, *Thalia geniculata*, *Tridens ambiguus*, *Tridens strictus*, *Typha angustifolia*, *Typha domingensis*, *Typha latifolia*, *Ulmus americana*, *Utricularia gibba*, *Utricularia macrorrhiza*, *Vaccinium elliotii*, *Vallisneria americana*, *Verbena hastata*, *Viola*, *Wisteria frutescens*, *Wolffia brasiliensis*, *Woodwardia virginica*, *Xanthium strumarium*, *Xyris difformis*.

2.1.6.12. ***Sagittaria guayanensis* Kunth** is a nonindigenous annual, which grows in ditches, pools (ephemeral), rice fields, and streams at elevations to 100 m. The plants typically produce broad floating leaves, which superficially resemble lily pads; only the inflorescence extends above the water surface. The substrates are described as mud. Flowering occurs from summer to fall. Unlike most of their congeners, these plants are andromonoecious, with individuals bearing staminate and perfect flowers. Here, the condition is believed to have been derived secondarily from a monoecious ancestry in order to facilitate self-pollination. The flowers are preanthesis cleistogamous. Consequently, they typically attract few pollinator visits, rarely outcross, and primarily are self-pollinating. In its native range, the seeds are well represented in the seed bank (up to 37 seeds m⁻²) and germinate well under ambient greenhouse temperatures. The plants have no well-developed means of asexual reproduction. **Reported associates (North America):** *Chara*, *Bacopa repens*, *Ammannia auriculata*, *Dopatrium junceum*, *Eriocaulon cinereum*, *Heteranthera limosa*, *Rotala ramosior*, *Sphenoclea zeylanica*.

2.1.6.13. ***Sagittaria isoetiformis* J.G. Sm.** is a perennial, which grows in shallow waters (2–70 cm; typically 20–40 cm) in bottoms (pond), clay pits, depressions, ditches, ponds (karst; sinkhole), pools, and along the shores of lakes, limesinks, ponds (drying), and rivers at elevations to 73 m. Exposures tend to receive full sunlight. The substrates are acidic (e.g., pH: 5.4) and are described as Basinger (spodic psammaquents), loamy fine sand (Albany), loamy sand, muck, mucky sand, peat, peaty sand, sand, sandy muck, sandy peat, and Troup (grossarenic paleudults). They contain relatively low levels of Ca, K, and Mg. Flowering and fruiting have been observed from June to October. These monoecious plants are highly sexual, with most female flowers producing numerous (up to 200) achenes. Although individuals are self-compatible, they primarily are outcrossed (the male and female flowers rarely open simultaneously) by insects (Insecta). Populations maintain relatively high levels of genetic variation (94% polymorphic loci; $H_{ES}=0.399$); however, they are fairly differentiated ($G_{ST}=0.399$). Although possible, geitonogamous pollen transfer probably occurs rarely, being limited by the temporally exclusive sex expression and by the close proximity of different phase genets, which simultaneously offer flowers of both sexes to potential pollinators. Though capable of clonal growth, the populations are not structured genetically as being highly clonal, but exhibit patterns of diverse genetic variation, which has been attributed to the recruitment of sexual propagules from the seed bank. The seeds can germinate in wet soil

or in several centimeters of water. Seed dispersal (primarily by water) likely occurs over small distances due to the lack of any obvious adaptations for long-distance dispersal. Vegetative reproduction occurs by stolons (also referred to as rhizomes), which produce small corms (yielding as many as 20 ramets annually). The corms persist for only a few weeks. Stolon connections do not persist between ramets. The plants differ from most of their congeners by their ability to implement a CAM photosynthetic pathway. **Reported associates:** *Andropogon glomeratus*, *Andropogon gyrans*, *Brasenia schreberi*, *Cabomba*, *Carex striata*, *Centella asiatica*, *Cephalanthus occidentalis*, *Coleataenia tenera*, *Cyperus*, *Dichantherium acuminatum*, *Drosera*, *Echinodorus*, *Eleocharis melano-carpa*, *Eleocharis obtusa*, *Eleocharis robbinsii*, *Eriocaulon compressum*, *Eubotrys racemosa*, *Eupatorium leptophyllum*, *Eupatorium leucolepis*, *Eupatorium mohrii*, *Fimbristylis perpusilla*, *Fuirena*, *Gratiola ramosa*, *Helanthium tenellum*, *Hydrocotyle umbellata*, *Hypericum denticulatum*, *Juncus repens*, *Lachnanthes caroliniana*, *Lachnocaulon anceps*, *Lechea*, *Leersia hexandra*, *Lobelia boykinii*, *Ludwigia linearis*, *Ludwigia spathulata*, *Lysimachia loomisii*, *Nymphaea odorata*, *Nymphoides cordata*, *Nyssa biflora*, *Panicum hemitomom*, *Panicum verrucosum*, *Panicum virgatum*, *Polygala cymosa*, *Pontederia*, *Proserpinaca palustris*, *Rhynchospora perplexa*, *Rhynchospora pusilla*, *Riccia*, *Scleria reticularis*, *Sclerolepis uniflora*, *Serenia repens*, *Smilax walteri*, *Spartina*, *Syngonanthus flavidulus*, *Taxodium distichum*, *Typha*, *Utricularia cornuta*, *Utricularia gibba*, *Utricularia resupinata*, *Verbena*, *Viola lanceolata*, *Xyris*.

2.1.6.14. ***Sagittaria kurziana* Glück** is a perennial, which grows in tidal or non-tidal canals, ditches (flowing), rivers (spring-fed), springs, and streams at elevations below 100 m. It inhabits cool, clear waters that are fresh to brackish (specific conductance: 36–878 $\mu\text{S cm}^{-1}$; chloride: 4–236 mg l⁻¹), clear, fast flowing (e.g., 300 cm s⁻¹), and moderately deep (to 1.8 m). They are circumneutral (pH: 4.4–8.7; $\bar{x}$: 6.9); and usually hard ($\bar{x}$ total CaCO₃ alkalinity: 36.2 mg l⁻¹) with a high total nitrogen ($\bar{x}$: 860 $\mu\text{g l}^{-1}$) and sulfur content ($\bar{x}$ sulfate: 21.8 mg l⁻¹). The substrates are alkaline ($\bar{x}$: pH: 8.3), low in organic matter, and high in Ca ($\bar{x}$: 1830 $\mu\text{g g}^{-1}$) and are described as limestone-shell sand or sandy. Unlike most of its congeners, this is an entirely submersed species, which is restricted to lotic riverine habitats, where it can grow densely to become the dominant component (by biomass). Transplant studies have failed to induce floating or emergent leaves on the plants. Flowering occurs from March to May. The flowers emerge from the otherwise inundated inflorescence during anthesis but sometimes open while underwater. The plants are monoecious, with the lower inflorescence whorl bearing three female flowers (occasionally two females and one male), and the next whorl is entirely male (rarely with one male and two female flowers or two male and one female flower); the remaining flowers are male. Further studies are needed on the pollination biology and seed ecology of this species. The plants reproduce vegetatively by the production of coarse rhizomes. **Reported associates:** *Cabomba caroliniana*, *Ceratophyllum demersum*, *Chara*, *Cladophora*,

Cryptocoryne beckettii, *Egeria densa*, *Eichhornia crassipes*, *Hydrilla verticillata*, *Hymenocallis rotata*, *Lemna*, *Lobelia cardinalis*, *Myriophyllum aquaticum*, *Myriophyllum heterophyllum*, *Myriophyllum laxum*, *Myriophyllum spicatum*, *Najas guadalupensis*, *Nuphar*, *Pistia stratiotes*, *Pontederia cordata*, *Potamogeton*, *Vallisneria americana*, *Zizania aquatica*.

2.1.6.15. ***Sagittaria lancifolia* L.** is a perennial, which grows in shallow (to 1.2 m), sluggish to still, tidal or non-tidal, brackish (oligohaline) to freshwaters on beaches or in baygalls, bogs, borrow pits, canals (drainage), depressions, ditches, dunes, flats, flatwoods, floodplains, lakebeds (dry), marshes (depression; floating; freshwater; salt), meadows, ponds (spring-fed), pools, rice fields, roadsides, savannahs, scrub, sinkholes, slopes (to 5%), sloughs, swales, swamps (dome; strand), and along the margins of bayous, lagoons, lakes, ponds, rivers, and streams (estuarine) at elevations to 31 m. The plants consistently occur in open exposures, where they receive full sunlight, and less often in partial shade. They can tolerate some brackish conditions but are killed at salinity levels of 15‰ (especially if grazed by herbivores). The leaves elongate proportionally with increased water depth. The waters are circumneutral (pH: 5.3–8.7; $\bar{x}$: 7.2), alkaline ($\bar{x}$ total alkalinity: 32.9 mg l⁻¹; $\bar{x}$ Ca: 23.9 mg l⁻¹; $\bar{x}$ chloride: 30.8 mg l⁻¹), and high in nitrogen ($\bar{x}$ total N: 1020 µg l⁻¹). The substrates often are brackish, but somewhat acidic ($\bar{x}$ = pH: 6.1), and have been characterized as clay (Schriever), clayey alluvium, dredge spoil, gravel, Lafitte-Clovelly association, loamy sand, marl, muck (Allemands; Kenner), Newhan-Corolla, peat, peaty muck, rock, sand (Duckston; Leon; Waveland), sandy loam (fine; Harleston), silt, silty clay loam (Cancienne), and silty loam. Although described as monoecious, the plants actually are subandrodioecious (mixtures of male and cosexual plants). The flowers are pollinated by insects (Insecta). Flowering and fruiting have been observed throughout the year (from January to December). The achenes float and are dispersed by water; however, the presence of resinous glands confers adhesiveness, which is believed to facilitate their attachment to animal vectors for epizoochorous dispersal. A seed bank (having up to 167 seeds m⁻²) develops; however, many of the seeds are not intact and are inviable. The achenes require light for germination, which occurs readily (100%) at 25°C. Warm stratification can promote germination. Germination rates are highest under inundated conditions and are reduced under anaerobic conditions; higher rates (67%) occur in saturated sites than in flooded sites (33%). Seed germination is inhibited completely at salinities of 2‰ or higher. Seedling densities of 20 m⁻² have been observed at several sites. The adult plants contain a milky latex sap and reproduce vegetatively by means of a thick rhizome. Genetic analyses (using allozymes) indicate that populations are characterized by only low levels of clonality. The leaves and inflorescences are larger on plants growing under high phosphorous conditions, but more biomass is allocated to roots and rhizomes under low phosphorous conditions. The plants can attain mean plot biomass values of 254 g DM m⁻². The roots are colonized by arbuscular mycorrhizae and dark septate endophytic Fungi. **Reported**

associates: *Acer rubrum*, *Acemella repens*, *Aeschynomene*, *Alternanthera philoxeroides*, *Ambrosia artemisiifolia*, *Ambrosia trifida*, *Ammannia latifolia*, *Ampelaster carolinianus*, *Ampelopsis arborea*, *Amphicarpum*, *Aristida palustris*, *Asclepias perennis*, *Asclepias rubra*, *Baccharis halimifolia*, *Bacopa monnieri*, *Berchemia scandens*, *Boehmeria cylindrica*, *Bolboschoenus robustus*, *Calopogon tuberosus*, *Celtis laevigata*, *Cephalanthus occidentalis*, *Cicuta maculata*, *Cirsium horridulum*, *Cirsium nuttallii*, *Cladium jamaicense*, *Cyperus articulatus*, *Cyperus odoratus*, *Cyperus strigosus*, *Cyperus virens*, *Decodon verticillatus*, *Desmanthus illinoensis*, *Diospyros virginiana*, *Echinochloa walteri*, *Eichhornia crassipes*, *Eleocharis cellulosa*, *Eleocharis fallax*, *Eleocharis montevidensis*, *Elephantopus carolinianus*, *Eragrostis elliotii*, *Eryngium aquaticum*, *Eupatorium*, *Fimbristylis spadicea*, *Fraxinus*, *Fuirena scirpoidea*, *Galium tinctorium*, *Gonolobus*, *Hibiscus laevis*, *Hydrocotyle verticillata*, *Hydrolea corymbosa*, *Hymenocallis rotata*, *Hypericum cistifolium*, *Hypericum fasciculatum*, *Ilex cassine*, *Ilex glabra*, *Ilex opaca*, *Ilex vomitoria*, *Ipomoea sagittata*, *Iris hexagona*, *Itea virginica*, *Iva annua*, *Juncus acuminatus*, *Juncus effusus*, *Juncus roemerianus*, *Juniperus virginiana*, *Lachnanthes caroliniana*, *Leersia hexandra*, *Leersia oryzoides*, *Leptochloa fusca*, *Liquidambar styraciflua*, *Ludwigia glandulosa*, *Ludwigia octovalvis*, *Ludwigia peploides*, *Ludwigia peruviana*, *Lythrum alatum*, *Lythrum lineare*, *Mikania scandens*, *Morus rubra*, *Myrica cerifera*, *Myriophyllum aquaticum*, *Nymphaea odorata*, *Nymphoides aquatica*, *Nyssa aquatica*, *Orontium aquaticum*, *Osmunda regalis*, *Packera glabella*, *Panicum amarum*, *Panicum dichotomiflorum*, *Panicum hemitomom*, *Panicum repens*, *Panicum virgatum*, *Parthenocissus*, *Paspalum distichum*, *Paspalum urvillei*, *Peltandra virginica*, *Persea*, *Persicaria glabra*, *Persicaria hydropiperoides*, *Persicaria punctata*, *Phragmites australis*, *Phyla lanceolata*, *Phyla nodiflora*, *Physostegia leptophylla*, *Pinus elliotii*, *Platanthera nivea*, *Polygala rugelii*, *Pontederia cordata*, *Ptilimnium capillaceum*, *Quercus*, *Ranunculus sardous*, *Rhaphidophyllum hystrix*, *Rhynchospora caduca*, *Rhynchospora elliotii*, *Rhynchospora fascicularis*, *Rhynchospora inundata*, *Rubus argutus*, *Rumex conglomeratus*, *Rumex crispus*, *Rumex obovatus*, *Sabal minor*, *Sabal palmetto*, *Sabatia calycina*, *Sacciolepis striata*, *Sagittaria graminea*, *Sagittaria latifolia*, *Sagittaria platyphylla*, *Salix caroliniana*, *Salix nigra*, *Sambucus*, *Samolus valerandi*, *Saururus cernuus*, *Schoenoplectus californicus*, *Schoenoplectus tabernaemontani*, *Scleria lacustris*, *Serenoa*, *Smilax smallii*, *Spartina alterniflora*, *Spartina bakeri*, *Spartina cynosuroides*, *Spartina patens*, *Sphagnum*, *Symphyotrichum elliotii*, *Symphyotrichum novi-belgii*, *Symphyotrichum subulatum*, *Taxodium distichum*, *Thelypteris palustris*, *Tillandsia*, *Toxicodendron radicans*, *Triadica sebifera*, *Typha dominicensis*, *Typha latifolia*, *Utricularia purpurea*, *Vigna luteola*, *Vitis*, *Woodwardia areolata*, *Xyris difformis*, *Zizania aquatica*, *Zizaniopsis miliacea*.

2.1.6.16. ***Sagittaria latifolia* Willd.** is a perennial, which inhabits shallow (average depth of 10 cm, but up to 1.2 m), intertidal, non-tidal, or tidal freshwaters of backwaters,

baygalls, beaches, bogs (quaking; sandy), bottomlands, canals (drainage), channels, depressions, dikes, ditches (roadside; verbal), fens (calcareous; poor; prairie; rich), flats (sand), floodplains, gravel pits, lagoons (dessicated), lakes (playa), marshes, meadows, mud flats, oxbows, pans (dune), ponds (sand), pools (ephemeral; roadside), prairies, rice fields, roadsides, seeps, shores, silt bars, slopes (to 1%), sloughs, springs, streams (intermittent), swales, swamps, vernal pools, woodlands, and the margins of lagoons, lakes, ponds, potholes, reservoirs, rivers, sloughs, and streams at elevations to 2625 m. The waters span a broad range of conditions (pH: 4.7–9.2; $\bar{x}$: 6.9–7.3; conductivity: 20–510 $\mu\text{mhos cm}^{-1}$; total alkalinity: 1.5–290 $\text{mg l}^{-1} \text{CaCO}_3$; $\bar{x}$ = 26.4 mg l^{-1} ; total N: 380–2470 $\mu\text{g l}^{-1}$). Exposures range from open sites in full sunlight to areas of partial shade. The substrates include alluvium, clay (heavy), clayey sand, granite, gravel, loam, muck, mucky sand, mud (organic; soft), peaty muck, peaty mud, rocky serpentine, sand, sandy mud, sandy silty alluvium, silt (river bottom), silty clay, silty gravel, and silty sand. Flowering occurs from May to November, with fruiting observed from June to October. The flowers are pollinated by generalist insects (Insecta), including bees and wasps (Hymenoptera) or flies (Diptera). Individuals can be monoecious or dioecious. Sex expression is controlled by two Mendelian loci (male and female sterility), where dioecious males are heterozygous at both loci, and monoecious individuals are homozygous for alleles dominant to male sterility in females and recessive to female sterility in males. Allozyme data indicate that individuals of each type remain genetically distinct and that both suffer substantially from inbreeding depression. Dioecious populations contain only a subset of the haplotype diversity found in monoecious populations, indicating the derivation of the former from the latter. Reproduction primarily is sexual in monoecious populations but vegetative in dioecious populations. Selfing rates are higher in monoecious populations. In dioecious individuals, the males have larger flowers but smaller floral displays than the female flowers, which remain open for a shorter time period than the males. The larger male flowers experience higher pollinator visitation rates, but larger male floral displays result in lower pollination success. Sexual expression is highly plastic in monoecious populations with higher numbers of female flowers produced at higher nutrient levels. In monoecious individuals, the female flowers increase proportionally with plant size, while the males do not. The flat seeds are dispersed by water. A persistent seed bank develops. Germination requires light and flooded conditions. Seeds from monoecious plants germinate freely, whereas those of dioecious plants require a period of stratification. The seeds can be recalcitrant but have been stored successfully in water at 3°C. They have germinated following 150 days of cold stratification under a 21°C/16°C day/night temperature regime. Vastly higher germination rates have been obtained for seeds whose seed coats are first “nipped” using scissors. Densities of up to 20 seedlings m^{-2} have been observed at field sites. Vegetative propagation occurs by the formation of rhizomes, which produce large tubers. The rhizomes normally extend from 4 to 6 cm below the surface, but can occur as deep as

10 cm. An essentially 1:1 trade-off exists between sexual reproduction (primarily the production of female flowers) and the extent of vegetative reproduction. The roots can harbor large colonies of methanotrophic bacteria. The plants can tolerate short-term intrusions of salinity but suffer from decreased seed germination, and seedling emergence, survival, and growth rates when exposed to saline conditions.

Reported associates: *Abutilon theophrasti*, *Acalypha*, *Acer negundo*, *Acer rubrum*, *Acer saccharinum*, *Acmella*, *Agalinis*, *Agrostis gigantea*, *Agrostis stolonifera*, *Alisma subcordatum*, *Alisma triviale*, *Alnus serrulata*, *Alternanthera philoxeroides*, *Amaranthus tuberculatus*, *Ambrosia artemisiifolia*, *Ammannia coccinea*, *Ammannia robusta*, *Amorpha fruticosa*, *Andropogon glomeratus*, *Anemone canadensis*, *Angelica atropurpurea*, *Apios americana*, *Apocynum cannabinum*, *Aristida purpurascens*, *Asclepias incarnata*, *Asclepias syriaca*, *Azolla*, *Baccharis halimifolia*, *Baccharis salicifolia*, *Betula*, *Bidens aristosus*, *Bidens beckii*, *Bidens cernuus*, *Bidens frondosus*, *Bidens laevis*, *Bistorta bistortoides*, *Boehmeria cylindrica*, *Bolboschoenus fluviatilis*, *Boltonia asteroides*, *Brasenia schreberi*, *Butomus umbellatus*, *Calamagrostis canadensis*, *Calla palustris*, *Caltha palustris*, *Campanula aparinoides*, *Carex bebbii*, *Carex comosa*, *Carex cristatella*, *Carex exilis*, *Carex haydenii*, *Carex hystericina*, *Carex lasiocarpa*, *Carex limosa*, *Carex livida*, *Carex lupuliformis*, *Carex lurida*, *Carex molesta*, *Carex muskingumensis*, *Carex pellita*, *Carex praegracilis*, *Carex rostrata*, *Carex stipata*, *Carex stricta*, *Carex utriculata*, *Carex vesicaria*, *Carex vulpinoidea*, *Cephalanthus occidentalis*, *Ceratophyllum demersum*, *Chamaedaphne calyculata*, *Chara*, *Chelone glabra*, *Cicuta bulbifera*, *Comarum palustre*, *Conium maculatum*, *Conoclinium*, *Coreopsis gladiata*, *Cornus amomum*, *Cornus sericea*, *Crataegus douglasii*, *Cyperus erythrorhizos*, *Cyperus esculentus*, *Cyperus odoratus*, *Cyperus squarrosus*, *Cyperus strigosus*, *Decodon verticillatus*, *Distichlis spicata*, *Doellingeria umbellata*, *Drosera anglica*, *Dryopteris*, *Dulichium arundinaceum*, *Echinochloa crus-galli*, *Echinochloa walteri*, *Eclipta prostrata*, *Egeria densa*, *Elaeagnus angustifolia*, *Eleocharis acicularis*, *Eleocharis bella*, *Eleocharis erythropoda*, *Eleocharis obtusa*, *Eleocharis ovata*, *Eleocharis palustris*, *Eleocharis parishii*, *Eleocharis quadrangulata*, *Eleocharis robbinsii*, *Elodea canadensis*, *Elymus canadensis*, *Equisetum arvense*, *Equisetum fluviatile*, *Eragrostis hypnoides*, *Eriocaulon aquaticum*, *Eupatorium perfoliatum*, *Eutrochium maculatum*, *Fallopia scandens*, *Festuca*, *Fimbristylis vahlii*, *Forestiera acuminata*, *Fraxinus nigra*, *Fraxinus pennsylvanica*, *Galium obtusum*, *Galium trifidum*, *Galium triflorum*, *Gentiana andrewsii*, *Glyceria borealis*, *Glyceria grandis*, *Glyceria striata*, *Gnaphalium palustre*, *Hedeoma hispida*, *Helenium autumnale*, *Helianthus tuberosus*, *Heliopsis helianthoides*, *Hippuris vulgaris*, *Hordeum jubatum*, *Humulus lupulus*, *Hydrocotyle verticillata*, *Hypericum canadense*, *Hypericum sphaerocarpum*, *Ilex cassine*, *Impatiens capensis*, *Iris pseudacorus*, *Iris virginica*, *Isoetes lacustris*, *Juncus acuminatus*, *Juncus effusus*, *Juncus nodosus*, *Laportea canadensis*, *Lathyrus palustris*, *Leersia oryzoides*, *Lemna minor*, *Lemna trisulca*, *Lepidium*

latifolium, *Leptochloa panicea*, *Lilaeopsis*, *Lilium michiganense*, *Lindernia dubia*, *Lipocarpa micrantha*, *Ludwigia palustris*, *Ludwigia peploides*, *Ludwigia polycarpa*, *Lycopus americanus*, *Lycopus rubellus*, *Lycopus uniflorus*, *Lycopus virginicus*, *Lysimachia ciliata*, *Lysimachia nummularia*, *Lysimachia vulgaris*, *Lythrum salicaria*, *Mazus pumilus*, *Melilotus albus*, *Mentha arvensis*, *Menyanthes trifoliata*, *Mimulus ringens*, *Murdannia*, *Myriophyllum sibiricum*, *Navarretia*, *Nuphar polysepala*, *Nuphar variegata*, *Nymphaea odorata*, *Nyssa biflora*, *Oenothera biennis*, *Panicum dichotomiflorum*, *Panicum hemitomon*, *Panicum virgatum*, *Paspalum dilatatum*, *Peltandra virginica*, *Penthorum sedoides*, *Persicaria amphibia*, *Persicaria arifolia*, *Persicaria coccinea*, *Persicaria hydropiperoides*, *Persicaria lapathifolia*, *Persicaria pensylvanica*, *Persicaria punctata*, *Persicaria sagittata*, *Phalaris arundinacea*, *Phanopyrum gymnocarpon*, *Phragmites australis*, *Phyla lanceolata*, *Physostegia virginiana*, *Poa nemoralis*, *Poa pratensis*, *Polytrichum*, *Pontederia cordata*, *Populus angustifolia*, *Potamogeton amplifolius*, *Potamogeton berchtoldii*, *Potamogeton crispus*, *Potamogeton foliosus*, *Potamogeton gramineus*, *Potamogeton illinoensis*, *Potamogeton natans*, *Potamogeton natans*, *Potamogeton pusillus*, *Potamogeton richardsonii*, *Potamogeton zosteriformis*, *Potentilla norvegica*, *Proserpinaca palustris*, *Prunus virginiana*, *Puccinellia*, *Pycnanthemum virginianum*, *Ranunculus aquatilis*, *Ranunculus flammula*, *Ranunculus pensylvanicus*, *Ranunculus recurvatus*, *Rhexia mariana*, *Rhododendron canescens*, *Rhus glabra*, *Rhynchospora inundata*, *Ribes americanum*, *Rorippa islandica*, *Rorippa palustris*, *Rosa setigera*, *Rubus argutus*, *Rudbeckia laciniata*, *Rumex altissimus*, *Rumex verticillatus*, *Sagittaria ambigua*, *Sagittaria australis*, *Sagittaria calycina*, *Sagittaria cuneata*, *Sagittaria engelmanniana*, *Sagittaria filiformis*, *Sagittaria graminea*, *Sagittaria lancifolia*, *Sagittaria montevidensis*, *Sagittaria platyphylla*, *Sagittaria rigida*, *Sagittaria sanfordii*, *Sagittaria teres*, *Salix amygdaloides*, *Salix exigua*, *Salix gooddingii*, *Salix interior*, *Salix lasiandra*, *Salix nigra*, *Sambucus nigra*, *Saururus cernuus*, *Scheuchzeria palustris*, *Schoenoplectus acutus*, *Schoenoplectus americanus*, *Schoenoplectus hallii*, *Schoenoplectus lacustris*, *Schoenoplectus tabernaemontani*, *Schoenoplectus triqueter*, *Scirpus atrovirens*, *Scirpus cyperinus*, *Scutellaria lateriflora*, *Sesbania drummondii*, *Sicyos angulatus*, *Silene nivea*, *Silphium perfoliatum*, *Sium suave*, *Solidago gigantea*, *Sonchus arvensis*, *Sparganium androcladum*, *Sparganium emersum*, *Sparganium eurycarpum*, *Sparganium natans*, *Sphagnum angustifolium*, *Sphagnum centrale*, *Sphagnum teres*, *Spiraea douglasii*, *Spirodela polyrhiza*, *Stuckenia pectinata*, *Stuckenia vaginata*, *Stylisma aquatica*, *Symphyotrichum lanceolatum*, *Symphyotrichum pilosum*, *Symphyotrichum puniceum*, *Symphyotrichum subulatum*, *Symplocarpus foetidus*, *Taxodium distichum*, *Thalia geniculata*, *Thalictrum dasycarpum*, *Toxicodendron radicans*, *Toxicodendron vernix*, *Tradescantia virginiana*, *Triadenum virginicum*, *Typha angustifolia*, *Typha domingensis*, *Typha latifolia*, *Urtica dioica*, *Utricularia macrorhiza*, *Utricularia purpurea*, *Vallisneria americana*, *Verbascum*

thapsus, *Verbena bonariensis*, *Verbena hastata*, *Vernonia fasciculata*, *Veronica anagallis-aquatica*, *Veronica catenata*, *Veronica peregrina*, *Viburnum lentago*, *Viola lanceolata*, *Vitis riparia*, *Wolffia brasiliensis*, *Wolffia columbiana*, *Xanthium strumarium*, *Zannichellia palustris*, *Zizania palustris*.

2.1.6.17. ***Sagittaria longiloba* Engelm. ex J.G. Sm.** is a perennial, which grows in shallow waters (to 45 cm) in canals (irrigation), cienegas, ditches (drainage; roadside), marshes, mudflats, playas, ponds, pools (alkaline; ephemeral), rice fields, and along the margins of lakes, ponds, rivers, and streams at elevations to 1676 m. This is a common species of playa lakes and similar habitats. The exposures typically are open and receive full sunlight. The substrates are described as alkaline and include clay, clay loam, mud, and sand. Flowering occurs from May to October, with fruiting observed from July to October. The plants are monoecious and probably are pollinated by insects (Insecta). Viable achenes are known to be passed through the digestive tracts of birds (Aves: Anatidae: *Anas platyrhynchos*; Charadriidae: *Charadrius vociferus*) after retention times ranging from 8 to 16 h, which implicates birds as agents of their long-distance dispersal. The achenes germinate in a few centimeters of water under ambient greenhouse conditions. The seedlings typically establish in sites that have been shallowly flooded for more than 2 weeks. In appropriately flooded sites, germination is continuous throughout the growing season. Seedling densities from 25 to 75 m⁻² have been observed in the field. Vegetative reproduction occurs by the production of tubers.

Reported associates: *Agropyron*, *Alisma triviale*, *Ambrosia grayi*, *Ammannia coccinea*, *Bacopa rotundifolia*, *Callitriche heterophylla*, *Chara*, *Cyperus digitatus*, *Digitaria sanguinalis*, *Echinochloa crus-galli*, *Echinodorus berteroi*, *Eleocharis macrostachya*, *Eleocharis palustris*, *Helianthus ciliaris*, *Heteranthera dubia*, *Heteranthera limosa*, *Heteranthera mexicana*, *Juncus*, *Juniperus*, *Lemna*, *Leptochloa fusca*, *Limosella aquatica*, *Ludwigia glandulosa*, *Ludwigia palustris*, *Marsilea vestita*, *Myriophyllum pinnatum*, *Paspalum distichum*, *Persicaria bicornis*, *Persicaria glabra*, *Persicaria hydropiperoides*, *Persicaria lapathifolia*, *Pontederia cordata*, *Populus fremontii*, *Potamogeton natans*, *Potamogeton nodosus*, *Rumex chrysocarpus*, *Rumex crispus*, *Sagittaria calycina*, *Sagittaria latifolia*, *Schoenoplectus californicus*, *Spirodela polyrhiza*, *Stuckenia pectinata*, *Symphyotrichum subulatum*, *Typha domingensis*, *Xanthium*.

2.1.6.18. ***Sagittaria macrocarpa* J.G. Sm.** is a perennial (or sometimes annual?), which is narrowly distributed and endemic to the inner coastal plain Sandhills Region of the southeastern United States. The plants occur in very shallow waters of ponds (artificial; beaver), pools, seepage bogs, streamheads (blackwater), and lakeshores at low elevations. The waters are acidic, darkly stained (blackwaters), and low in nutrients. The substrates have been described as clay, clayey sand, mud, peaty sand, and sand. The plants are monoecious and flower during summer (their specific flowering period has not been clarified). The plants reproduce vegetatively by the production of slender stolons. Much life history information is needed for

this species, which until recently had been regarded as a synonym of *S. graminea* (see *Systematics*). **Reported associates:** *Dichanthelium*, *Eleocharis flavescens*, *Eleocharis robbinsii*, *Juncus debilis*, *Lachnanthes caroliniana*, *Mayaca fluviatilis*, *Nymphaea odorata*, *Nymphoides*, *Nyssa biflora*, *Panicum hemitomon*, *Potamogeton diversifolius*, *Sagittaria engelmanniana*, *Sagittaria graminea*, *Schoenoplectus etuberculatus*, *Sparganium americanum*, *Sphagnum*.

2.1.6.19. ***Sagittaria montevidensis* Cham. & Schlecht.** is a perennial, which colonizes shallow waters or exposed substrates in ditches (landscaped), mudflats (riverine), sloughs (roadside), and along the margins of swamps (roadside) at elevations to 10 m. The substrates are described as muddy clay. The plants are monoecious, with the female flowers lacking the ring of stamens found in *S. calycina*. The petals possess a bright crimson spot, which presumably serves as an attractant to potential pollinators. Flowering occurs from July to October. Aside from these few details, most of the North American information for this taxon has been attributed incorrectly and refers instead to *S. calycina*, a distinct, native species (see *Systematics*). Reliable information pertaining correctly to the North American occurrences of this nonindigenous species is scarce and should be compiled. **Reported associates (North America):** *Nymphaea capensis*, *Sagittaria latifolia*, *Sagittaria platyphylla*.

2.1.6.20. ***Sagittaria papillosa* Buch.** is a perennial, which grows in shallow (e.g., 6.5–20 cm depth), brackish to freshwaters of bogs, borrow pits, ditches (roadside), flats, flatwoods (pine), marshes, meadows, pools (roadside), prairies (coastal; saline), savannahs, swamps, terraces (river), wastelands, woodlands (sparse), and along the margins of lakes and ponds at elevations to 67 m. Exposures are described as open. The substrates are acidic (mean values: pH: 4.9–5.2; organic matter: <1–3.5%; Ca (as CaO): 118–308 ppm; K (as K₂O): 34–78 ppm; Mg (as MgO): 30–104 ppm; P (as P₂O₅): 7–39.5 ppm). Flowering and fruiting occur from April to September. The plants normally are racemose and monoecious, but occasionally produce branched inflorescences (panicles) having staminate and bisexual flowers on the lowest branches (i.e., they are andromonoecious); the stamens of the bisexual flowers are functional. Individuals are self-compatible, which allows for self-pollination to occur. The natural pollinators of open-pollinated plants have not been enumerated, but likely are insects (Insecta). Only racemose, monoecious plants have been observed to develop under greenhouse conditions (and from F₂ crosses), indicating that the anomalous floral features are environmentally plastic and not strictly determined genetically. Additional information on the pollination biology or seed ecology of this species is unavailable. The plants reproduce vegetatively by the production of coarse rhizomes, from which new vegetative plantlets develop. The connections with the maternal plant sever by the onset of anthesis, which yields clonal ramets in near proximity. **Reported associates:** *Acer negundo*, *Baccharis halimifolia*, *Bacopa caroliniana*, *Boehmeria cylindrica*, *Carex amphibola*, *Carex arkansana*, *Celtis laevigata*, *Centella asiatica*, *Cephalanthus occidentalis*, *Cornus foemina*, *Crataegus mollis*, *Crataegus viridis*,

Cyrilla racemiflora, *Eleocharis macrostachya*, *Eleocharis quadrangulata*, *Eleocharis wolfii*, *Eupatorium rotundifolium*, *Euthamia leptoccephala*, *Helenium flexuosum*, *Hydrolea ovata*, *Hymenocallis lirioides*, *Ilex*, *Iris brevicaulis*, *Iris hexagona*, *Isoetes melanopoda*, *Juncus acuminatus*, *Juncus brachycarpus*, *Juncus dichotomus*, *Juncus effusus*, *Juncus marginatus*, *Juncus nodatus*, *Limnoscium pinnatum*, *Ludwigia*, *Ludwigia palustris*, *Mikania scandens*, *Myrica*, *Oplismenus hirtellus*, *Panicum hemitomon*, *Paspalum geminatum*, *Paspalum wrightii*, *Persicaria hydropiperoides*, *Pinus palustris*, *Pluchea*, *Pontederia cordata*, *Proserpinaca palustris*, *Quercus*, *Ranunculus hispidus*, *Rhynchospora corniculata*, *Sabal minor*, *Sagittaria graminea*, *Salix nigra*, *Sambucus nigra*, *Samolus valerandi*, *Sarracenia*, *Schoenolirion croceum*, *Scutellaria integrifolia*, *Sesbania drummondii*, *Steinchisma hians*, *Thalia dealbata*, *Tridens strictus*, *Typha latifolia*.

2.1.6.21. ***Sagittaria platyphylla* (Engelm.) J.G. Sm.** is a perennial, which grows in shallow (e.g., 8–50 cm deep), tidal or non-tidal, brackish or freshwaters of bayous, bogs (hillside), bottoms (lake), canals (drainage), cobble bars, ditches (drainage; roadside), flats, flatwoods, gravel pits, lagoons, levees (wooded), mudflats, lakes, marshes, mudflats, ponds (farm; retention; seasonal), pools, rice fields, roadsides, sand pits, spillways, streams, swales, swamps (roadside), woodlands, and along the margins or shores of lakes, ponds, pools, and reservoirs at elevations to 316 m. Although the plants occur occasionally in brackish sites, their biomass declines at salinities of 3 ppt; salinity levels of 6‰ are lethal. In cultivation, the plants thrive in water temperatures from 20°C to 24°C. Exposures typically are open sites with full sunlight, and uncommonly are characterized by shade. The substrates are acidic (mean pH: 5.8), high in organic matter (mean: 23.8%), and include clay, clayey alluvium, gravel, muck (tidal), mud, sand (fine; Mascotte), sandy clay, sandy silt, silt, silty clay, and silty clay loam (Schriever). Flowering and fruiting extend from April to December. The plants are monoecious and likely pollinated by insects (Insecta). The fruits are buoyant and dispersed by water currents. Although no persistent seed banks have been reported, the seeds are known to remain viable for several years when stored in uncontaminated water. In one study, all *S. platyphylla* accessions surveyed genetically possessed a single multilocus isozyme genotype (13 loci), indicating extremely low levels of genetic variation in the species. Those results contrast with a study of invasive populations in Australia, where each surveyed individual possessed a unique (AFLP) genotype, which indicated that seeds are the primary propagules involved in dispersal. Vegetative reproduction occurs by means of rhizomes, from which large tubers are produced. Detached tubers sink initially, then float to the surface once the shoots develop, but eventually sink again when the roots develop. They also are dispersed by water. Compared to other aquatic species, *S. platyphylla* has a relative slow exponential leaf decay rate (0.053 day⁻¹). **Reported associates:** *Acmella repens*, *Alternanthera philoxeroides*, *Ammannia coccinea*, *Ampelopsis arborea*, *Asclepias*, *Azolla filiculoides*, *Bacopa monnieri*, *Briza minor*,

Bromus catharticus, *Caperonia*, *Cephalanthus occidentalis*, *Ceratophyllum demersum*, *Colocasia esculenta*, *Commelina diffusa*, *Corchorus*, *Cyperus difformis*, *Cyperus flavicomus*, *Cyperus haspan*, *Cyperus pseudovegetus*, *Cyperus strigosus*, *Cyperus virens*, *Dichanthelium*, *Diodia virginiana*, *Diospyros virginiana*, *Echinochloa crus-galli*, *Echinodorus berteroi*, *Echinodorus cordifolius*, *Egeria densa*, *Eleocharis ambigens*, *Eleocharis baldwinii*, *Eleocharis montana*, *Eleocharis obtusa*, *Elymus virginicus*, *Eupatorium capillifolium*, *Euphorbia*, *Fagus grandifolia*, *Fimbristylis dichotoma*, *Gleditsia aquatica*, *Hydrilla verticillata*, *Hydrocleys nymphoides*, *Hydrocotyle umbellata*, *Hydrocotyle verticillata*, *Hydrolea ovata*, *Hydrolea uniflora*, *Ilex glabra*, *Juncus effusus*, *Juncus megacephalus*, *Juncus repens*, *Justicia ovata*, *Kyllinga brevifolia*, *Leersia oryzoides*, *Lepidium virginicum*, *Leptochloa*, *Liquidambar styraciflua*, *Lobelia*, *Lonicera japonica*, *Ludwigia alternifolia*, *Ludwigia octovalvis*, *Ludwigia palustris*, *Ludwigia peploides*, *Ludwigia repens*, *Marsilea vestita*, *Micranthemum umbrosum*, *Mikania scandens*, *Myrica cerifera*, *Najas guadalupensis*, *Najas minor*, *Nyssa biflora*, *Paspalum urvillei*, *Persicaria punctata*, *Phyla nodiflora*, *Pinus taeda*, *Plantago patagonica*, *Potamogeton crispus*, *Potamogeton diversifolius*, *Potamogeton illinoensis*, *Potamogeton nodosus*, *Quercus nigra*, *Rhynchospora colorata*, *Rhynchospora corniculata*, *Rotala ramosior*, *Rubus trivialis*, *Rumex conglomeratus*, *Rumex crispus*, *Sabal palmetto*, *Sagittaria australis*, *Sagittaria calycina*, *Sagittaria lancifolia*, *Sagittaria latifolia*, *Sagittaria montevidensis*, *Salix*, *Schoenoplectus americanus*, *Sesbania*, *Solidago altissima*, *Sphenoclea zeylanica*, *Taxodium distichum*, *Triadica sebifera*, *Typha domingensis*, *Typha latifolia*, *Vallisneria americana*, *Verbena brasiliensis*, *Zizania texana*.

2.1.6.22. ***Sagittaria rigida* Pursh** is a perennial, which grows in shallow to deep (e.g., 0.2–1.8 m), still or flowing, brackish to fresh, tidal or non-tidal waters of bays, bogs, canals, channels, depressions, ditches, meadows, mudflats, oxbows, ponds (artificial; dried; farm; natural; shallow; small; stock; upland), sinkholes (depression), swales, thickets (swamp), and along the margins or shores (receding) of lakes, ponds, reservoirs, rivers, streams, and swamps at elevations to 1385 m. The plants are tolerant of turbidity and fairly eutrophic conditions. In standing waters, they often occur at greater depths (>1.0 m). Exposures typically receive full sunlight. The waters (pH: 5.4–8.9; $\bar{x}$ = 7.4; specific conductance: 319–340 $\mu\text{S cm}^{-1}$; total alkalinity as CaCO_3 : 10–140 mg l^{-1}) have been characterized as brackish, calcareous, or hard. The substrates (pH: 5.9; 2.7% organic matter) include muck (marly), mucky sand, mud (alluvial), rock, sand, and sandy muck. Flowering and fruiting extend from May to September. The plants are monoecious. The pollination system has not been described but probably is mediated by small insects (Insecta). A persistent seed bank develops, with a mean density of up to 119 seeds m^{-2} reported from shallowly flooded sites. Seeds that are freshly collected in the spring have germinated well following several days of cold (4°C), wet storage. Seedling establishment occurs optimally during drawdown conditions. The plants reproduce vegetatively by rhizomes, from which tubers can develop.

Reported associates: *Alisma triviale*, *Bacopa rotundifolia*, *Bolboschoenus fluviatilis*, *Brasenia schreberi*, *Butomus umbellatus*, *Carex gynandra*, *Carex interior*, *Carex lupulina*, *Cephalanthus occidentalis*, *Ceratophyllum demersum*, *Ceratophyllum echinatum*, *Cyperus bipartitus*, *Dulichium arundinaceum*, *Eleocharis erythropoda*, *Eleocharis obtusa*, *Eleocharis palustris*, *Elodea canadensis*, *Eriophorum angustifolium*, *Heteranthera limosa*, *Heteranthera multiflora*, *Heteranthera reniformis*, *Heteranthera rotundifolia*, *Hibiscus*, *Hypericum mutilum*, *Iris pseudacorus*, *Isoetes riparia*, *Juncus acuminatus*, *Justicia americana*, *Kyllinga gracillima*, *Leersia oryzoides*, *Lemna minor*, *Lindernia dubia*, *Ludwigia palustris*, *Lythrum salicaria*, *Marsilea vestita*, *Menyanthes trifoliata*, *Myriophyllum sibiricum*, *Nelumbo lutea*, *Nuphar polysepala*, *Nymphaea odorata*, *Orontium aquaticum*, *Peltandra virginica*, *Persicaria amphibia*, *Persicaria bicornis*, *Persicaria coccinea*, *Persicaria hydro-piperoides*, *Persicaria punctata*, *Phalaris arundinacea*, *Phragmites australis*, *Phyla lanceolata*, *Pontederia cordata*, *Potamogeton foliosus*, *Potamogeton nodosus*, *Potamogeton richardsonii*, *Potamogeton vaseyi*, *Ranunculus ambigens*, *Rumex altissimus*, *Rumex crispus*, *Rumex stenophyllus*, *Sagittaria brevirostra*, *Sagittaria graminea*, *Sagittaria latifolia*, *Sagittaria sanfordii*, *Saururus cernuus*, *Schoenoplectus acutus*, *Schoenoplectus heterochaetus*, *Schoenoplectus pungens*, *Schoenoplectus smithii*, *Schoenoplectus tabernaemontani*, *Scirpus cyperinus*, *Sparganium americanum*, *Sparganium emersum*, *Sphagnum magellanicum*, *Sphagnum palustre*, *Sphagnum subsecundum*, *Thelypteris palustris*, *Typha angustifolia*, *Typha latifolia*, *Utricularia macrorhiza*, *Wolffia columbiana*, *Zizania aquatica*, *Zizania palustris*.

2.1.6.23. ***Sagittaria sanfordii* Greene** is a perennial, which inhabits waters (to 1 m deep) in canals, ditches, floodplains, lakes (vernal), marshes, mudflats, pools (alkaline; vernal), rice fields, river bottoms (drying), sloughs, streams and the margins of canals, lakes, ponds (beaver; stock), rivers, and streams at elevations to 609 m. The habitats are categorized as alkaline, with substrates described as alluvium (rocky), clay, loam (gummy), mud (drying), and Tuscan mudflow. Flowering occurs from May to October. The plants are monoecious, but occasionally produce perfect (but normally pistillate) flowers with functional stamens. The plants reproduce vegetatively by rhizomes, which produce spherical tubers. Little additional information exists on the reproductive or seed ecology. This is a relatively rare species, which has become extirpated in many areas due to habitat loss. Its life history deserves a comprehensive evaluation. **Reported associates:** *Alisma*, *Artemisia douglasiana*, *Callitriche*, *Carex*, *Cyperus eragrostis*, *Eleocharis macrostachya*, *Eleocharis quadrangulata*, *Iris pseudacorus*, *Isoetes*, *Juncus effusus*, *Legenere valdiviana*, *Ludwigia peploides*, *Marsilea*, *Polygonum*, *Potamogeton*, *Ranunculus*, *Sagittaria calycina*, *Sagittaria latifolia*, *Sagittaria rigida*, *Schoenoplectus acutus*, *Typha*.

2.1.6.24. ***Sagittaria secundifolia* Kral** is a perennial, which inhabits clear, slow to swift, riverine waters associated with pools (shallow), rapids, riffles (shallow), and shoals at elevations to 466 m. The plants can grow in exposed shallows or

at depths of up to 75 cm. They are intolerant of pollution and epiphytic growths of filamentous algae. Exposures typically receive full sunlight, with populations declining where a wooded overstory is present. The substrates are characterized as boulders (small), cobble, rocky (sandstone) crevices, sand, and slabs (flat; jointed; sandstone). The plants do not occur in highly turbulent water, deep pools, or on substrates consisting of large boulders. Plants growing in swift, shallow water are short in stature, sterile, and reproduce vegetatively by thick, elongate rhizomes (to 10 cm), which anchor amidst the cracks and fissures in the rocky substrate. In quieter waters, the plants produce longer leaves, shorter rhizomes, and are fertile. Flowering occurs from May to August, with fruiting from July to September. The flowers (which appear to float on the water surface) develop only under full sunlight and on plants growing near the water surface, which are conditions associated with low water flow periods. Most of the plants are devoid of flowers and reproduce asexually; however, preliminary studies indicate that populations retain a fair level of genetic variability. The perianth is essentially absent on pistillate flowers, but of normal proportions in the staminate flowers. Pollination presumably is facilitated by bees (Insecta: Hymenoptera), but the reproductive biology and seed ecology of this species remain virtually unknown. **Reported associates:** *Justicia americana*, *Lindernia*, *Ludwigia*, *Myriophyllum*, *Persicaria*, *Potamogeton*, *Najas*, *Podostemum ceratophyllum*.

2.1.6.25. ***Sagittaria subulata* (L.) Buch.** is a perennial, which inhabits shallow (to 61 cm), coastal, brackish (salinity: 0.5–18 ppt), tidal or non-tidal waters in bays, canals, depressions, hammocks, marshes (tidal), mudflats, streams, and along the margins of ponds and rivers at elevations <100 m. The plants occur commonly in areas that become exposed at low tide. The waters are circumneutral (pH: 4.8–8.3; $\bar{x}$: 6.6–6.7), low in total alkalinity (0.4–56.4 mg l⁻¹; $\bar{x}$: 18.5–20.3 mg l⁻¹), with a relatively low total nitrogen content ($\bar{x}$: 700 µg l⁻¹). In cultivation, the plants thrive in water temperatures from 18°C to 28°C. The substrates include mud, muddy peat, sand, sandy gravel, silty clay, and silty mud. Flowering can extend from March to November. The individuals are monoecious, with the flowers pollinated by small flies (Insecta: Diptera). In deeper waters, the upper (male) flowers open only partially, with the lower (pistillate) flowers rarely becoming emersed above the water surface. Few seeds are produced and nothing is known regarding their germination requirements. The plants primarily reproduce vegetatively by the production of stolons, from which tubers can develop. The leaves lack Kranz anatomy but exhibit CAM-like concentrations of malate, which indicates a similar but modified C₄ photosynthetic pathway. **Reported associates:** *Acer*, *Alternanthera philoxeroides*, *Azolla filiculoides*, *Bacopa rotundifolia*, *Bidens bidentoides*, *Bidens eatonii*, *Bidens hyperboreus*, *Callitriche heterophylla*, *Cardamine longii*, *Carex glaucescens*, *Carya cordiformis*, *Ceratophyllum demersum*, *Cornus foemina*, *Crassula aquatica*, *Crotalaria spectabilis*, *Cyperus virens*, *Echinodorus berteroi*, *Egeria densa*, *Eichhornia crassipes*, *Eleocharis acicularis*, *Eleocharis diandra*, *Eleocharis engelmannii*, *Eleocharis flavescentis*, *Eleocharis obtusa*, *Eleocharis*

parvula, *Eriocaulon parkeri*, *Festuca filiformis*, *Fimbristylis autumnalis*, *Fraxinus*, *Heteranthera multiflora*, *Heteranthera reniformis*, *Hydrilla verticillata*, *Hydrocotyle umbellata*, *Hydrolea quadrivalvis*, *Isoetes mattaponi*, *Lemna valdiviana*, *Lilaeopsis chinensis*, *Limosella australis*, *Lindernia dubia*, *Ludwigia palustris*, *Luziola fluitans*, *Micranthemum micranthemoides*, *Najas guadalupensis*, *Nuphar advena*, *Nymphaea*, *Nyssa biflora*, *Orontium aquaticum*, *Persicaria arifolia*, *Persicaria hydropiperoides*, *Persicaria punctata*, *Pistia stratiotes*, *Planera aquatica*, *Pontederia cordata*, *Potamogeton diversifolius*, *Potamogeton illinoensis*, *Potamogeton pusillus*, *Proserpinaca palustris*, *Ptilimnium capillaceum*, *Rhynchospora glomerata*, *Rhynchospora microcephala*, *Ruppia maritima*, *Sagittaria calycina*, *Sagittaria graminea*, *Salvinia*, *Schoenoplectus smithii*, *Spergularia salina*, *Taxodium distichum*, *Typha domingensis*, *Utricularia gibba*, *Utricularia inflata*, *Vallisneria americana*, *Zannichellia palustris*.

2.1.6.26. ***Sagittaria teres* S. Wats.** is a perennial, which grows in shallow (to 100 cm) waters of borrow pits, swamps, and along the margins or shores of lakes and ponds at elevations to 64 m. Exposures are open and receive full sunlight. The waters are acidic (pH: 4.5–6.7; $\bar{x}$ = 5.2) and very soft (total alkalinity 4–7 mg l⁻¹; $\bar{x}$ = 5.5 mg l⁻¹). The substrates can include cobble, gravel, or sand (mucky; pure; silty; white). Flowering and fruiting extend from July to September. The plants are monoecious. The fruits normally develop and ripen underwater and can differ morphologically if ripened above water. Only scarce information exists on the reproductive biology and seed ecology. Allozyme analyses indicate high levels of genetic variation in populations, which implicates recruitment from the seed bank as a principal means of population persistence (although seed bank data are not available). Vegetative reproduction occurs by the production of stolons, from which minute tubers can develop. However, genetic analyses also indicate that populations are not highly clonally structured, despite their capacity for asexual reproduction. **Reported associates:** *Carex longii*, *Coreopsis rosea*, *Cyperus squarrosus*, *Drosera filiformis*, *Drosera intermedia*, *Drosera rotundifolia*, *Dulichium arundinaceum*, *Eleocharis robbinsii*, *Eleocharis tricostata*, *Eleocharis tuberculosa*, *Eriocaulon aquaticum*, *Eupatorium leucolepis*, *Eupatorium perfoliatum*, *Fimbristylis autumnalis*, *Fuirena pumila*, *Gratiola aurea*, *Hypericum adpressum*, *Hypericum mutilum*, *Isoetes echinospora*, *Juncus militaris*, *Juncus pelocarpus*, *Lipocarpus micrantha*, *Lobelia dortmanna*, *Najas flexilis*, *Nymphaea odorata*, *Nymphoides cordata*, *Panicum verrucosum*, *Pontederia cordata*, *Potamogeton illinoensis*, *Potamogeton perfoliatus*, *Proserpinaca pectinata*, *Rhexia virginica*, *Rhynchospora inundata*, *Rhynchospora macrostachya*, *Rhynchospora scirpoides*, *Rotala ramosior*, *Sabatia kennedyana*, *Sagittaria graminea*, *Sagittaria latifolia*, *Schoenoplectus etuberculatus*, *Scleria reticularis*, *Sparganium angustifolium*, *Utricularia cornuta*, *Utricularia geminiscapa*, *Utricularia gibba*, *Utricularia resupinata*, *Vallisneria americana*, *Viola lanceolata*, *Xyris difformis*, *Xyris smalliana*.

Use by wildlife: The starchy tubers of various *Sagittaria* species are eaten by beavers (Mammalia: Castoridae: *Castor canadensis*), muskrats (Mammalia: Cricetidae: *Ondatra zibethicus*), and waterfowl (Aves: Anatidae). The plants (species unspecified) host many insects (Insecta), including beetles and weevils (Coleoptera: Chrysomelidae: *Donacia caerulea*, *Galerucella nymphaea*, *Plateumaris rufa*; Curculionidae: *Brachybamus electus*, *Listronotus turbatus*, *Onychylis angustus*, *O. nigrirostris*), flies (Diptera: Ephydriidae: *Hydrellia deceptor*, *H. griseola*), and larval moths (Lepidoptera: Noctuidae: *Acronicta oblongata*, *Argyrogramma verruca*, *Bellura obliqua*, *Homophoberia cristata*). The seeds of *Sagittaria ambigua* reportedly are eaten by birds (Aves). The flowers of *S. australis* are visited (and pollinated) primarily by generalist bees (Insecta: Hymenoptera: Apidae: *Ceratina*; Halictidae: *Augochlora*, *Lasioglossum*). The tubers are eaten by weevils (Insecta: Coleoptera: Curculionidae: *Listronotus caudatus*, *L. echinodori*); the flowers are attacked by *L. appendiculatus*. The plants provide cover and shade for small fish. The nutlets of *S. calycina* are eaten by canvasbacks (Aves: Anatidae: *Aythya valisineria*) and by other ducks (Aves: Anatidae: *Anas*) in low to locally high quantities. *Sagittaria cristata* is colonized by various freshwater sponges (Bryozoa: Cristatellidae: *Cristatella mucedo*; Fredericellidae: *Fredericella sultana*; Paludicellidae: *Paludicella articulata*; Pectinatellidae: *Pectinatella magnifica*; Plumatellidae: *Hyalinella punctata*, *Plumatella emarginata*, *P. repens*). It is a minor food item for ducks (Aves: Anatidae). The foliage of *S. cuneata* contains 21.8% crude protein, 17.3% crude fiber and is high in K, Fe, and Mo. The plants are grazed by muskrats (Mammalia: Cricetidae: *Ondatra zibethicus*) and domestic livestock (Mammalia: Bovidae) including cattle (*Bos taurus*) and sheep (*Ovis aries*). The achenes and tubers are eaten by various waterfowl (Aves: Anatidae) including Canada geese (*Branta canadensis*), mallards (*Anas platyrhynchos*), and wood ducks (*Aix sponsa*). The plants also are host to weevils (Insecta: Coleoptera: Curculionidae: *Listronotus rubt-zoffi*). They have been found to harbor more than 39 million nitrifying bacteria. The flower heads, leaves, and roots of *S. engelmanniana* are fed upon by weevils (Insecta: Coleoptera: Curculionidae: *Listronotus appendiculatus*, *L. neocallosus*, *L. sordidus*). Various weevils (Insecta: Coleoptera: Curculionidae) also are hosted by *S. graminea* (*Listronotus neocallosus*), *S. filiformis* (*L. neocallosus*) and *S. lancifolia* (*Listronotus cryptops*). The foliage of *S. graminea* is eaten by grass carp (Vertebrata: Osteichthyes: Cyprinidae: *Ctenopharyngodon idella*) and nutria (Mammalia: Myocastoridae: *Myocastor coypus*); its tubers (15.9% crude protein; 16.1% crude fiber) are consumed by canvasbacks (Aves: Anatidae: *Aythya valisineria*) and wood ducks (Aves: Anatidae: *Aix sponsa*) during winter months. The plants are categorized overall as a good food for ducks (Aves: Anatidae). In Asia, *S. guayanensis* is fed to pigs (Mammalia: Suidae: *Sus scrofa*) as fodder. The leaves of *S. kurziana* support large populations of larval flies (Insecta: Diptera: Chironomidae) and provide habitat for the Ichetucknee siltsnail (Mollusca: Gastropoda: Hydrobiidae: *Floridobia mica*). *Sagittaria*

lancifolia is a host of smut (Fungi: Basidiomycota: Doassansiaceae: *Doassansia sagittariae*; *Doassansiopsis deformans*). The foliage is used for oviposition by Florida applesnails (Mollusca: Gastropoda: Ampullariidae: *Pomacea paludosa*), and is eaten by grasshoppers (Insecta: Orthoptera: Romaleidae: *Romalea microptera*) and white-tailed deer (Mammalia: Cervidae: *Odocoileus virginianus seminolus*); the flower buds (primarily the males) are eaten by weevils (Insecta: Coleoptera: Curculionidae: *Listronotus appendiculatus*). *Sagittaria latifolia* is eaten by moose (Mammalia: Cervidae: *Alces americanus*) and white-tailed deer (Mammalia: Cervidae: *Odocoileus virginianus*); its tubers are consumed by pintail ducks (Aves: Anatidae: *Aythya valisineria*) and other waterfowl. The seeds and foliage are eaten by American wigeons (Aves: Anatidae: *Anas americana*) and occasionally by bullfrogs (Amphibia: Ranidae: *Rana catesbeiana*). The plants host numerous insects (Insecta), including aphids (Homoptera: Aphididae: *Rhopalosiphum nymphaeae*), beetles and weevils (Coleoptera: Chrysomelidae: *Donacia caerulea*, *D. subtilis*; Coccinellidae: *Coleomegilla maculata*; Curculionidae: *Hyperodes solutus*, *Listronotus appendiculatus*, *L. delumbis*, *L. echinodori*, *L. squamiger*, *Lixellus lutulentus*), caddis flies (Trichoptera: Lemnephilidae: *Pycnopsyche*; Leptoceridae: *Leptocerus americanus*, *Nectopsyche*, *Triaenodes abus*, *T. ignitus*, *T. injustus*, *T. marginatus*; Polycentropodidae: *Neureclipsis crepuscularis*, *Polycentropus*), flies (Diptera: Itonididae), grasshoppers (Orthoptera: Acrididae: *Paroxya atlantica*, *P. clavuliger*, *Romalea microptera*), leafhoppers (Homoptera: Cicadellidae: *Draeculacephala*), moths (Lepidoptera: Crambidae: *Munroessa icciusalis*, *Paraponyx obscuralis*; Noctuidae: *Cryptocala acadiensis*), and stink bugs (Hemiptera: Pentatomidae: *Amaurochrous cinctipes*). The flowers are visited by a variety of potentially pollinating insects (Insecta), including bees (Hymenoptera: Apidae: *Apis mellifera*, *Bombus*, *Ceratina*; Halictidae: *Augochlora*, *Halictus*, *Lasioglossum*), beetles (Coleoptera: Cantharidae: *Chauliognathus pennsylvanicus*; Chrysomelidae: *Diabrotica undecimpunctata*; Coccinellidae: *Coleomegilla maculata*), butterflies (Lepidoptera: Hesperidae: *Ancyloxypha numitor*), flies (Diptera: Syrphidae: *Allograpta*, *Criorhina*, *Eristalis*, *Heliophilus*; Tachinidae: *Linnaemya*), and wasps (Hymenoptera: Vespidae: *Euodynerus*). The foliage is colonized by freshwater sponges (Paludicellidae: *Paludicella articulata*; Plumatellidae: *Plumatella repens*). *Sagittaria longiloba* is eaten by sandhill cranes (Aves: Gruidae: *Grus canadensis*) and waterfowl (Aves: Anatidae). The seeds are eaten by ducks (Aves: Anatidae: *Anas platyrhynchos*) and killdeer (Charadriidae: *Charadrius vociferus*). The plants are fed on by weevils (Insecta: Coleoptera: Curculionidae: *Listronotus manifestus*, *L. scapularis*). *Sagittaria platyphylla* is eaten by feral swine (Mammalia: Suidae: *Sus scrofa*), nutria (Mammalia: Myocastoridae: *Myocastor coypus*), and white-tailed deer (Mammalia: Cervidae: *Odocoileus virginianus*). The leaf axils provide refuge for larval dragonflies (Insecta: Odonata: Libellulidae: *Pachydiplax longipennis*), and emergent portions of the plant are used as mating sites by adult

dragonflies (Insecta: Odonata: Coenagrionidae *Telebasis salva*). The foliage provides an oviposition site for fountain darters (Osteichthyes: Percidae: *Etheostoma fonticola*), cover and habitat for fish (Osteichthyes: Cyprinidae: *Notropis chalybaeus*), and serves as an attachment substrate for ciliophorans (Protozoa: Peritrichida: Operculariidae: *Opercularia wallgreni*). The large (e.g., 2.5 cm) tubers (19.9% crude protein; 56.1% total digestible nutrients) provide an important food for turtles (Reptilia: Emydidae: *Pseudemys texana*) and various waterfowl (Aves: Anatidae), including canvasbacks (*Aythya valisineria*), gadwalls (*Anas strepera*), mallards (*Anas platyrhynchos*), pintails (*Anas acuta*), and ring-necked ducks (*Aythya collaris*). The foliage of *S. rigida* (14.78% crude protein; 23.69% crude fiber; Fe: 2083 ppm) is eaten by muskrats (Mammalia: Cricetidae: *Ondatra zibethicus*). The plants are inhabited by beetles (Insecta: Coleoptera: Chrysomelidae: *Donacia caerulea*). The tubers (11.6% crude protein; 2.0% crude fiber; 0.6% crude fat) are consumed by canvasback ducks (Aves: Anatidae: *Aythya valisineria*) and tundra swans (Aves: Anatidae: *Cygnus columbianus*). The seeds and tubers of *S. subulata* are consumed occasionally by waterfowl (Aves: Anatidae). *Sagittaria teres* is eaten by pintail ducks (Aves: Anatidae: *Anas acuta*).

Economic importance: food: The tubers of *Sagittaria* species are rich in starch and were eaten by Native Americans and European settlers, who boiled them to temper the bitter taste imparted by their milky sap. Tubers of *S. cuneata* were eaten by the Klamath and Menominee, Montana, Ojibwa, and Paiute tribes. *Sagittaria guayanensis* is eaten as a rainy season vegetable in Laos. *Sagittaria latifolia* contains 13.7% crude protein. Its tubers were eaten by the Chippewa, Cocopa, Dakota, Klamath, Lakota, Meskwaki, Omaha, Pawnee, Pomo, Potawatomi, Thompson, and Winnebago tribes, who often stored them as a winter food; **medicinal:** The Cheyenne and Chippewa administered *S. cuneata* medicinally for various ailments. The plants were regarded as an analgesic by the Navajo, and the corms were eaten by the Ojibway to treat indigestion. Decoctions prepared from *Sagittaria guayanensis* are used in parts of Asia as a body wash ('Banarbhega') to control fever; the plant juices (mixed with honey) are drunk to facilitate recovery following childbirth. *Sagittaria lancifolia* was used by the Florida Seminoles to treat alligator bites. Extracts from the plant have been found to inhibit several Bacteria (Pseudomonadaceae: *Pseudomonas aeruginosa*; Staphylococcaceae: *Staphylococcus aureus*). Infusions of *S. latifolia* were used by the Cherokee to treat fevers (leaves) and by the Chippewa as a remedy for gastrointestinal disorders (roots). The Iroquois used infusions from the plant for treating rheumatism and fabricated various compound decoctions as remedies for boils, constipation, and itching. The species also was used medicinally by the Lakota and the Potawatomi, the latter applying a poultice from the corms to heal wounds; **cultivation:** Several *Sagittaria* species are grown as ornamental water garden plants. 'Benni' is a patented cultivar of *S. australis* (US PP12,198 P2); 'Crushed Ice' is a cultivar of *S. graminea*. *Sagittaria lancifolia* and *S. montevidensis* are used as water garden ornamentals. *Sagittaria*

platyphylla is distributed occasionally as an aquarium plant, whereas *S. subulata* is a popular decorative aquarium species; **misc. products:** *Sagittaria lancifolia* and *S. latifolia* have been used in wetland restoration projects. The Iroquois used a root decoction of *S. latifolia* as a medicine to improve corn yields; **weeds:** *Sagittaria guayanensis* is a rice-field weed in Louisiana and also in Brazil and Peru. It has developed resistance to ALS inhibitor herbicides (bensulfuron-methyl) in Malaysia; bensulfuron-methyl resistant strains of *S. montevidensis* occur in California. *Sagittaria latifolia* has been reported as a rice-field weed in California; *S. longiloba* is a common rice-field weed in the western United States. *Sagittaria montevidensis* is a nuisance rice-field weed in South America; herbicide resistant strains have evolved (various ALS inhibitors) in Australia, Brazil, China, and the United States (California). *Sagittaria sanfordii* is regarded as a rice-field weed in California; **nonindigenous species:** *Sagittaria graminea* has been introduced to Washington state. It is invasive in China and has been introduced to Australia and France, where it also is problematic. *Sagittaria guayanensis* was introduced to Louisiana from tropical America. *Sagittaria latifolia* has been introduced widely throughout Europe. It is possible that *S. longiloba* was introduced to California, where nearly all of the records are associated with rice fields. *Sagittaria montevidensis* has been introduced to Australia, China, and the southeastern United States, where it has been distributed commercially as an ornamental; it also has been introduced to California, reportedly as an inadvertent consequence of disposed shipping ballast. *Sagittaria platyphylla* is nonindigenous to Australia and European Russia. *Sagittaria rigida* has been introduced to California, Idaho, and Washington in the United States, and to Ireland and the United Kingdom in Europe. *Sagittaria subulata* has been introduced to the British Isles.

Systematics: *Sagittaria* remains in need of taxonomic revision, with even basic species boundaries yet to be determined reliably. There is still some debate whether to subdivide the genus by excluding *Lophotocarpus*, which contains those annual species having perfect flowers with hypogynous stamens. Because the *Lophotocarpus* group resolves phylogenetically as the sister clade to the remainder of *Sagittaria* (Figure 1.7), either taxonomic disposition could be reconciled. In either case, *Sagittaria* appears to be monophyletic, with *Astonia*, *Limnophyton*, and *Wiesneria* among its most closely related genera (e.g., Figures 1.3 and 1.7). Several species (which retain OBL designations) are now regarded as various synonyms. *Sagittaria chapmanii* and *S. weatherbiana* are treated as subspecies of *S. graminea*. Although each taxon appears to be distinct phylogenetically (Figure 1.7), the nuclear data used to construct that tree do not exclude the possibility that *S. chapmanii* and *S. weatherbiana* could be of hybrid origin, with both having *S. graminea* as one parent. This hypothesis is consistent with results from crossing studies, which have shown *S. graminea* to be highly interfertile with *S. isoetiformis* (with which *S. chapmanii* resolves), and at least partially interfertile with *S. fasciculata* (with which *S. weatherbiana* resolves; Figure 1.7). Although *S. chapmanii*

FIGURE 1.7 Interspecific relationships in *Sagittaria* as indicated by analysis of 5S-NTS data (modified from Keener, 2005). North American taxa designated as OBL indicators are highlighted in bold. The species recognized by some authors within the segregate genus *Lophotocarpus* resolve within a clade as indicated. The disjunct placement of *S. graminea* subspecies possibly reflects their hybrid origin (see text).

(= *S. graminea* subsp. *chapmanii*) is interfertile with *S. graminea*, the allozymically determined genetic identity of these two taxa is remarkably low (0.473). Also, in contrast with the typical subspecies, *S. graminea* subsp. *chapmanii* is quite variable genetically. Both factors could be a consequence of hybridization involving more distant species. *Sagittaria graminea* is well isolated reproductively from *S. cristata* and *S. teres*. *Sagittaria spatulata* is treated as a synonym of *S. calycina*. Although regarded by some authors as a synonym of *S. montevidensis*, *S. calycina* is retained here as a distinct species in accordance with its unique morphological features and genetic distinctness from the former (e.g., Figure 1.7). It seems clear that *S. montevidensis* and *S. calycina* should not be treated as synonyms. However, *S. calycina* includes a variety (*S. calycina* var. *spongiosa*), which some authors have distinguished as *S. spatulata*. In any case, both are closely related

sister taxa (Figure 1.7). *Sagittaria macrocarpa* has been recognized as a synonym of *S. fasciculata*; however, morphological and genetic evidence (e.g., Figure 1.7) indicate its status as a distinct species, which has been accepted here (but does not preclude the possibility that *S. fasciculata* might be of hybrid origin). DNA sequence data resolve *S. macrocarpa* as the sister species of *S. cristata* (Figure 1.7). Though *S. cuneata* and *S. latifolia* bear a superficial morphological similarity, they are distinct genetically (e.g., by both isozyme and DNA markers). Furthermore, crossing studies have demonstrated that strong infertility barriers exist among *S. australis*, *S. brevirostra*, *S. cuneata*, *S. engelmanniana*, and *S. latifolia*, which all are well isolated reproductively. Allozyme data indicate that *S. isoetiformis* and *S. teres* are a closely related progenitor-derivative species pair. Specimens of *S. filiformis*, *S. kurziana*, and *S. subulata* often show a history of confused identifications, which has been attributed to extensive phenotypic plasticity relating to water depth. Observations of extensive variation in leaf morphology have raised doubts regarding the distinctness of these three taxa, which are separated by relatively minor fruit features and share a close phylogenetic interrelationship (Figure 1.7). Furthermore, because artificial hybridizations between *S. filiformis* and *S. kurziana* (Figure 1.7) have produced fertile F_1 offspring, the recognition of these three taxa at the species level should be re-evaluated by additional genetic studies.

Distribution: *Sagittaria cuneata* is widespread throughout northern North America; *S. graminea* occurs in eastern North America and is disjunct in Washington State; *S. latifolia* is widespread in eastern North America and sporadic in the west. *Sagittaria australis*, *S. brevirostra*, *S. calycina*, and *S. platyphylla* occur primarily in the eastern United States; *S. rigida* occurs in the eastern United States and southeastern Canada, with nonindigenous stations in Idaho and Washington; *S. cristata* occurs throughout the upper Great Lakes region. *Sagittaria engelmanniana*, *S. filiformis*, *S. isoetiformis*, and *S. lancifolia* occur along the southeastern Coastal Plain of the United States. *Sagittaria subulata* occurs along the eastern and southeastern coastal areas of the United States; *S. teres* is restricted to the coastal plain of the northeastern United States. *Sagittaria longiloba* occurs in the southwestern United States, and extends into Mexico and Central America. Species with more restricted distributions include *S. ambigua* (Illinois, Indiana, Kansas, and Missouri), *S. demersa* (New Mexico and elsewhere restricted to a small region of central Mexico), *S. fasciculata* (North and South Carolina), *S. kurziana* (Florida), *S. papillosa* (Arkansas, Louisiana, Oklahoma, and Texas), *S. macrocarpa* (endemic to the Sandhills Region of the Carolinas), *S. sanfordii* (endemic to California), and *S. secundifolia* (Alabama and Georgia). *Sagittaria guayanensis* has been introduced to Louisiana from the New World tropics; *S. montevidensis* was introduced to the southeastern United States and to California.

References: Abbott & Scott, 2001; Adair et al., 2012; Adams & Godfrey, 1961; Ainsworth, 2006; Alves Pagotto et al., 2011; Atwood, 1950; Badzinski et al., 2006; Baldwin & Mendelssohn, 1998; Baskin & Baskin, 1998; 2015; Baxter, 2007; Beal, 1977;

Beal et al., 1982; Bowes et al., 2002; Bowker, 1991; Bowyer et al., 2005; Boyd & McGinty, 1981; Broadhurst & Chong, 2011; Brewis, 1975; Brown, 1942; Bushnell, Jr., 1966; Calhoun & King, 1998; Chafin, 2007; Colle et al., 1978; Collon & Velasquez, 1989; Cooperrider, 1955; Coulter, 1955; Craven & Hunt, 1984; Crocker, 1907; Crow, 1969; Cruden, 1988; Das et al., 2006; Davis, 1993; Delesalle & Blum, 1994; De Oliveira et al., 2015; DeVlaming & Proctor, 1968; Diamond, 2016; Dirrigl, Jr. & Mohlenbrock, 2012; DiTomaso & Healy, 2003; Dorken & Barrett, 2003; 2004a; 2004b; 2004c; Dorken et al., 2002; Edwards & Sharitz, 2000; 2003; Emerson, 1921; Enser & Caljouw, 1989; Everitt et al., 1999; Fassett, 1957; Ferren, Jr., 1973; Ferren, Jr. & Schuyler, 1980; Fields et al., 2003; Fraser et al., 1980; Frost & Hicks, 2012; Glaettli & Barrett, 2008; Gleason et al., 2003; Gluck, 1927; Godfrey & Adams, 1964; Gonzalez et al., 1983; Grabowski, 2001; Grace & Ford, 1996; Graves, 1984; Grier, 1916; Hamel & Parsons, 2001; Harms & Grodowitz, 2009; Harrison & Knapp, 2010; Harvey & Haines, 2003; Hauber & Lege, 1999; Haukos & Smith, 1997; 2001; Haynes & Hellquist, 2000a; Haynes & Holm-Nielsen, 1994; Haynes & Les, 2004; Heilman & Carlton, 2001; Hellquist & Crow, 1981; Hendricks & Goodwin, Jr., 1952; Hestand & Carter, 1974; Hoagland & Buthod, 2007; Hoagland et al., 2001; Hohman et al., 1990; Hooper, 1951; Howard & Mendelssohn, 1995; Hoyer et al., 1996; Huang, 2003; Huang et al., 2000; Hussner, 2012; Jacono, 2001; 2002; Johnson & Rohwer, 2000; Kandalepas et al., 2010; Kasselmann, 2003; Kaul, 1976; 1979; 1991; Kenow & Lyon, 2009; Kissoon et al., 2013; 2015; Knapton & Pauls, 1994; Koch, 1970; Korschgen & Moyle, 1955; Kral, 1982; Labisky et al., 2003; Lagueux et al., 1995; Laidig & Zampella, 1996; Landers et al., 1977; Lavoie et al., 2003; Leck & Graveline, 1979; Lehman et al., 2009; Lehtonen, 2009; Les & Tippet, 2013; Linn et al., 1975; Little, Jr., 1938; Lot et al., 2002; Low & Bellrose, Jr., 1944; Luken & Thieret, 2001; MacGillivray, 1903; MacRoberts & MacRoberts, 2010; Manandhar, 1985; Mancera et al., 2005; Manolis, 2016; Marburger, 1993; Martin & Shaffer, 2005; Mason, 1957; Mattson et al., 1995; Matulewich & Finstein, 1978; McAtee, 1939; McGaha, 1952; McKee & Mendelssohn, 1989; McPherson & Paskewitz, 1984; Middleton, 1989; Mitchell, 1926; Mohr, 1901; Morrone, 2013; Moyle, 1945; Muenchow, 1998; Muenchow & Delesalle, 1992; 1994; Mulhouse, 2004; Nakamura & Nelson, 2001; Newberry, 1991; Norquist, 1990; O'Brien, 1997; Padgett et al., 2004; Pates & Madsen, 1955; Perkin et al., 2012; Perry & Dorken, 2011; Pezeshki et al., 2000; Phillips, 1911; Phillips et al., 2011; Pollux, 2011; Power, 1996; Profous & Loeb, 1984; Quinlan et al., 2008; Reid et al., 2010; Rhodes, 1978; Richards & Ivey, 2004; Robinson & Frye, 1986; Rosen, 2007; Rubtsov, 1975; Sarkissian et al., 2001; Sasser et al., 1995a; Sawyer et al., 2005; Schlickeisen et al., 2003; Schuyler & Gordon, 2002; Shaffer et al., 1992; Schaffner, 1924; Self et al., 1975; Sharitz et al., 2010; Skinner & Telfer, 1974; Sletten & Larson, 1984; Smith, 1895; 1900; Smith & Capinera, 2005; Sneddon & Lamont, 2010; Snyder, 1988; Sorrie et al., 2006; 2007; Stevens, 1957; Strong & Kellogg, 1994; Sugden & Driver, 1980; Sullivan, 1981; Takos, 1947; Terrell et al., 1978; Thieret, 1969; 1970; Thompson &

McKinney, 2006; Tom & Karr, 2013; Turner, 1996; Turner et al., 2012; USFWS, 1983; 2014; Vamosi et al., 2006; Van der Valk & Rosburg, 1997; Van der Valk et al., 2009; Van Drunen & Dorken, 2012; Vidal, 1960; Wallis, 2007; Wang et al., 2006; Wang et al., 2012a; Wellborn & Robinson, 1987; Weller, 1988; Wells & Alexander, 2014; West, 1945; Whetstone et al., 1987; Whyte & Cain, 1981; Wilson, 1937; Wooten, 1970; 1971; 1973a; 1973b; 1978; 1986; Wooten & Brown, 1983; Yanovsky, 1936; Yatskievych & Jenkins, 1981; Zaremba & Lamont, 1993; Zebryk, 2004; Zhang et al., 2010a; 2013a; Zhang et al., 2014a.

Family 2.2. Butomaceae [1]

Although once recognized as a somewhat broader taxon that included members of the former Limnocharitaceae (now merged with Alismataceae), Butomaceae currently are circumscribed as a monotypic family comprising only *Butomus* and the single species *B. umbellatus* (Cronquist, 1981). Phylogenetic analysis of sequence data from the *rbcL* gene provided supportive evidence that Butomaceae were not only distinct from Limnocharitaceae but resolved as the sister group to Hydrocharitaceae rather than Alismataceae, where the limnocharit genera were included (Les et al., 1997a). The same sister-group association of Butomaceae and Hydrocharitaceae has been recovered in many subsequent analyses (see Les & Tippet, 2013), including those incorporating sequence data from complete cpDNA genomes (Ross et al., 2016; Figure 1.2).

This is a fairly distinctive group of aquatics bearing linear, distichous, sheathing leaves that arise from an elongate rhizome, and perfect, hypogynous, trimerous flowers with an apocarpous gynoecium of nectariferous, basally connate, distally unsealed carpels, which mature into follicles; placentation is laminar (Cronquist, 1981). The flowers are arranged in large, showy, determinate umbels, which terminate an elongate, naked scape. Other aspects of the life history, economic uses, etc. are discussed below under the generic treatment.

Butomaceae are indigenous to temperate Eurasia and North Africa, but introduced to North America. One North American genus contains OBL indicators:

2.2.1. *Butomus* L.

2.2.1. *Butomus*

Flowering rush; butome à ombelle

Etymology: after the Greek *bous tomos* ("ox cutting") in reference to the unsuitability of the plant for fodder

Synonyms: none

Distribution: **global:** Africa (northern); Eurasia; North America; **North America:** north central

Diversity: **global:** 1 species; **North America:** 1 species

Indicators (USA): obligate wetland (OBL): *Butomus umbellatus*

Habitat: freshwater; lacustrine, palustrine, riverine; **pH:** 7.3–7.6; **depth:** 0–2.5 m; **life-form(s):** emergent, floating-leaved, or submersed (rosulate) herb

Key morphology: plants stemless, rhizomatous (to 40 cm), emersed, floating-leaved, or submersed; leaves (to 2.7 m)

basal, sessile, sheathed, linear, triangular in section, flattened distally; inflorescence an erect, scapose, umbel (to 25-flow-ered), the scape (to 150 cm) naked, triangular in section; flow-ers (to 2.5 cm) bisexual, pedicellate (to 10 cm), hypogynous, trimerous; tepals (to 11.5 mm) six, pinkish purple, the veins darker; stamens (to 5.5 mm) nine, in two cycles; gynoecium apocarpous (but coherent basally), pistils six, placentation laminar, ovules ~50; follicles (to 1 cm) leathery, beaked

Life history: duration: perennial (bulbils, rhizomes); **asexual reproduction:** bulbils, rhizomes; **pollination:** self; insect; **sexual condition:** hermaphroditic; **fruit:** follicles (infrequent); **local dispersal:** bulbils (water), rhizome frag-ments (water), seeds (gravity, wind); **long-distance disper-sal:** bulbils (water), seeds (birds, water)

Imperilment: 1. *Butomus umbellatus* [G5]

Ecology: general: Monotypic (see next).

2.2.1.1 *Butomus umbellatus* L. is a nonindigenous perennial, which inhabits exposed substrates to relatively deeper waters (typically 0.9–1.3 m but up to 4.5 m) in backwaters (diked), bays, bogs (floating), channels (dried), ditches, flats (river), floodplains, gravel pits, lakes, marshes, meadows, mudflats, ponds (retention), rivers, sand/mud bars, shoals, shores (reced-ing), sloughs, streams, swales, and along the margins of canals, lakes, ponds, reservoirs, rivers, and streams at elevations to 1372 m. Site exposures are open and receive full sunlight. The sites typically are alkaline (e.g., pH: 7.3–7.6; total alkalinity: 55–153 mg l⁻¹). The plants grow as emergent, floating-leaved, or completely submersed life-forms and occur often in swift currents. The biomass peaks at 1.3 m depth and decreases in deeper water. The plants have a strong affinity for coarse sub-strates but occur on clay, clayey sand, gravel, muck, mucky cobble, mud, rock, sand, and silt. Flowering occurs from June to October with fruiting extending from July to October. The flowers of diploids are self-compatible (the triploids being sterile). However, they are protandrous (with a short, initial male phase) and require pollinators to achieve seed set. At the umbel level, the plants are synchronously dichogamous, with nearly three quarters of the female flowers being recep-tive while the male phase is absent. Pollen is shed sequentially from 3 to 11 hr after anthesis and is completely removed from the flowers by 12 hr; the stigmas sequentially become recep-tive at about 15 hr from the onset of anthesis, continuing until about 21 hr after the initial floral opening. Pollen retains high viability for 7 hr, but becomes inviable after 24 hr; wet pollen rapidly loses viability. During the male phase, the dehiscence of anthers is “reversible”; i.e., being able to reclose in wet con-ditions and reopen subsequently (within 13–20 min) under dryer conditions. The insect (Insecta) pollinators include bees (Hymenoptera: Apidae) and flies (Diptera: Syrphidae). The highest floral visitation rates occur on sunny days when the flowers are dry. Polymorphic gynoecium color (pink or white) has been observed in China, where pink morphs (the com-mon type) produce more pollen and ovules (and exhibit cor-respondingly higher seed production) than the white morphs. A single plant can produce 35,000 small (0.16 mg) seeds on average, with larger plants yielding an estimated 500 fruits and 258,000 seeds. Typically, the seeds fall directly on the

ground beneath the maternal plant or are dispersed locally by wind; however, they are buoyant and can remain afloat for several days, which facilitates longer distance dispersal by water. The seeds also are believed to be dispersed by becom-ing entangled within the feathers of birds (Aves). The seeds reportedly germinate adequately (20–50%) after being cold stratified for several months in water and then subjected to an 8/16-hr light/dark regime at 25°C/10°C. They require light for germination, which also has been achieved successfully for stratified seeds incubated at 20°C–30°C under long-day conditions. The seeds are known to retain up to 68% viability after 5 years of storage in cold water. The seedlings grow well in cultivation under a 14/10 hr, 30°C/20°C, light/temperature regime (70% relative humidity). The seedlings grow slowly, are capable of floatation, and require at least 2 months of unshaded conditions in order to establish. Vegetative bulbils can replace flowers in the inflorescence and also develop from the rhizomes; either can function as asexual propagules. There are somewhat conflicting reports regarding the production of vegetative structures relative to different cytotypes. In native European populations, triploid plants reproduce primarily by vegetative reproduction involving prolific, detachable, rhizome buds and the development of inflorescence bulbils, which both are capable of water dispersal; the diploids produce fewer rhi-zome buds and lack floral bulbils. Individual plants consis-tently can produce upward of 200 vegetative bulbils annually. However, in the introduced North American plants, diploid plants were found to invest highly in sexual structures as well as in clonal bulbils, whereas the triploids were sterile and did not produce vegetative bulbils. Plants in introduced regions also produce a greater number of sexual inflorescences and asexual bulbils and invest more biomass in each reproductive mode than those in native populations, which may account for their successful invasion ability. The bulbils appear in mid-August when water temperatures approach 22.5°C and can be produced by plants less than 25 cm in length. They reach their highest density (averaging 200–300 buds m⁻²) at depths from 0.3 to 1.6 m. The plants spread rapidly during periods of low water, which results in more substrate for colonization by sexual and vegetative propagules. The average ramet den-sity can approach 100 m⁻². Genetic studies have confirmed that reduced variability and fewer genets characterize the introduced North American populations, which presumably underwent a severe bottleneck at their time of introduction. North American plants emerge from May to June and reach peak DM biomass by late July, which can exceed 108 g m⁻².

Reported associates (North America): *Alisma subcordatum*, *Asclepias incarnata*, *Bidens cernuus*, *Bidens trichospermus*, *Bolboschoenus fluviatilis*, *Carex cristatella*, *Ceratophyllum demersum*, *Chara*, *Drepanocladus*, *Echinochloa crus-galli*, *Eleocharis erythropoda*, *Eleocharis obtusa*, *Elodea canadensis*, *Glyceria grandis*, *Glyceria striata*, *Heteranthera dubia*, *Hippuris vulgaris*, *Hydrocharis morsus-ranae*, *Iris pseudacorus*, *Iris virginica*, *Leersia oryzoides*, *Lemna minor*, *Lindernia dubia*, *Ludwigia palustris*, *Ludwigia polycarpa*, *Lycopus virginicus*, *Lythrum salicaria*, *Mentha arven-sis*, *Myriophyllum hippuroides*, *Myriophyllum sibiricum*,

Myriophyllum spicatum, *Najas flexilis*, *Nitella*, *Nuphar advena*, *Nuphar variegata*, *Nymphaea odorata*, *Nymphoides peltata*, *Peltandra virginica*, *Persicaria amphibia*, *Persicaria lapathifolia*, *Phalaris arundinacea*, *Phragmites australis*, *Poa palustris*, *Pontederia cordata*, *Populus angustifolia*, *Populus deltoides*, *Potamogeton amplifolius*, *Potamogeton crispus*, *Potamogeton foliosus*, *Potamogeton gramineus*, *Potamogeton illinoensis*, *Potamogeton nodosus*, *Potamogeton praelongus*, *Potamogeton pusillus*, *Potamogeton richardsonii*, *Potamogeton robbinsii*, *Potamogeton zosteriformis*, *Potentilla anserina*, *Ranunculus aquatilis*, *Ranunculus flabellaris*, *Ricciocarpus*, *Rorippa aquatica*, *Rosa woodsii*, *Rumex altissimus*, *Rumex crispus*, *Rumex verticillatus*, *Sagittaria cuneata*, *Sagittaria latifolia*, *Salix exigua*, *Schoenoplectus acutus*, *Schoenoplectus pungens*, *Schoenoplectus tabernaemontani*, *Scirpus atrovirens*, *Sparganium androcladum*, *Sparganium eurycarpum*, *Stuckenia pectinata*, *Trapa natans*, *Typha angustifolia*, *Typha latifolia*, *Utricularia macrorhiza*, *Vallisneria americana*, *Xanthium strumarium*, *Zannichellia palustris*, *Zizania aquatica*.

Use by wildlife: The leaves of *Butomus umbellatus* are eaten by muskrats (Mammalia: Cricetidae: *Ondatra zibethicus*), and the bulbils are consumed by blue-winged teal (Aves: Anatidae: *Anas discors*). North American plants also are host to chytrids (Fungi: Blastocladiomycota: Physodermataceae: *Physoderma butomi*), Fungi (Ascomycota: Nectriaceae: *Fusarium oxysporum*; Pestalotiopsidaceae: *Pestalotiopsis guepinii*; Xylariaceae: *Dicyma ovalispora*, *Virgaria nigra*; Basidiomycota: Agaricaceae: *Phoma*), larval caddisflies (Insecta: Trichoptera: Leptoceridae: *Ylodes*; *Ceraclea*, *Oecetis*, *Triaenodes*), larval flies (Insecta: Diptera: Chironomidae: *Chironomus*, *Rheotanytarsus*), and snails (Mollusca: Gastropoda: Lymnaeidae: *Lymnaea stagnalis*; Physidae: *Physa*).

Economic importance: food: The rhizomes and bulbils of *Butomus umbellatus* are high in starch and have been eaten (when dried or roasted) or ground into flour for bread making; **medicinal:** Acetone extracts of *Butomus umbellatus* are inhibitory to some microbes (Bacteria: Bacillaceae: *Bacillus subtilis*); **cultivation:** *Butomus umbellatus* is grown as an ornamental water garden plant and has been distributed under the cultivar names 'Rosenrot' and 'Schneeweisschen'; **misc. products:** The Iroquois made a decoction using whole plants of *Butomus*, which they added to livestock feed as a treatment for parasitic worms; **weeds:** *Butomus umbellatus* is a weed of North American wetlands, where it has been described as being more invasive than purple loosestrife (Lythraceae: *Lythrum salicaria*); **nonindigenous species:** *Butomus umbellatus* is nonindigenous to the New World, introduced to North America sometime prior to 1897. Morphological and genetic data indicate that there have been several separate introductions of the species from different regions of Eurasia. The first introductions presumably resulted from the seed-contaminated ballast and packing materials disposed by ships along the St. Lawrence River. Introductions have continued, primarily via the escape of horticultural specimens.

Systematics: Molecular phylogenetic analyses consistently resolve the monotypic *Butomus* as the sister group of Hydrocharitaceae (e.g., Figures 1.2 and 1.3). Being monotypic, the genus also is monophyletic. Although two species have been proposed by some researchers, most evidence (including transplant studies) indicates that there is a single but cytotypically variable species. The base chromosome number of *Butomus* is $x=13$. *Butomus umbellatus* has diploid ($2n=26$) and triploid ($2n=39$) cytotypes, which both occur in New World populations. Triploid populations are believed to have multiple origins. All coding regions for the chloroplast and mitochondrial genomes of *B. umbellatus* have been sequenced, providing ample data for phylogenetic studies. *Butomus* is not known to hybridize.

Comments: *Butomus umbellatus* occurs throughout central North America, north of the glacial maxima.

References: Anderson et al., 1974; Barrett et al., 2008; Bhardwaj & Eckert, 2001; Brown & Eckert, 2005; Core, 1941; Countryman, 1970; Cuenca et al., 2013; Delisle et al., 2003; Eckert et al., 2000; Fernald & Kinsey, 1943; Fernando & Cass, 1996; Gunderson et al., 2016; Harms & Shearer, 2015; Haynes, 2000a; Hroudová & Zákavský, 1993; 2003; Hroudová et al., 2004; Huang & Tang, 2008; Les & Mehrhoff, 1999; Les & Tippet, 2013; Li et al., 2012; Lohammar, 1954; Lui et al., 2005; Madsen et al., 2016; Maki & Galatowitsch, 2004; Muenscher, 1936; Özbay & Alim, 2009; Ross et al., 2016; Salisbury, 1976; Sparrow, 1974; Stuckey, 1968; Turnage et al., 2012.

Family 2.3. Hydrocharitaceae [17]

With approximately 127 entirely aquatic species, Hydrocharitaceae are among the most diverse hydrophyte families. Every member of the group is designated as an OBL indicator throughout North America. Although not large in terms of species, the family contains an impressive assortment of growth forms (emergent, floating-leaved, free-floating, submersed), habits (annual, perennial, rosulate, vitatte), and pollination systems (anemophily, entomophily, epiphytically, hypohydrophily, self-pollination). It is the only known angiosperm family to contain an unusual water-mediated pollination system, which involves detached, free-floating, male flowers. Moreover, it is one of only three angiosperm families to contain "seagrasses" (i.e., angiosperms adapted marine habitats) as well as freshwater species. Leaf and floral morphology are equally diverse.

Various phylogenetic studies (e.g., Les & Haynes, 1995; Les & Tippet, 2013; Les et al., 1993; 1997c; 2006a; Petersen et al., 2006; Ross et al., 2016; Shaffer-Fehre, 1991) have clarified the circumscription of the family to include the former Najadaceae, whose highly reduced morphology has made it difficult to place among other alismatid monocots. All of these studies, which encompass morphological as well as DNA sequence data (from mitochondrial, nuclear, and plastid genomes), have consistently supported the merger of Najadaceae and Hydrocharitaceae as a single clade. Similar lines of evidence (e.g., Figures 1.2 and 1.3) support Butomaceae as the sister group.

Economically, the family is important as a source of ornamental water garden and aquarium plants, which are represented by a large number of genera. For decades, introductory botany courses have used *Egeria densa* as a “classic example” for illustrating the phenomenon of cytoplasmic streaming. Many species provide food and cover for a variety of wildlife. The three marine genera (*Enhalus*, *Halophila*, and *Thalassia*) are of particular importance to the ecology of coastal marine habitats. However, a number of genera (e.g., *Egeria*, *Hydrilla*, *Hydrocharis*, *Lagarosiphon*, *Najas*) also include noxious, weedy species, which have seriously disrupted the ecology of many freshwater systems. In North America, all such cases represent nonindigenous introductions. Some of the resulting infestations have had significant economic consequences and are responsible for millions of dollars in annual expenditures directed at their control.

Eleven genera occur in North America and all contain OBL indicators:

- 2.3.1. *Blyxa* Noronha ex Thouars
- 2.3.2. *Egeria* Planch.
- 2.3.3. *Elodea* Michx.
- 2.3.4. *Halophila* Thouars
- 2.3.5. *Hydrilla* Rich.
- 2.3.6. *Hydrocharis* L.
- 2.3.7. *Limnobium* Rich.
- 2.3.8. *Najas* L.
- 2.3.9. *Ottelia* Pers.
- 2.3.10. *Thalassia* Banks & Sol. ex K.D. Koenig
- 2.3.11. *Vallisneria* L.

2.3.1. *Blyxa*

Bamboo plant, blyxa

Etymology: thought to be derived from the Greek *blyzo* (“to flow”), in reference to the habitat

Synonyms: *Diplosiphon*; *Enhydrias*; *Hydrilla* (in part); *Hydrolirion*; *Hydrotrophus*; *Saivala*; *Vallisneria* (in part)

Distribution: **global:** Africa; Asia; Australia; North America*; **North America:** southern United States

Diversity: **global:** 12 species; **North America:** 1 species

Indicators (USA): obligate wetland (OBL): *Blyxa aubertii*

Habitat: brackish, freshwater; lacustrine; **pH:** 6.0–7.4; **depth:** <1 m; **life-form(s):** submersed (rosulate)

Key morphology: stems (to 3 cm) cormose; leaves (to 60 cm) basal, submersed, linear, sessile, the margins finely serrate; inflorescence solitary, peduncled (to 50 cm) or sessile (rarely), with flattened spathe; flowers (to 15 cm) bisexual, trimerous, emersed (then chasmogamous) or submersed (then cleistogamous); sepals (to 10 mm) green; petals (to 17 mm) linear, white or reddish; stamens (to 5.8 mm) 3; capsules (to 80 mm) terete, cylindrical, 1-locular, style single, stigmas (to 15 mm) linear; seeds (to 1.8 mm) numerous, the surface smooth or with up to 12 warty ridges

Life history: **duration:** annual (fruits/seeds); **asexual reproduction:** none; **pollination:** autogamy; **sexual condition:** hermaphroditic; **fruit:** capsules (common); **local dispersal:** seeds (water); **long-distance dispersal:** seeds (birds)

Imperilment: 1. *Blyxa aubertii* [GNR]

Ecology: general: All *Blyxa* species are submersed, obligately aquatic plants, with only their flowers emerging from the water during sexual reproduction. The species include rosulate or vittate annuals and perennials, with the latter developing stolons. The flowers can be bisexual or unisexual (then arranged dioeciously). The bisexual flowers are either emergent and chasmogamous or submersed and cleistogamous (when growing in deeper water), with both types being highly autogamous. The unisexual flowers are emergent and are pollinated by insects (Insecta: Diptera; Odonata). The seeds are smooth or spiny (sometimes variable within a species), with the latter capable of tangling together and then being dispersed as a larger unit. Local dispersal occurs by water and probably over greater distances by animal vectors (presumably by seeds attached in adhering mud). The seeds are known to be eaten by birds (Aves), but it has not determined whether they remain viable after passage through their digestive tract. Large seed banks can develop in some species. The highest seed germination occurs on the sediment surface.

2.3.1.1. *Blyxa aubertii* Rich. is an annual which grows in borrow pits, lakes (artificial), pools, and rice fields at elevations to 70 m. In North America, the plants occur primarily in turbid waters (to 91 cm depth), which are associated with anthropogenically disturbed habitats. In portions of the native range, the waters are circumneutral (pH: 6.0–7.4) and often are characterized by iron precipitation. The plants have been cultivated successfully in subalkaline waters of medium hardness at 20°C–28°C. In North America, the substrates are nutrient poor and have been described as clay, clay mud, and mud. Flowering in North America has been observed from July to December. The plants can allocate up to 38.1% of their DM biomass to sexual reproduction. The flowers are bisexual, self-compatible, and chasmogamous when emersed but cleistogamous when submersed (which occurs when excessive water depth precludes floral emergence). Because the anthers dehisce before the perianth and the stigmas expand beyond the calyx (pollen is collected as their expansion ensues), both types are highly autogamous and have comparable levels of seed set. During anthesis (lasting just 2 days), little pollen is exposed to potential pollinators, and no biotic pollinators have been observed. Studies of populations in Japan found there to be from 10 to 71 flowers/plant, 45.3 seeds/fruit, and 92.9% seed set on average. Individual plants are capable of producing from 340 to 4224 seeds, with larger plants producing higher seed numbers. Mechanisms of seed dispersal in this species are uncertain, but presumably include water (locally) and adherence to mud on the feet of migrating waterfowl (Aves: Anatidae) over greater distances. Seeds also have been dispersed inadvertently by transport within contaminated rice (Poaceae: *Oryza*) seed. **Reported associates (North America):** *Ceratophyllum demersum*, *Egeria densa*, *Juncus repens*, *Limnophila indica*, *Limnophila xludoviciana*, *Najas minor*, *Nymphaea odorata*, *Potamogeton diversifolius*, *Sagittaria platyphylla*.

Use by wildlife: *Blyxa* seeds are eaten by black-winged stilts (Recurvirostridae: *Himantopus himantopus*). The foliage is eaten by snails (Mollusca: Gastropoda).

Economic importance: food: *Blyxa aubertii* is eaten as a green leaf vegetable in Vietnam; **medicinal:** *Blyxa* is mentioned in Ayurveda medical texts as a universal remedy; **cultivation:** Due to its fragile leaves (and annual habit), *Blyxa aubertii* is cultivated only occasionally as an aquarium plant; **misc. products:** none; **weeds:** *Blyxa aubertii* is a rice-field weed in Asia and North America. Korean populations of *B. aubertii* have become resistant to ALS inhibitor type herbicides; **nonindigenous species:** *Blyxa aubertii* was introduced to Louisiana rice fields around the 1960s.

Systematics: Molecular phylogenetic analyses consistently resolve *Blyxa* and *Ottelia* as sister genera; however, further taxon sampling will be necessary in order to determine whether *Ottelia* is monophyletic and distinct from *Blyxa* (e.g., Figure 1.8). *Blyxa aubertii* possesses a seed amino acid profile similar to that of *B. echinosperma*, which some authors treat as a variety of the former. The two taxa undoubtedly are closely related if not conspecific. The basic chromosome number of *Blyxa* probably is $x=6$. Several anomalous counts ($2n=16$, 24, and 40) have been reported for *B. aubertii* and the cytology of this species requires further clarification. No *Blyxa* hybrids have been reported.

Distribution: In North America, *Blyxa aubertii* currently is known only from Louisiana and Mississippi.

References: Bhunia & Mondal, 2014; Cook, 1996a; 1996b; Cook & Lüönd, 1983; Feitoza et al., 2009; Haynes, 2000b; Jiang & Kadono, 2001; Kasselman, 2003; McNair & Alford, 2014; Ogle et al., 2001; Quattrocchi, 2012; Sullivan, 1981; Thieret et al., 1969.

2.3.2. Egeria

Brazilian elodea, Brazilian waterweed, South American waterweed

Etymology: after the Latin *Aegeria*, a legendary Roman nymph of springs

Synonyms: *Anacharis* (in part); *Elodea* (in part); *Philotria* (in part); *Udora* (in part)

Distribution: global: New World; **North America:** United States, British Columbia (Canada)

Diversity: global: 3 species; **North America:** 2 species

Indicators (USA): obligate wetland (OBL): *Egeria densa*, *E. naias*

Habitat: brackish (coastal), freshwater; lacustrine, riverine; **pH:** 5.2–8.9; **depth:** to 3 m; **life-form(s):** submersed (vittate)

Key morphology: stems (to 3 m+) completely submersed or floating, single or branched, rooted in the substrate (or water); leaves cauline, in whorls (of 4–5+), dense (internodes to 2.4 cm), sessile, the blades (to 40 mm) linear, flat or recurved, the margins finely to strongly serrate, the apex tipped by a single spine; flowers unisexual (plants dioecious); inflorescence (♂) 2–5-flowered, enclosed in a sessile spathe (to 12 mm), the flowers raised above the surface by an elongate peduncle (to 80 mm); sepals 3, green (to 4.4 mm); petals (to 10.5 mm) 3, white, shiny; stamens 9, the filaments (to 4.5 mm) clavate, papillose, yellow, contracted below anthers (to 1.8 mm); pistillate flowers (♀) either absent or smaller than the male flowers; when present, the spathes (to 8 mm) 1–2-flowered, the flowers

FIGURE 1.8 Phylogenetic relationships in Hydrocharitaceae as indicated by a 167-taxon analysis of *rbcl* sequence data (adapted from Les & Tippers, 2013). The result is similar to an analysis of full cpDNA data (Ross et al., 2016) by resolving four distinct clades corresponding to subfamilies Anacharidoideae, Hydrilloideae, Hydrocharitoideae, and Stratiotoideae; however, the interrelationships among these clades are resolved somewhat differently in the two studies. Although the entire family is aquatic, the OBL North American taxa (highlighted in bold) are scattered throughout the phylogeny.

raised above the water surface by their elongate hypanthium (to 48+ mm); the petals 3 (to 8.5 mm), white, conspicuous, with 3 orangish or reddish, papillose staminodes (to 2.4 mm); nectaries (3) present; ovary (to 3 mm) inferior, styles (to 3.8 mm) 3, each with 2–4 lobed stigmas, ovules (to 9) erect; capsules (to 14.5 mm) irregularly dehiscent; seeds (to 7.2 mm) beaked (to 3.7 mm), ellipsoidal

Life history: duration: perennial (whole plants); **asexual reproduction:** shoot fragments; **pollination:** insect; **sexual condition:** dioecious; **fruit:** capsules (absent); **local**

dispersal: shoot fragments (water); **long-distance dispersal:** shoot fragments (humans, water)

Imperilment: 1. *Egeria densa* [G5]; *E. naias* [unranked]

Ecology: general: The genus *Egeria* is entirely aquatic, with all species occurring as submersed growth forms where only the flowers emerge above the water surface. The flowers are unisexual and are arranged in a dioecious condition. They are produced almost continuously when water temperatures are within 15°C–25°C. The flowers are nectariferous, scented, and appear to be pollinated by small insects such as flies (Insecta: Diptera). However, in at least one species, the non-indigenous North American material is comprised entirely of male plants, thereby lacking any ability for sexual reproduction. Little is known regarding the seed production or germination requirements of the plants in their indigenous range. In North America, the plants are vegetatively vigorous and exclusively reproduce asexually by the production and spread of vegetative shoot fragments.

2.3.2.1. ***Egeria densa* Planch.** inhabits still or flowing (e.g., 30 cm s⁻¹), tidal or non-tidal, brackish to freshwaters (to 3.0 m; to 7.0 m in its native range) in bayous, canals, channels (drainage), ditches (irrigation), floodplains, lagoons (gravel pit), lakes, ponds (irrigation), pools, puddles, reservoirs, rivers, sloughs, springs, and streams at elevations to 2165 m. The plants can tolerate exposures ranging from full sunlight to deep shade; however, light reduction (e.g., to 25%) has been observed to reduce relative growth rates. The experimentally determined optimal light intensity is only about 108 lumens and the plants do not acclimate well to higher light intensities. The waters span a broad range of acidity (pH: 6.0–8.9; $\bar{x}$: 7.4) and are relatively high in alkalinity ($\bar{x}$: 38.2 mg l⁻¹ CaCO₃) and specific conductance ($\bar{x}$: 184 μ S cm⁻¹), but relatively low in inorganic nitrogen ($\bar{x}$: 100 μ g l⁻¹) and phosphorous ($\bar{x}$: 68 μ g l⁻¹). The plants are particularly susceptible to iron deficiency. Optimal water temperatures range from 16°C to 28°C, but temperatures up to 35°C are tolerated. Fertilization experiments indicate that the plants do not respond positively to increased sediment nutrient levels as do potential competitors such as *Hydrilla* (Hydrocharitaceae). Growth rates and biomass production generally correlate negatively with pH, which is due to the higher concentrations of free CO₂ in more acidic waters. However, the plants are adapted to the lower inorganic carbon levels in waters of higher pH by their ability to use bicarbonate (HCO₃⁻) as an alternative carbon source. They also possess a high-affinity nitrate transporter (NRT₂), which facilitates nitrate uptake, especially by the shoots. Under stressful conditions (high light and temperature), the shoots induce a C4-like photosynthetic mechanism by increasing expression levels of PEP carboxylase and malic enzyme. Studies in the western United States indicate that the lowest total nonstructural carbohydrate reserves (35–51% starch) occur from March to June. The substrates include boulders, clay, clay loam, logs (submerged), mud (organic), sand (granite), sandy shell, sandy silt, silt, and silty loam (Congaree). In North America the plants flower from March to November; however, only male plants of this dioecious species have been introduced to the United States, making it

reliant entirely on asexual reproduction. The plants essentially are evergreen and overwinter on the bottom (even under ice cover) as intact, short, dormant shoot fragments or rootstocks (sometimes more than 113 m⁻²), with their vegetative growth resuming when water temperatures warm to 10°C–15°C. The starch concentration is highest in leaves (25.4%) and stems (22.6%) during the winter months. Optimal growth (in cultivation) occurs at 20.7°C and the plants are strong competitors in warm water environments (20°C–30°C). Bimodal growth peaks (late spring and fall) have been observed in some areas. Dispersal occurs primarily by the generation of shoot fragments, which float on the water surface and are transported by currents. The fragments average 7.3 cm in length and 88% retain full regeneration capacity after 4 weeks. They also survive desiccation well (e.g., during drawdown), especially if mixed among mounds of other stranded vegetation. Fragments on the exposed sediment surface die within 22 days, but 32% of shoot apices on fragments at the bottom of exposed vegetation mounds have remained viable for more than 34 days. The fragments are tolerant of chlorates (ClO₃⁻) and significant exposure (to 1,000 mg l⁻¹) does not influence their extent of desiccation. Human-mediated transport of the fragments on boating and fishing equipment also facilitates their spread. Surveys of nonindigenous populations using RAPDs markers have shown very limited levels of variation, which indicates that genetic bottlenecks have occurred at the times of introduction, and/or that introduced plants have spread widely as clonally derived ramets. **Reported associates (North America):** *Bidens beckii*, *Brasenia schreberi*, *Cabomba caroliniana*, *Callitriche*, *Ceratophyllum demersum*, *Ceratophyllum echinatum*, *Eichhornia crassipes*, *Eleocharis acicularis*, *Eleocharis palustris*, *Elodea canadensis*, *Heteranthera*, *Hydrilla verticillata*, *Isoetes*, *Lemna minor*, *Limnobium spongia*, *Ludwigia*, *Myriophyllum heterophyllum*, *Myriophyllum hippuroides*, *Myriophyllum spicatum*, *Najas flexilis*, *Najas guadalupensis*, *Nelumbo lutea*, *Nitella*, *Nuphar polysepala*, *Nymphaea capensis*, *Nymphaea odorata*, *Peltandra virginica*, *Pistia stratiotes*, *Potamogeton crispus*, *Potamogeton diversifolius*, *Potamogeton foliosus*, *Potamogeton richardsonii*, *Potamogeton robbinsii*, *Ranunculus aquatilis*, *Sagittaria montevidensis*, *Spirodela polyrhiza*, *Utricularia macrorhiza*, *Vallisneria americana*, *Vallisneria neotropicalis*, *Wolffia*, *Zizaniopsis miliacea*.

2.3.2.2. ***Egeria naias* Planch.** is a nonindigenous, submersed perennial, which grows in lakes to depths of 1 m. It occurs preferentially in warmer (optimum temperature: 15°C–26°C), clear to tannin stained, somewhat acidic to alkaline (pH: 5.2–7.6) waters. In its native range, the plants are more tolerant to low light (compensation point: 6–22 μ M m⁻² s⁻¹ PAR) and turbid water conditions than are those of the congeneric *E. densa* (see above). Although they are bicarbonate (HCO₃⁻) users, they thrive less in higher bicarbonate/conductivity waters than *E. densa*, which exhibits a higher carbon uptake efficiency under low CO₂ conditions. The plants rely on sediment nutrients (N and P) for optimal growth, but neither nutrient appears to be a growth limiting factor. In the indigenous range, the total number of male flowers ordinarily outnumber

the female flowers by ratios of 3–4:1. Levels of sexual reproduction appear to be reasonably high in native populations, which contain a fair level of genetic variability as indicated by allozyme and RAPD markers. Although the plants can tolerate turbid, eutrophic conditions, the regeneration of vegetative fragments occurs most rapidly in less-turbid, oligotrophic, and sand-dominated sites. Higher growth rates occur in vegetative fragments that retain the apical meristems. In their native range, the plants have exhibited low tolerance to drawdown conditions, which substantially impact the populations. **Reported associates (North America):** none. This species has only recently been found in Florida (USA) where it is known from a single locality.

Use by wildlife: *Egeria densa* contains 75.1% digestible dry matter and 17.4% crude protein. North American plants are eaten by apple snails (Mollusca: Gastropoda: Ampullariidae: *Pomacea*), crayfish (Crustacea: Decapoda: Cambaridae: *Procambarus acutus*, *P. spiculifer*), grass carp (Vertebrata: Teleostei: Cyprinidae: *Ctenopharyngodon idella*), larval leaf-cutter moths (Insecta: Lepidoptera: Crambidae: *Parapoynx diminutalis*), redbelly tilapia (Vertebrata: Teleostei: Cichlidae: *Tilapia zilli*), and Suwannee River cooters (Reptilia: Emydidae: *Pseudemys concinna suwanniensis*). The plants also provide rearing habitat for largemouth bass (Vertebrata: Teleostei: Centrarchidae: *Micropterus salmoides*). Several species of birds (Aves) intensely forage in *Egeria densa* beds, including common moorhens (Rallidae: *Gallinula chloropus*), little blue herons (Ardeidae: *Egretta caerulea*), and tricolored herons (Ardeidae: *Egretta tricolor*); they are foraged to a lesser extent by blue-winged teals (Anatidae: *Anas discors*), great blue herons (Ardeidae: *Ardea herodias*), pied-billed grebes (Podicipedidae: *Podilymbus podiceps*), snowy egrets (Ardeidae: *Egretta thula*), and wood ducks (Anatidae: *Aix sponsa*).

Economic importance: food: Neither *Egeria densa* nor *E. naias* is reported to be edible; **medicinal:** no medicinal uses for *Egeria densa* or *E. naias* are known; **cultivation:** *Egeria densa* is one of the most common plants sold commercially for freshwater aquariums (see also next). *E. naias* also is widely grown as an aquarium plant but only recently has become popular in the United States; **misc. products:** *Egeria densa* has been used widely as a botanical subject for various physiological experiments pertaining to cyclosis and photosynthesis. Meal made from dried *E. densa* has been used as a feed for chickens (Aves: Phasianidae: *Gallus gallus*). *Egeria densa* is under investigation as a potential renewal energy source (biomethane) via the process of continuous anaerobic digestion. Dead *E. densa* plants have shown to be effective biosorptives for the removal of copper ions (Cu_2^+) from contaminated water; **weeds:** *Egeria densa* and *E. naias* are weedy in their native range and seriously invasive throughout their nonindigenous range; **nonindigenous species:** *Egeria densa* was introduced to the United States sometime before 1893 and also has been introduced (with variable persistence) to Africa, Australia, Chile, Denmark, England, France, Germany, Iceland (geothermal springs), Italy, Japan, The Netherlands, New Zealand, Russia, and Spain. The introductions have occurred by the careless disposal of plants used as botanical

laboratory specimens or as aquarium ornamentals. The presence of plants in nonindigenous sites has been detected successfully from environmental DNA (eDNA) samples. *Egeria naias* was first detected in 2017 from a site in west-central Florida, which appears to have resulted from the careless disposal of aquarium plants.

Systematics: The monophyly of *Egeria* is uncertain, with phylogenetic analyses placing *E. densa* closer to *Elodea* than to its congener *Egeria najas* (Figure 1.8). Without further sampling of *Egeria* (*E. heterostemon*) and *Elodea* species, it is unclear whether *Egeria* should best be retained as a distinct genus or merged with *Elodea* (which often has been done in the past). The basic chromosome number of *Egeria* also is uncertain. Several different cytotypes ($2n=16, 24, 46$) have been attributed to plants identified putatively as *Egeria densa*, which raises doubts on the identification of the source material, especially because some of the cytotypes ($2n=16, 24$) also are quite divergent genetically. No natural hybrids involving *E. densa* or *E. najas* have been reported. Experimental reciprocal crosses between these two species also have failed to set seed, which indicates the presence of an effective genetic isolating mechanism. Intergeneric crosses involving *Elodea*, *Hydrilla*, and *Lagarosiphon* also have been unsuccessful.

Distribution: *Egeria densa* occurs sporadically throughout the warmer parts of the United States; *E. naias* currently is known only in west-central Florida.

References: Baker et al., 2010; Barnes et al., 2013; Bartodziej & Weymouth, 1995; Bini & Thomaz, 2005; Blackburn et al., 1961; Boschilia et al., 2012; Boyd & McGinty, 1981; Carter & Sytsma, 2001; Catling & Wojtas, 1986; Catling & Mitrow, 2001; Conrad et al., 2016; Cook & Urmi-König, 1984a; Crutchfield, Jr. et al., 1992; De Abreu Pietrobelli et al., 2009; DiTomaso & Healy, 2003; Dugdale et al., 2012; Ernst-Schwarzenbach, 1945; 1953; Fujiwara et al., 2016; Haramoto & Ikusima, 1988; Haynes, 2000b; Hoyer et al., 1996; Hussner, 2012; Hussner et al., 2010a; 2016; Kasselmann, 2003; Kadono, 2004; Kadono et al., 1997; Koehler & Bove, 2001; Lagueux et al., 1995; Lara et al., 2002; Les & Tippery, 2013; Maurice et al., 1984; Mony et al., 2007; Mori et al., 1999; 2012; Mühlberg, 1982; Palma et al., 2013; Parker & Hay, 2005; Pennington & Sytsma, 2009; Pierinia & Thomaz, 2004; Pine & Anderson, 1991; Pulgar & Izco, 2005; Redekop et al., 2016; Riis et al., 2012; Rixon et al., 2005; Santos et al., 2011; Silveira et al., 2009; Sultana et al., 2013; Takahashi & Asaeda, 2014; Takayanagi et al., 2012; Tanaka et al., 2004; Tavechio & Thomaz, 2003; Thomaz et al., 2007; Umetsu et al., 2012; Wasowicz et al., 2014; Yarrow et al., 2009; Yeo, 1966; Zhen et al., 2016.

2.3.3. Elodea

Waterweed; Elodée

Etymology: after the Greek *helodes* (“wetland”) in reference to the habitat

Synonyms: *Anacharis*; *Diplandra*; *Helodea*; *Hydora*; *Philotria*; *Serpicula*; *Udora*

Distribution: global: Asia*; Australia*; Europe*; New World; New Zealand*; **North America:** widespread

Diversity: global: 5 species; **North America:** 3 species

Indicators (USA): obligate wetland (OBL): *Elodea bifoliata*, *E. canadensis*, *E. nuttallii*

Habitat: freshwater; lacustrine, riverine; **pH:** 5.6–10.2; **depth:** 0.1–12 m; **life-form(s):** submersed (vittate)

Key morphology: stems (to 4+ m) submersed, branching, flexuous, sometimes with turion-like buds and adventitious roots; foliage opposite or in whorls of 3- and 6-ranked, the leaves (to 15.5–24.8 mm) sessile, linear to ovate, often clustered apically; plants dioecious; spathes (♂ to 8.2–42.0 mm; ♀ to 17.6–67.0 mm) sessile, with 1–2 flowers; ♂ flowers: essentially sessile (to 0.5 mm) and detaching or long-pedicelled (to 15+ cm) and attached, floating and opening at water surface; sepals (to 3.4–6.1 mm) 3, green; petals (to 2.6–6.2 mm) 3, reduced, whitish, translucent; stamens 9; ♀ flowers: sepals (to 3.5 mm) 3, green; petals (to 3 mm) 3, reduced, whitish, translucent; staminodia (to 1.4 mm) 3, hypanthium elongate (to 32 cm); ovary syncarpous (3 carpels), inferior, styles (to 4 mm) 3, recurved, entire or bifid; capsules (to 10 mm) irregularly dehiscent, several-seeded (to 10), beaked (to 6.5–20.0 mm); seeds (to 5.7 mm) fusiform, smooth or covered by hairs (to 1 mm)

Life history: duration: perennial (dormant apices, rhizomes, winter buds); **asexual reproduction:** rhizomes, shoot fragments, winter buds; **pollination:** epihydrophily; **sexual condition:** dioecious; **fruit:** capsules (rare to common); **local dispersal:** seeds, shoot fragments (water); **long-distance dispersal:** shoot fragments (birds, water)

Imperilment: 1. *Elodea bifoliata* [G4/G5]; S1 (KS, NE, UT); S2 (AB, MT, SK, WY); 2. *E. canadensis* [G5]; S1 (AL, NC, UT); S2 (SK, WY); S3 (IL, KY, NS); 3. *E. nuttallii* [G5]; S1 (KS, MB, NS, PE, WY); S2 (KY, MT, NB, NC, TN); S3 (BC, IL, ON, QC, VT, WV)

Ecology: general: All *Elodea* species are submersed aquatic plants, which extend only their flowers above the water surface. All three North American species are ranked as OBL indicators throughout their ranges. Although retained as OBL indicators in the National list, *Elodea callitrichoides* and *E. schweinitzii* have been excluded here. The former was erroneously reported for North America and the latter is not accepted taxonomically as a distinct species (see *Systematics*). When water clarity is high, the species can colonize depths up to 12 m, which is the greatest maximum depth recorded for any freshwater aquatic angiosperm. All of the species are dioecious perennials, which possess an epihydrophilous water pollination system. The male flowers either detach from the submersed male plants and rise to the surface where they float and open or they remain attached to the male plants by long pedicels and open once they reach the surface. In either case, the pollen is shed from the male flowers onto the water surface, where it is transported by currents to the female plants. The female flowers also float, but remain attached to the maternal plants by an elongate hypanthium; once reaching the surface, they open and extend their stigmas into the water, where the floating pollen grains are encountered. Despite this rather intricate pollination system, there typically are few seeds produced (except in one species) and most of the reproduction is

asexual. Vegetative reproduction occurs by the fragmentation of the shoots, which can remain viable having only a few nodes intact. The plants (or at least large fragments) also are known to overwinter readily, even in waters having thick ice cover. Requirements for seed germination have not been elucidated. The seeds and vegetative fragments are dispersed locally by water, and over greater distances by birds (Aves) as well as by human-mediated transport. Phenotypic plasticity is extensive and facilitates adaptation of the plants to variable local conditions. It is strongly advised that the taxonomic issues involving *E. canadensis* and *E. nuttallii* (see *Systematics*) be taken into account before attempting to interpret the ecological data provided for these species.

2.3.3.1. *Elodea bifoliata* **H. St. John** inhabits still or slow-moving (e.g., $0.57 \text{ m}^{-3} \text{ s}^{-1}$) waters (to 7.0 m deep) of canals, lakes, ponds, pools, potholes, reservoirs, rivers, sloughs, and streams at elevations to 3088 m. The plants occur in open exposures to partial shade. They often are found floating on the surface of the water, or are washed ashore from sites established in deeper water. The waters are described as alkaline. The substrates have been characterized as mud, rock, sand, and sandy clay. Flowering occurs from July to August with fruiting extending through September. The plants are highly fertile and there has been some suspicion (but no definitive evidence) that they might be monoecious. Further life history information is lacking for this species.

Reported associates: *Alisma subcordatum*, *Azolla filiculoides*, *Carex microptera*, *Ceratophyllum demersum*, *Chara*, *Crypsis schoenoides*, *Elatine brachysperma*, *Elatine californica*, *Elatine rubella*, *Eleocharis acicularis*, *Eleocharis palustris*, *Eleocharis parishii*, *Glyceria*, *Gratiola*, *Lemna minor*, *Limosella*, *Marsilea mollis*, *Myriophyllum sibiricum*, *Myriophyllum spicatum*, *Najas guadalupensis*, *Najas marina*, *Persicaria amphibia*, *Persicaria coccinea*, *Potamogeton diversifolius*, *Potamogeton foliosus*, *Potamogeton gramineus*, *Potamogeton natans*, *Potamogeton nodosus*, *Potamogeton pusillus*, *Potamogeton richardsonii*, *Potamogeton richardsonii*, *Ranunculus aquatilis*, *Ranunculus longirostris*, *Schoenoplectus acutus*, *Sparganium*, *Stuckenia pectinata*, *Utriculata*, *Veronica*, *Wolffia columbiana*, *Zannichellia palustris*.

2.3.3.2. *Elodea canadensis* **Michx.** inhabits standing freshwaters (to 12.0 m deep) in backwashes, backwaters, bays, beaches, bottomlands (river), canals, channels, depressions, ditches (drainage; irrigation; roadside), floodplains, flumes, gravel pits, lagoons, lakes, mudflats, ponds, pools, potholes, reservoirs, rivers, sloughs, springs, and streams at elevations to 3326 m. The plants occur occasionally in slightly brackish water but can tolerate only low salinity levels (<3.5 ppt). Habitats can span a broad range of acidity (pH: 6.5–10.2), but typically are mesotrophic to eutrophic, alkaline waters (pH: $\bar{x}$ = 7.6–7.8) of higher alkalinity (to $300 \text{ mg l}^{-1} \text{ CaCO}_3$) and conductivity (to $650 \text{ } \mu\text{mhos cm}^{-1}$). Optimum water temperatures range from 15°C to 20°C. Exposures range from open sites to partial shade. The plants tolerate relatively high light levels with an optimum near $16,000 \text{ lumens m}^{-2}$. Net photosynthesis is saturated at light intensities from 18,000 to 38,000

lumens m⁻² (15–30% of full sunlight). However, they also tolerate deep shade, suffering less than a 20% decrease in biomass compared to unshaded conditions. Shoot fragments can sustain growth at light levels as low as 90% shade, at which point they can still survive but without additional growth. The plants also are fairly tolerant of disturbances due to cutting and competition. The shoots take up nutrients and minerals directly from the water and are capable of removing large amounts of nitrogen (e.g., 39.8 kg ha⁻¹) and phosphorous (12.1 kg ha⁻¹). The foliage can concentrate heavy metals (e.g., As: 307 mg kg⁻¹; Cd: 32.33 µg g⁻¹; Pb: 160.9 µg g⁻¹) at up to several thousand times their ambient concentrations. The plants are capable of using bicarbonate (HCO₃⁻) when concentrations of free CO₂ are low in the ambient waters. Bicarbonate use is reduced proportionally with increasing CO₂ concentrations. The majority of sediment-derived phosphorous (54%) is translocated from the roots to shoots. The plants are limited by sediment nitrogen (rather than phosphorous) levels. The substrates include alluvium, clay, cobbly sandy loam, gravel, humic soil over clay, loam, marl, muck, mud, ooze, peat, rocks (basalt), sand, sandstone, sandy gravel, sandy muck, silt, silty mud, and stones. Flowering has been observed from June to October; the fruits are seldom encountered but have been reported in August. Most reproduction is asexual and involves the production and dispersal of vegetative shoot fragments, which are produced readily by the relatively brittle stems. The apical foliage often becomes tightly clustered, developing into well-insulated winter buds, which enable the plants to persist throughout the cold season. The plants die back during autumn, releasing manganese and other ions into the water. They decompose rapidly, losing 50% of their biomass (DM) within a week and 95% of their biomass within 47–57 days. Spring regrowth occurs from the dormant stem fragments or winter buds. The fragments rapidly regenerate roots and quickly establish, even when in deep (e.g., 94%) shade. The fragments have high survival rates (>80%) whether rooted or not. Their ability to establish on sediments is higher in the autumn than in the spring. Fragments have been observed to be draped around the necks and backs of waterfowl (Aves: Anatidae), which can disperse them over fairly long distances. The fragments are fairly tolerant to desiccation and can remain viable in the open air for at least 23 hr. On a dry mass basis, the plants consume 0.2–2.8 mg O₂ g⁻¹ hr⁻¹ while fixing 1.16–2.97 mg C g⁻¹ hr⁻¹ during the growing season. Biomass production (DM) can reach levels to 11.7 kg ha⁻¹ day⁻¹ for a seasonal total of up to 2320 kg ha⁻¹. Genetic analyses (microsatellite markers) of introduced populations (where reproduction is entirely asexual) have shown an unexpectedly high level of genetic variation (e.g. 2–5 alleles/locus; 0.19–0.37 expected heterozygosity), which indicates an elevated level of somatic mutation, given a low probability of multiple introductions. The roots are not colonized by mycorrhizal Fungi. **Reported associates:** *Acorus calamus*, *Alisma subcordatum*, *Beckmannia syzigachne*, *Bidens beckii*, *Brasenia schreberi*, *Cabomba caroliniana*, *Callitriche palustris*, *Carex gynandra*, *Carex pellita*, *Cephalanthus occidentalis*, *Ceratophyllum demersum*, *Chara*, *Eleocharis acicularis*, *Eleocharis palustris*, *Elodea*

nuttallii, *Equisetum fluviatile*, *Fontinalis*, *Glyceria borealis*, *Gnaphalium*, *Gratiola*, *Heteranthera dubia*, *Hippuris vulgaris*, *Hydrocharis morsus-ranae*, *Hydrocotyle vulgaris*, *Iris pseudacorus*, *Isoetes bolanderi*, *Juncus balticus*, *Juncus marginatus*, *Justicia americana*, *Lemna minor*, *Lemna obscura*, *Lemna trisulca*, *Lilaeopsis*, *Marsilea mollis*, *Marsilea vestita*, *Myosotis laxa*, *Myriophyllum heterophyllum*, *Myriophyllum sibiricum*, *Myriophyllum spicatum*, *Najas flexilis*, *Najas guadalupensis*, *Nasturtium officinale*, *Nitella*, *Nuphar advena*, *Nuphar polysepala*, *Nuphar variegata*, *Nymphaea odorata*, *Nyssa*, *Persicaria amphibia*, *Persicaria coccinea*, *Persicaria hydropiper*, *Phalaris arundinacea*, *Potamogeton alpinus*, *Potamogeton amplifolius*, *Potamogeton berchtoldii*, *Potamogeton crispus*, *Potamogeton diversifolius*, *Potamogeton foliosus*, *Potamogeton friesii*, *Potamogeton gramineus*, *Potamogeton illinoensis*, *Potamogeton natans*, *Potamogeton nodosus*, *Potamogeton perfoliatus*, *Potamogeton praelongus*, *Potamogeton pusillus*, *Potamogeton richardsonii*, *Potamogeton robbinsii*, *Potamogeton zosteriformis*, *Ranunculus aquatilis*, *Ranunculus flabellaris*, *Ranunculus flammula*, *Ranunculus longirostris*, *Ranunculus subrigidus*, *Sagittaria cuneata*, *Sagittaria latifolia*, *Sagittaria rigida*, *Schoenoplectus acutus*, *Schoenoplectus hallii*, *Schoenoplectus triqueter*, *Scirpus microcarpus*, *Sium suave*, *Sparganium angustifolium*, *Sparganium emersum*, *Spiraea douglasii*, *Spirodela polyrhiza*, *Stuckenia filiformis*, *Stuckenia pectinata*, *Stuckenia vaginata*, *Typha latifolia*, *Utricularia gibba*, *Utricularia macrorhiza*, *Utricularia minor*, *Vallisneria americana*, *Veronica*, *Zannichellia palustris*.

2.3.3.3. *Elodea nuttallii* (Planch.) H. St. John inhabits flowing or still freshwater, tidal or non tidal waters (to 6.1 m deep) in backwaters, bayous, bottoms (lake; tank), brooks, canals, ditches (channelized; drainage; roadside), flats (mud; river), gravel pits, lakes, marshes, oxbows (drying), ponds (hatchery; sinkhole; strip mine), pools (channel), potholes, reservoirs, rivers, sloughs, streams, and swamps at elevations to 3201 m. The waters (to 3 m deep) are described as calcareous (pH: 5.6–9.2; $\bar{x}$: 6.9–7.0; alkalinity to 160 mg l⁻¹ CaCO₃; chloride: to 1.6 ppm; conductivity to 310 µmhos cm⁻¹). The plants are fairly resistant to currents; however, turbulence can decrease their total chlorophyll content by as much as 40%. They typically are found in sunny exposures but are fairly shade tolerant; they are less tolerant of anoxic or hypoxic conditions. The plants are very resistant to desiccation and have been observed to rapidly recolonize a wetland, which had been drawn down for 10 weeks during summer. Increased sediment PO₄³⁻ concentration has been observed to reduce growth, while increasing growth in shoots that have been trimmed; an opposite effect occurs when PO₄³⁻ and NH₄⁺ levels are increased simultaneously. Like the preceding species, *E. nuttallii* similarly possesses the ability to use bicarbonate ions (HCO₃⁻) during conditions of low free CO₂ availability (e.g., at higher pH levels). The ability to uptake and accumulate heavy metals is similar to that of the preceding species as well. Experiments have indicated a higher overall growth rate in *Elodea nuttallii* than *E. canadensis*, but with foliar (vs. root) uptake being greater in the latter. The former also

is more shade tolerant than the latter. The substrates include cobble (river), gravel, marl, mucky silt, mud, rock, sand, sandy mud, sandy silt, silt, and silty gravel. Flowering has been observed from June to August, with fruiting in August. The species is believed to form a transient soil seed bank, with the seeds persisting for <1 year. However, fruiting is rare and most reproduction is asexual, occurring by means of stem fragmentation. During the growing season, the shoots usually do not fragment unless they are subjected to current velocities above 2.4 m s^{-1} ; however, fragmentation becomes widespread at the end of the season. The fragments (with as few as four nodes) have high survival rates (>70%) whether rooted or not. They are known to establish effectively under virtually any light regime including 94% shade. The fragments survive cold water conditions well and can resume growth when mean daily water temperatures surpass 4°C . Their ability to establish on sediments is higher in the spring than in the autumn. The plants produce a number of allelochemicals (α -linolenic acid, β -ionone, dihydroactinidiolide, linoleic acid, pentadecanoic acid, and stearic acid), which inhibit the growth of phytoplankton. **Reported associates:** *Azolla*, *Brasenia schreberi*, *Cabomba caroliniana*, *Callitriche hermaphrodita*, *Carex diandra*, *Carex stipata*, *Carex vesicaria*, *Cephalanthus occidentalis*, *Ceratophyllum demersum*, *Ceratophyllum echinatum*, *Chara*, *Eichhornia crassipes*, *Elatine chilensis*, *Elatine minima*, *Elatine triandra*, *Eleocharis acicularis*, *Elodea canadensis*, *Eriocaulon aquaticum*, *Glossostigma cleistanthum*, *Gratiola aurea*, *Heteranthera dubia*, *Hippuris vulgaris*, *Isoetes echinospora*, *Isoetes xatoni*, *Juncus balticus*, *Juncus bulbosus*, *Juncus nevadensis*, *Leersia oryzoides*, *Lemna minor*, *Lemna trisulca*, *Lemna turionifera*, *Ludwigia palustris*, *Lythrum salicaria*, *Menyanthes trifoliata*, *Myriophyllum heterophyllum*, *Myriophyllum heterophyllum* $\times$ *Myriophyllum laxum*, *Myriophyllum humile*, *Myriophyllum pinnatum*, *Myriophyllum sibiricum*, *Myriophyllum spicatum*, *Myriophyllum tenellum*, *Myriophyllum verticillatum*, *Najas canadensis*, *Najas flexilis*, *Najas gracillima*, *Najas guadalupensis*, *Najas marina*, *Najas minor*, *Nasturtium officinale*, *Nelumbo lutea*, *Nuphar polysepala*, *Nuphar variegata*, *Nymphaea odorata*, *Persicaria amphibia*, *Persicaria glabra*, *Potamogeton amplifolius*, *Potamogeton berchtoldii*, *Potamogeton bicupulatus*, *Potamogeton crispus*, *Potamogeton epihydrus*, *Potamogeton foliosus*, *Potamogeton gramineus*, *Potamogeton natans*, *Potamogeton nodosus*, *Potamogeton perfoliatus*, *Potamogeton praelongus*, *Potamogeton pulcher*, *Potamogeton pusillus*, *Potamogeton richardsonii*, *Potamogeton robbinsii*, *Potamogeton spirillus*, *Potamogeton zosteriformis*, *Proserpinaca palustris*, *Ranunculus aquatilis*, *Ranunculus longirostris*, *Riccia fluitans*, *Ricciocarpus natans*, *Sagittaria cuneata*, *Schoenoplectus acutus*, *Sparganium eurycarpum*, *Spirodela polyrhiza*, *Stuckenia filiformis*, *Stuckenia pectinata*, *Typha latifolia*, *Utricularia gibba*, *Utricularia macrorhiza*, *Utricularia minor*, *Utricularia purpurea*, *Utricularia radiata*, *Vallisneria americana*, *Wolffia brasiliensis*, *Wolffia columbiana*, *Zannichellia palustris*.

Use by wildlife: *Elodea canadensis* comprises 18–27% protein and is consumed by a number of herbivores. The plants are

eaten by rusty crayfish (Crustacea: Decapoda: Cambaridae: *Orconectes rusticus*), muskrats (Mammalia: Cricetidae: *Ondatra zibethicus*), and mute swans (Aves: Anatidae: *Cygnus olor*). Insect (Insecta) herbivores include larval caddisflies (Trichoptera: Leptoceridae: *Leptocerus americanus*, *Nectopsyche*), flies (Diptera: Ephydriidae: *Hydrellia discursa*, *H. harti*, *H. trichaeta*), and moths (Lepidoptera: Crambidae: *Acentria ephemerella*, *A. nivea*). The plants also are host to several Fungi (Ascomycota: Helotiaceae: *Varicosporium elodeae*; Chytridiomycota: Chytridiaceae: *Chytridium elodeae*; Cladochytriaceae: *Megachytrium westonii*). The presence of *E. canadensis* can reduce the level of larval mosquitoes (Insecta: Diptera: Culicidae) by as much as 34%. Dense growths of the plants also interfere with foraging activities of juvenile bluegills (Osteichthyes: Centrarchidae: *Lepomis macrochirus*) and other fish.

Economic importance: food: *Elodea* shoots are eaten as a snack in Estonia. However, given the ability of the shoots to concentrate heavy metals, consumption of the plants is inadvisable; **medicinal:** The Iroquois prepared an infusion from *Elodea canadensis*, which was used as an emetic. *Elodea nuttallii* contains β -sitosterol, which is used to treat enlarged prostates; **cultivation:** *Elodea canadensis* and *E. nuttallii* are widely grown as cold water aquarium plants; **misc. products:** *Elodea canadensis* and *E. nuttallii* are used routinely in various plant physiological experiments. *Elodea nuttallii* has been used as a co-substrate (with maize silage) for biogas generation. The plants also have been considered for wastewater treatment, where they are capable of achieving high annual removal rates of ammonia (75%), 5-day biochemical oxygen demand (90%), total nitrogen (47%), and total phosphorus (38%) from primary wastewater; **weeds:** *Elodea canadensis* and *E. nuttallii* are regarded as weeds throughout their nonindigenous range (and often also within their indigenous range); **nonindigenous species:** *Elodea* (*E. canadensis* and/or *E. nuttallii*) has been introduced throughout the world, including Africa, Australia (~1931), Europe [Croatia (~2006), England (~1847), France (~1850), Germany (~1860), Hungary (~1870), Ireland (~1836), Italy (~1892), Switzerland (~1869)], New Zealand (~1872), and Russia (~1970)].

Systematics: Phylogenetic analyses indicate that *Elodea* is most closely related to *Egeria* (Figure 1.9) and somewhat more distantly to *Apalanthe*. Although some authors have advocated the merger of *Elodea* and *Egeria*, crosses between these genera (also between *Elodea* and *Hydrilla* or *Lagarosiphon*) are inviable, which indicates that the genera are well isolated genetically. Accessions of three *Elodea* species included in phylogenetic analyses resolve as a clade, which substantiates the monophyly of the genus as far as it has been sampled (Figure 1.9). *Elodea* is extremely difficult taxonomically. Due to their frequent sterility, specimens of *E. canadensis* and *E. nuttallii* typically are identified by their leaf morphology (shorter, ovate leaves in the former; elongate, linear leaves in the latter). However, genetic analyses have indicated that many of the specimens observed in the field are *E. canadensis* $\times$ *E. nuttallii* hybrids, and that “*E. canadensis*” phenotypes commonly associate with “*E. nuttallii*” genotypes

FIGURE 1.9 Phylogenetic relationships of *Elodea* and related genera as indicated by analysis of nrITS sequence data (adapted from Les & Tippery, 2013). As sampled, *Elodea* is monophyletic and closely related to *Egeria* (the placement of *Egeria najas* notwithstanding). Many *E. canadensis* × *E. nuttallii* hybrids have been detected by the recovery of cloned parental alleles originating from both species. The hybrids can resemble either parental species, at least vegetatively. Taxa designated as OBL North American indicators are highlighted in bold.

and vice versa. The author also has observed phenotypically plastic specimens clearly having “*E. canadensis*” foliage on one portion of the shoot and distinctly “*E. nuttallii*” foliage on another part of the same shoot. Consequently, it is virtually impossible to identify material of either taxon morphologically, at least when in vegetative condition. Yet, the two taxa are distinct genetically (Figure 1.9), despite their bewildering mosaic of phenotypic variability. *Elodea* also is problematic cytologically. The basic chromosome number of *Elodea* is uncertain but probably is $x=8$, given a $2n=16$ count reported for the South American *Elodea callitrichoides*. However, that base number would indicate that *E. bifoliata* ($2n=24$) is triploid, which would be unusual given its relatively high fertility. The counts reported for *E. canadensis* and *E. nuttallii* are so variable ($2n=24, 32, 40, 48, 56, 64, 72, 96$) that their ploidy levels are indeterminable; yet they consistently are based on $x=8$. Extensive somatically derived aneuploidy ($2n=32, 42, 43, 44, 48$) reportedly has arisen within a single strain of *E. nuttallii* that was cultivated over a 73-year period. Experimental hybridizations involving *E. callitrichoides* × *E. canadensis* are inviable; however, reciprocal crosses between *E. canadensis* and *E. nuttallii* are fully interfertile. Genetically determined hybrids between *E. canadensis* and *E. nuttallii* have been collected throughout their range; however, it is not understood whether hybrid plants occur frequently or if their widespread distribution is due to the broad dispersal of fewer ramets. The complete chloroplast genome of *E. canadensis* has been sequenced.

Distribution: *Elodea bifoliata* occurs in western North America. *Elodea canadensis* and *E. nuttallii* are essentially sympatric throughout much of North America, except for the extreme northern and southern regions where neither is common.

References: Abernethy et al., 1996; Atapaththu & Asaeda, 2015; Bailey et al., 2008; Barrat-Segretain, 2004; Barrat-Segretain et al., 2002; Barrat-Segretain & Cellot, 2007; Beck-Nielsen & Madsen, 2001; Bishop & Eighmy, 1989; Catling & Wojtas, 1986; Ciutti et al., 2011; Cook & Urmikönig, 1985; Crow & Hellquist, 1982; Eighmy et al., 1991; Ernst-Schwarzenbach, 1945; 1953; Eugelink, 1998; Fulmer & Robinson, 2008; Green, 2016; Greulich & Tremolieres, 2006; Gross et al., 2001; Harms & Grodowitz, 2009; Harrel & Dibble, 2001; Haynes, 2000b; Hoffmann et al., 2014a; Huotari & Korpelainen, 2012; Huotari et al., 2011; Hussner et al., 2010b; Kalle & Söukand, 2013; Kasselman, 2003; Király et al., 2007; Kočić et al., 2014; Kravtsova et al., 2010; Kunii, 1981; Kuntz et al., 2014; Les & Philbrick, 1993; Mayes et al., 1977; Mielecki & Pieczynska, 2005; Löve, 1982; Peters et al., 2008; Preston & Croft, 1997; Riis et al., 2010; Robinson et al., 2007; Sand-Jensen & Gordon, 1986; Sheldon & Boylen, 1977; Spencer & Ksander, 2003; Thiébaud et al., 2010; Vincent & Bertola, 2012; Wang et al., 2014a; Zaman & Asaeda, 2013; Zefferman, 2014.

2.3.4. Halophila

Seagrass, star grass

Etymology: from the Greek *hals philos* (“salt loving”) in reference to the marine habitat

Synonyms: *Barkania*; *Caulinia* (in part); *Kerneria* (in part); *Lemnopsis*; *Serpicula* (in part); *Thalassia* (in part); *Zostera* (in part)

Distribution: **global:** cosmopolitan; **North America:** southern (Gulf and Atlantic coasts)

Diversity: **global:** 10–13 species; **North America:** 3 species

Indicators (USA): **obligate wetland (OBL):** *Halophila decipiens*, *H. engelmannii*, *H. ovalis*

Habitat: marine; oceanic; **pH:** 7.9–8.3; **depth:** to 90 m; **life-form(s):** submersed (vittate)

Key morphology: foliage arising directly from rhizomes or in pseudowhorls (to 8 leaves) from short, erect, unbranched stems, the rhizomes thin or thick (to 2 mm), with 2 scales per node; leaves sessile or petiolate (to 12 cm), the blades (to 30 mm) linear-oblong, linear-lanceolate, oblong, or oblong-elliptic, the margins entire or serrulate; flowers unisexual (the plants dioecious or monoecious), enclosed in a spathe; ♀ flowers (to 9 mm) essentially sessile, styles (to 30 mm) 3; ♂ flowers (to 4 mm), pedicellate (to 2 cm), the pollen released in chains from linear anthers (to 2 mm); capsules (to 6 mm) ovoid, beaked (to 6 mm); seeds (to 0.3 mm) few-30, reticulate

Life history: **duration:** perennial (rhizomes); **asexual reproduction:** rhizomes; **pollination:** water (hypohydrophily); **sexual condition:** dioecious, monoecious; **fruit:** capsules (common); **local dispersal:** fruits (gravity), shoot fragments (water); **long-distance dispersal:** fruits (water), seeds (birds, water)

Imperilment: **1.** *Halophila decipiens* [G4/G5]; **2.** *H. engelmannii* [G3/G5]; S1 (LA, MS); **3.** *H. ovalis* [G2]; S2 (FL)

Ecology: **general:** All *Halophila* species are submersed, perennial, marine, hydrophilous plants, and all North American taxa are OBL wetland indicators. The genus occurs

within one of three major clades of “seagrasses,” which represent the relatively few angiosperms adapted to life in the ocean. By their ability to survive in saltwater, the species typically encounter salinities of 34–35‰ and an alkaline pH of 8.1. Both features can vary due to freshwater intrusion from rainfall, proximity to freshwater sources, temperature, and other factors. *Halophila* species can occur in fairly deep waters and have been recorded at depths of up to 90 m. Although these are the smallest of the seagrasses physically, they also exhibit the highest rates of sexual reproduction. All of the species have unisexual flowers (the plants dioecious or monoecious) and are water pollinated. The pollen grains are ellipsoid and form linear moniliform strands, which typically are dispersed while submersed but occasionally float to the water surface. The grains are captured by the elongate, papillate stigmas of the female flowers. The fruits contain from 7 to 60 seeds, which are not particularly buoyant, are released at or below the sediment surface, and typically are dispersed within distances of only a few centimeters. Although the fruits are not particularly vagile, their concentration of stored seeds facilitates the rapid colonization of newly exposed sites. In some cases, the fruits are buoyant and able to float for some distance. Recent studies have shown that the seeds can retain viability after passage through the digestive tract of waterfowl (Aves: Anatidae), which implicates birds as potential vectors for long-distance dispersal. Transient or persistent seed banks can develop at densities of up to 70,000 seeds m⁻². The seeds are not dormant but do require light for germination. Rates of natural seed germination range from 12% to 63%. Like all seagrasses, *Halophila* species also reproduce asexually by means of rhizomes, and occasionally by stem fragmentation. Although “*Halophila johnsonii*” is designated as an OBL indicator, that taxon has been merged here with *H. ovalis* in accordance with the results of various systematic investigations (see *Systematics*). However, the ecological information compiled for this taxon is based primarily on information from reports specifically referencing “*H. johnsonii*.”

2.3.4.1. *Halophila decipiens* Ostenf. inhabits coastal marine communities in waters ranging from 24.3‰ to 38.0‰ salinity and extends from subtidal zones to depths as great as 85 m (in clear waters). The plants are ruderal and able to survive in reduced or fluctuating light; however, deeper water populations are intolerant of high irradiance levels (>1000 $\mu\text{E m}^{-2} \text{ s}^{-1}$) and reduced salinity (<35 ppt). Typical water depths are 10–30 m with temperatures ranging from 21.0°C to 36.0°C. Plant cover diminishes noticeably when illumination falls below 10% of surface incident light. The plants thrive in sites where disturbance has eliminated competition by ordinarily more persistent species. The substrates can include coral, limestone, muddy coral sand, muddy sand, sand, shell hash, and silt. The plants are monoecious and the flowers are protandrous. Flower density can vary from 50 to 1925 m⁻². Pollination is hypohydrophilous, occurring entirely underwater. In North America, flowering has been reported from July to September with fruiting from July to August. The flowers typically are open during a 9-hr period extending from first light until mid-afternoon. On average the fruits contain 36.8

seeds, which readily sink into the substrate. Large seed banks (to 13,500 seeds m⁻²) have been observed within the upper 3 cm of sediments; more typical values range from 134 to 3,414 seeds m⁻². Seed germination has been observed from October to January. Buried seeds germinate well (to 86%) within 2–9 days after exposure to light, but will remain dormant in the dark at 24°C. Seed germination occurs at salinities from 25% to 34% but is inhibited at 42%. Although the seeds are deposited locally, their movement *en masse* within large quantities of sediment dislodged by disturbance (e.g. hurricanes) can result in far greater dispersal distances. Seedling densities are highest during the winter. The biomass attained by the plants varies widely, ranging from 0.02 to 12 g m⁻²; it is lowest during fall and winter. Production rates (e.g., 0.023 g C m⁻² day⁻¹) can reach a total of 4.56×10^8 g C day⁻¹ during the peak growing season. The ratio of aboveground to belowground biomass is higher in shallow sites, with more storage occurring in underground organs at deeper sites. The plants can occupy extensive ranges of 7,500 km² or more. The foliage decomposes rapidly, losing more than 50% of its original mass within 3 days. The plants have been cultured successfully *in vitro*. **Reported associates:** *Halodule wrightii*, *Halophila engelmannii*, *Halophila ovalis*, *Ruppia maritima*, *Syringodium filiforme*, *Thalassia testudinum*.

2.3.4.2. *Halophila engelmannii* Asch. inhabits coasts (oceanic), lagoons, and tidal flats at depths to 90 m. The plants can tolerate salinity to 60‰ and occur where water temperatures vary from 13.3°C during winter to 31.6°C during summer. They decline during periods of increased precipitation, which favors species with lower salinity tolerances. The plants are intolerant of ultraviolet-A and UV-B radiation and typically are shaded by epiphytes or occur in the shade of other seagrasses. The substrates include limestone, mud, muddy clay, muddy sand, sand (gray), and sandy mud. The plants are dioecious. Flowering has been observed from March to June; however, under laboratory conditions, flowers have been produced continuously from January to September. The flowers open during a 9-hr period extending from first light until mid-afternoon. Although typically hypohydrophilous, some pollen has been observed to entrap gas bubbles, which enables them to rise to the water surface, where epihydrophily (surface pollination) conceivably could occur. An extensive seed bank can develop (100–800 m⁻²; $\bar{x}$: 74 m⁻²). Seeds collected from mid-May to mid-June are not dormant and have germinated within 4 weeks. Germination requires light and at 24°C–27°C, initiates within 7–10 days (if collected from November to May) and in 27–33 days if collected in October. Seed collected in June (and stored for 18 weeks in the dark at 24°C–27°C) germinated in the light within 27–38 days; seed stored for 30 weeks in the dark eventually germinated after 9–12 days. Many seeds most likely remain dormant in the sediment until they are exposed to light by disturbance. Seeds stored in the dark can remain viable for at least 2 years. Seedlings that have germinated under laboratory conditions represented a 64:46 ratio of male and female flowers; however, a 42:58 ratio of staminate to pistillate shoots has been observed in a natural population. Biomass has been observed to range

from 0.25 to 6.0 g m⁻². The plants have been cultured successfully *in vitro*. **Reported associates:** *Acetabularia*, *Caulerpa*, *Codium*, *Halimeda*, *Halodule wrightii*, *Halophila decipiens*, *Halophila ovalis*, *Penicillus*, *Ruppia maritima*, *Syringodium filiforme*, *Thalassia testudinum*, *Udotea*.

2.3.4.3. *Halophila ovalis* (R. Br.) Hook. f. inhabits the intertidal and subtidal zones (to 3 m depth) of coastal marine and riverine environments, including channel bottoms, lagoons, sand bars, and sand flats. These physiologically plastic plants are tolerant of higher irradiances, turbidity, fluctuations in salinity and temperature, and contain intracellular UV-absorbing pigments (numerous flavonoids), all factors that enable them to colonize shallower water depths in exclusion of deeper dwelling seagrass taxa. They acclimate rapidly to high UV-B and PAR levels. Their maximum growth occurs at salinities of 30 ppt. The plants will experience complete mortality if rapidly exposed to 10‰ salinity for 10 days; however, tolerance to 10‰ can be maintained if the reduction in salinity occurs gradually or in brief pulses. The substrates have been characterized as mud and sand (coarse). The plants are dioecious, with flowering (in this case ♀) observed from April to October; no seeds are produced. The North American populations probably are derived from the founding of a single female clone, which is incapable of seed set due to the lack of male plants and associated pollination. The plants can be dispersed vegetatively by fragments; however, these are relatively short-lived and remain viable only for 4–8 days. Radioisotope tracers have shown that the plants store few carbon reserves. Carbon is allocated more to younger portions of a genet and to ramets in proportion to their proximity, but is not allocated preferentially to ramets experiencing stress. These factors make it difficult for the plants to persist vegetatively over unsuitable substrates, which compromise their ability to withstand disturbances resulting in habitat loss. Biomass has been measured at 43.0 (above-ground) and 53.5 (belowground) g DM m⁻². **Reported associates (North America):** *Caulerpa prolifera* (Chlorophyta: Caulerpaceae), *Halodule wrightii*, *Halophila decipiens*, *Halophila engelmannii*, *Ruppia maritima*, *Syringodium filiforme*, *Thalassia testudinum*.

Use by wildlife: The queen conch (Mollusca: Gastropoda: Strombidae: *Strombus gigas*) is known to graze on epiphytes that clothe the foliage of *Halophila decipiens*. The foliage of *H. decipiens* is low in total protein (2.5–6.2% by DM) and soluble carbohydrate (4.3–8.2%) but is eaten by green sea turtles (Reptilia: Testudines: Cheloniidae: *Chelonia mydas*); *H. engelmannii* also is eaten by the turtles. Various organisms graze on the epiphytic algae found on the foliage of *H. ovalis*. **Economic importance: food:** not edible; **medicinal:** Crude extracts of *Halophila decipiens* are inhibitory to some Fungi (Ascomycota: Lulworthiaceae: *Lindra thalassiae*; Nectriaceae: *Fusarium*); **cultivation:** not cultivated; **misc. products:** none; **weeds:** none; **nonindigenous species:** The occurrence of *Halophila ovalis* along a small portion of the Atlantic coast is enigmatic, given the existence there only of genetically similar female plants, which have spread as asexual ramets. Although these plants have been treated as an

endemic, federally (USA) threatened taxon ("*H. johnsonii*"), it is almost certain that a single female clone was introduced to the region either by natural dispersal vectors or as a consequence of the intense international shipping in that area. Morphologically and genetically similar plants of *H. ovalis* (both with narrower leaves and fewer ovules than typical populations) have been documented in Antigua, indicating at least that the plants are not endemic to Florida.

Systematics: Various phylogenetic analyses have confirmed that *Halophila* is monophyletic. However, there remains some discrepancy on the number of species in the genus, even though most taxa have now been sampled and included in phylogenetic analyses. The most contentious issue involving North American material is the taxonomic status of "*Halophila johnsonii*," which was discovered relatively recently (1980) along the Atlantic coast of Florida. These plants consist entirely of genetically similar, female clones and reproduce only asexually. Given its rarity and precarious reproductive issues, *H. johnsonii* was recognized as a threatened endemic species in the United States, following numerous studies which demonstrated its morphological, ecological, and genetic distinctness from the more common *H. decipiens*. However, it was later shown that the Florida plants actually were not only unrelated to *H. decipiens*, but instead were closely related to *H. ovalis* and resolved within that clade in several phylogenetic studies (e.g., Figure 1.10). Although the Florida populations have narrower leaves and fewer ovules than other *H. ovalis* populations surveyed, they are similar genetically (identical nrITS sequences) and morphologically to *H. ovalis* populations from Antigua. Together, these results indicate that "*H. johnsonii*" should not be regarded as a distinct endemic species, but at best as a thin-leaved variant of the more widely ranging *H. ovalis*. The basic chromosome number of *Halophila* is $x=9$. *Halophila ovalis* ($2n=18$) is diploid; counts for *H. decipiens* and *H. engelmannii* are unavailable. No hybrids involving any *Halophila* species have been reported.

Distribution: *Halophila decipiens* occurs along the Gulf Coast of Florida and *H. ovalis* occurs along the Atlantic coast of Florida; both are widespread in tropical and subtropical waters worldwide. *Halophila engelmannii* occurs on the Atlantic coast of Florida and along the Gulf of Mexico coast.

References: Ackerman, 2006; Ballantine & Humm, 1975; Bell et al., 2008; Bird & Jewett-Smith, 1994; Bird et al., 1998; Bortone, 2000; Dawes et al., 1989; Dean & Durako, 2007; Duarte, 1991; Duarte & Chiscano, 1999; Durako et al., 2003; Eiseman & McMillan, 1980; Fourqurean et al., 2001; Gabriel et al., 2015; Gavin & Durako, 2011; 2012; 2014; Green & Short, 2003; Griffin & Durako, 2012; Hall et al., 2006; Hammerstrom et al., 2006; Hartog, 1970; Haynes, 2000b; Herbert, 1986; Howell, 2012; Humm, 1956; Inglis, 1999; Jewett-Smith & McMillan, 1990; Jewett-Smith et al., 1997; Josselyn, 1986; Kahn & Durako, 2008; 2009; Kahn et al., 2013; Kenworthy, 1999; Kunzelman et al., 2005; Larkum, 1995; Les, 1988; Les & Tippery, 2013; Les et al., 1997a; McDermid et al., 2007; McMillan, 1976; 1987; 1988; 1988a; 1988b; 1989; 1990; 1991; McMillan & Jewett-Smith, 1988; Meng et al., 2008; MNFS, 2002; Onuf, 1996;

FIGURE 1.10 Phylogenetic tree constructed for *Halophila* using nrITS sequence data (adapted from Short et al., 2010). These results (and those of Uchimura et al., 2008) show "*Halophila johnsonii*" to be embedded within a large *H. ovalis* clade. The nrITS sequence of "*H. johnsonii*" is identical to material from Antigua, which also is similar morphologically. The three OBL North American *Halophila* species (in bold) originate from various parts of the tree, indicating a broad phylogenetic diversity in the region.

Orth et al., 2000; 2006; Pettitt & Jermy, 1974; Phillips, 1960; Phillips & Meñez, 1988; Ross et al., 2008; Short & Wyllie-Echeverria, 1996; Short et al., 2010; Torquemada et al., 2005; Trocine et al., 1981; 1982; Uchimura et al., 2008; Waycott et al., 2002; 2006; Wu et al., 2016; Xu et al., 2011; York et al., 2008.

2.3.5. Hydrilla

Florida elodea, hydrilla, water thyme; hydrille

Etymology: derived from the Greek *Hydra*, a mythological lake-dwelling serpent

Synonyms: *Elodea* (in part); *Epigynanthus*; *Hydora* (in part); *Hydrospondylus*; *Ixia* (in part); *Serpicula* (in part); *Udora* (in part); *Vallisneria* (in part)

Distribution: **global:** Africa, Australia, Eurasia, North America*, South America (northern)*; **North America:** eastern, southern, and western United States

Diversity: **global:** 1 species; **North America:** 1 species

Indicators (USA): **obligate wetland (OBL):** *Hydrilla verticillata*

Habitat: brackish (coastal), freshwater, freshwater (tidal); lacustrine, palustrine, riverine; **pH:** 5.4–8.6; **depth:** to 15 m; **life-form(s):** submersed (vittate)

Key morphology: subterranean shoots horizontal, rhizomatous or stoloniferous, sometimes producing white to brownish turion-like tubers at the stolon termini, roots unbranched; leafy shoots (to 8.5 m) submersed, branched or unbranched, erect in water column, sometimes bearing hard, olive-green, conelike turions; leaves cauline, in whorls of 3–8, the blades (to 20 mm) linear, sessile, single-nerved, margins finely serrulate, abaxial surface with midvein prickles, base tapering to stem; inflorescences single-flowered, sessile to subsessile (pedicels to 0.5 mm), enclosed by a spathe of 2 connate bracts; flowers unisexual (plants dioecious or monoecious), perianth trimerous, translucent or reddish to whitish; ♂ flowers released under water in bud, rising to surface, the enclosed

staminal filaments distinct, springing apart explosively to release pollen from anthers as the free-floating flowers open at water surface; ♀ flowers floating on perianth, attached by an elongate, translucent to purplish floral hypanthium (to 50 mm); staminodes (3) minute; ovary tricarpellate, 1-locular, styles (to 0.75 mm) 3; fruits indehiscent, cylindrical, smooth or spiny; seeds (to 5) fusiform, smooth

Life history: **duration:** perennial (rhizomes, stolons, turions, whole plants); **asexual reproduction:** rhizomes, shoot fragments, stolons, tubers, turions (stem, stolons); **pollination:** abiotic (ballistic); **sexual condition:** dioecious, monoecious; **fruit:** capsular [indehiscent] (rare); **local dispersal:** shoot fragments, tubers, turions (water, waterfowl); **long-distance dispersal:** shoot fragments, tubers, turions (humans, water, waterfowl)

Imperilment: 1. *Hydrilla verticillata* [GNR]

Ecology: **general:** Although viewed almost universally as monotypic, *Hydrilla* represents a complex of cryptic, genetically variable taxa, which exhibit a number of cytological, ecological, and morphological differences. Nevertheless, all of the ecological information assembled for the genus over the past century has been attributed to one single, variable, wide-ranging species and is summarized below in that respect.

2.3.5.1. Hydrilla verticillata (L. f.) Royle is a nonindigenous species, which inhabits still or flowing, tidal, intertidal, or non-tidal, brackish to fresh (0–11‰ salinity) waters in backwaters, bayous, canals, coves, ditches (drainage, irrigation, roadside), gravel pits, lagoons (river), lakes (freshwater), marshes (floating, tidal), ponds (artificial, farm, fire, fish, floodplain, irrigation, koi, retention, sinkhole, stagnant), pools (riverbed, shallow), potholes (drying), reservoirs, spillways, springs, and the margins of channels (bayou, boat), embayments, lakes, rivers, and streams (spring-fed) at elevations (North America) to 860 m. Exposures can range from full sunlight to shade (e.g., along banks). The plants can colonize a variety of still to flowing waters from 0.7 to 15.0 m deep, with slow flow

rates $<0.2 \text{ m s}^{-1}$ apparently being optimal. They can grow in clear to turbid waters (e.g., Secchi depth: 0.6 m) at light levels as low as $10\text{--}12 \mu\text{E m}^{-2} \text{ s}^{-1}$. The plants are known to grow where percent transmittance of light is only 0.46 of that at the surface; they exhibit a decreasing chlorophyll A:B ratio with depth, which is attributed as an adaptation to reduced light levels. Shoot growth has been observed to continue for up to 10 weeks when the plants are kept in total darkness. The substrates (North America) are diverse and include alluvium (clayey, loamy), granite, gravel (limestone), limestone, marl, mud, rocky silt, sand, sandy silt, silt, silty clay, and silty clay loam (Cancienne); however, a high sediment organic content (e.g., $13\% \text{ dw}^{-1}$) is deleterious to growth. The plants occur most often in freshwater (salinity $<0.5\text{‰}$) with their growth seriously impacted at salinities $>13\text{‰}$. Otherwise, broad spectrum of water conditions is tolerated (water temperature: $18.2^{\circ}\text{C}\text{--}18.8^{\circ}\text{C}$; specific conductance: $27.0\text{--}400.8 \mu\text{S cm}^{-1}$; $\bar{x} = 183 \mu\text{S cm}^{-1}$; pH: $5.4\text{--}8.6$; $\bar{x} = 7.1$; total alkalinity: $1.7\text{--}164.0$; $\bar{x} = 29.9 \text{ mg l}^{-1} \text{ CaCO}_3$; total P: $10\text{--}106$ ($\bar{x} = 49$) $\mu\text{g l}^{-1}$; total N: $310\text{--}1,820$ ($\bar{x} = 900$) $\mu\text{g l}^{-1}$). Although exhibiting C_3 photosynthesis, hydrilla also is capable of fixing CO_2 into C_4 acids for subsequent decarboxylation through an inducible C_4 -like mechanism. Flowering (North America) occurs nearly year-round (January–November). Two major genetic strains (commonly referred to as “biotypes”) occur in North America, and are represented either by monoecious individuals or as pistillate clones of a dioecious strain (entirely staminate plants remain unknown in North America). The abiotic pollination system of *Hydrilla* is unique and difficult to characterize. The staminate flowers are released in bud from either male or monoecious shoots, and float individually to the water surface. The stamens remain reflexed under tension until the flower buds reach the surface before opening as distinct, free-floating structures. Concurrently, the pistillate flowers arise from female or monoecious shoots on which they remain attached by an elongate floral hypanthium, which extends them to the water surface. The pistillate flowers open at the water surface, where the stigmatic surfaces are exposed to the air (but are kept dry) within the floating flowers. A sudden release of the stamen filaments from their tensed orientation occurs when the staminate flowers open at the water surface, which results in an explosive, ballistic discharge of pollen in the form of an aerial shower. The fortuitous landing of some grains upon a nearby, receptive stigma is necessary in order to achieve pollination. Both pollen and stigma remain dry during the process. From this description it is easy to see why seed set often is low to non-existent, and seeds rarely are found in (monoecious) North American plants. However, high seed production has occurred in Asian plants and experimentally manipulated crosses using various strains of international provenance also have produced numerous seeds, with a success rate of 71% between dioecious and monoecious strains. Such crosses have produced highly viable (90%) seeds characterized by high seedling survival. Detached shoots can remain buoyant for 1–6 days, during which time they can transport attached sexual or vegetative propagules across the water surface. Seeds in Asian

populations have germinated within 1 week when incubated in light at $23^{\circ}\text{C}\text{--}28^{\circ}\text{C}$. Those stored in darkness (in water or dry) for up to 1 year have germinated readily when brought under light. *Hydrilla* plants are perennials, which possess an incredible capacity for rapid, vegetative growth and reproduction by means of stem fragmentation, turions, stolons, and tubers (a.k.a. subterranean turions). They are known to reach expansive surface coverages ranging from 8.5 to 405 ha. Biomass estimates up to 2.275 kg m^{-2} (FW) have been reported. The doubling time of shoots is about 19.8 days, but occurs much more rapidly (2.5–11 days) for tubers. Stem fragments comprising a single node are capable of regrowth, with 68%+ regrowth observed for fragments having 3–5 nodes. Tubers and turions can develop from October to April. Individual tuber production can reach 375 month^{-1} resulting in sediment densities of 6046 m^{-2} and several million ha^{-1} . Although the tubers can survive in the sediments for more than 4 years, the turions are thought to live for only a single year. Natural germination rates under drawdown conditions have reached 80%. The tubers germinate best (88–100%) in the light at temperatures from 22°C to 30°C ; however, low temperatures (15°C) have resulted in reduced tuber germination in the monoecious (35–68%) and dioecious (~3%) strains. Both tubers and turions have survived desiccation by maintaining physiological activity after drying (e.g., 16 hr @ 30°C , 40% RH). However, tolerance to drying increases with the number of leaf whorls present and single node fragments can succumb to drying in as short as 2 hr. The tubers survive longer, with 16.7% viability observed after drying for 64 hr; whereas turion viability declines sharply as drying time approaches 8 hr. Turion production is enhanced under short photoperiods ($<12 \text{ hr}$ light) and in free-floating (non-rooted) plants but declines as plant density increases. The subterranean turions of monoecious plants are much more resistant to cold temperatures than intact dioecious plants. When kept in cold (4°C) water for 105 days, mortality increased to 98% for dioecious plants but only to 48% for monoecious turions. **Reported associates (North America):** *Acorus calamus*, *Alternanthera philoxeroides*, *Bacopa monnieri*, *Brasenia schreberi*, *Cabomba caroliniana*, *Callitriche*, *Ceratophyllum demersum*, *Ceratophyllum echinatum*, *Chara contraria*, *Cynodon dactylon*, *Cyperus strigosus*, *Echinodorus cordifolius*, *Egeria densa*, *Eichhornia crassipes*, *Elodea nuttallii*, *Heteranthera dubia*, *Heteranthera multiflora*, *Hydrocotyle umbellata*, *Hygrophila polysperma*, *Juncus acuminatus*, *Lemna minor*, *Lemna perpusilla*, *Limnobium spongia*, *Ludwigia grandiflora*, *Ludwigia octovalvis*, *Luziola fluitans*, *Myriophyllum aquaticum*, *Myriophyllum laxum*, *Myriophyllum spicatum*, *Najas flexilis*, *Najas gracillima*, *Najas guadalupensis*, *Najas minor*, *Nelumbo lutea*, *Nitella*, *Nuphar*, *Nymphaea odorata*, *Nymphoides aquatica*, *Nyssa aquatica*, *Ottelia alismoides*, *Pistia stratiotes*, *Pontederia cordata*, *Potamogeton amplifolius*, *Potamogeton crispus*, *Potamogeton diversifolius*, *Potamogeton foliosus*, *Potamogeton nodosus*, *Potamogeton perfoliatus*, *Potamogeton pusillus*, *Potamogeton spirillus*, *Potamogeton zosteriformis*, *Sagittaria kurziana*, *Sagittaria latifolia*, *Salvinia minima*, *Spirodela polyrrhiza*, *Stuckenia*

pectinata, *Taxodium distichum*, *Trapa natans*, *Utricularia foliosa*, *Utricularia gibba*, *Vallisneria americana*, *Xyris*.

Use by wildlife: *Hydrilla verticillata* is grazed by Suwannee cooters (Reptilia: Testudines: Emydidae: *Pseudemys concinna suwanniensis*), which on average consume 850 g (WM) [68 g DM] turtle⁻¹ day⁻¹. *Hydrilla* collections from the southern United States have documented as many as 131 associated insect (Insecta) species. Of these, the plants are damaged or grazed primarily by aphids (Hemiptera: Aphididae: *Rhopalosiphum nymphaeae*), caddisflies (Trichoptera: Leptoceridae: *Leptocerus americanus*, *Nectopsyche tavra*, *Oecetis cinerascens*, *Triaenodes*), midges (Diptera: Chironomidae: *Ablabesmyia rhamphe*, *Apedilum elachistus*, *Cricotopus bicinctus*, *C. tricinctus*, *C. politus*, *C. sylvestris*, *Dicrotendipes*, *Endochironomus*, *Glyptotendipes*, *Larsia decolorata*, *Nanocladius alternantherae*, *Parachironomus hazelriggi*, *Pentaneura inconspicua*, *Pseudochironomus richardsoni*, *Tanytarsus buckleyi*), moths (Lepidoptera: Crambidae: *Oxyelophila callista*, *Paraponyx allionealis*, *P. diminulatis*, *P. obscuralis*, *Synclita oblitalis*), and shore flies (Diptera: Ephydriidae: *Hydrellia bilobifera*). The plants also are eaten by grass carp (Vertebrata: Teleostei: Cyprinidae: *Ctenopharyngodon idella*). Although hydrilla typically is viewed as a noxious weed, some studies have found enhanced benthic productivity where the plants have been established in previously unvegetated zones. The plants also have been found to increase foraging access in several bird (Aves) species, including American coots (Rallidae: *Fulica americana*), ducks (Anatidae), and pied-billed grebes (Podicipedidae: *Podilymbus podiceps*). *Hydrilla* is used for nest construction by the invasive brown hoplo catfish (Vertebrata: Teleostei: Callichthyidae: *Hoplosternum littorale*). *Hydrilla* plants also host epiphytic Cyanobacteria (Notocales: Hapalosiphonaceae: *Aetokthonos hydrillicola*), which produce a toxin known to cause avian vacuolar myelinopathy in the federally endangered Florida snail kite (Aves: Accipitridae: *Rostrhamus sociabilis*).

Economic importance: **food:** *Hydrilla* foliage contains about 19–25% (dw) crude protein and from 0.1% to 2% of 16 amino acids (nine essential); however, it has not been used as a human food; **medicinal:** *Hydrilla* extracts contain natural antioxidants (free radical scavenging activity: 29.6% inhibition at 100 µg ml⁻¹) and exhibit antimicrobial activity (primarily against Gram-positive bacteria); **cultivation:** *Hydrilla verticillata* has been popular as an aquarium plant, but due to its aggressive growth characteristics, its cultivation is emphatically discouraged anywhere beyond its indigenous range; **misc. products:** *Hydrilla* plants have been used for the phytoremediation of aqueous solutions contaminated by dyes and heavy metals and for domestic wastewater treatment. They also have been evaluated for compost production, biofuel production, and in the phytofabrication of silver nanoparticles. Feed for domestic laying hens (Aves: Phasianidae: *Gallus gallus domesticus*) has been supplemented by including up to 7.5% hydrilla without inducing any deleterious dietary effects. *Hydrilla* plants also have been considered as a viable feed for domestic cattle

(Mammalia: Bovidae: *Bos taurus*); **weeds:** *Hydrilla verticillata* is listed as a Federal noxious weed in the United States and is regarded as a notorious weed throughout its nonindigenous range. Some Florida populations exhibit varying levels of resistance to carotenoid biosynthesis inhibiting herbicides (e.g., Fluridone), which arise from somatic mutations occurring at a single codon in the phytoene desaturase (*pds*) gene; **nonindigenous species:** *Hydrilla* is nonindigenous throughout the New World. It was introduced to North America in the mid-20th century (~1959) through the careless disposal of aquarium plants. The nonindigenous New World range of *Hydrilla* has expanded southward into Central America and more recently (~2005) to South America (Brazil). Molecular data indicate that the US “monoecious biotype” originated from China or South Korea, and the US “dioecious biotype” from India. Recently, a third genetic strain has been documented from the United States (Connecticut River, CT), which is similar genetically to plants occurring in Ireland, Japan, Korea, and Latvia. Adventive *Hydrilla* populations also occur in Ireland, New Zealand, and South Africa. Ecological niche models have predicted a future increase of about 17% in potential North American hydrilla habitat due to changing climatic conditions.

Systematics: Phylogenetic analyses typically place the monotypic *Hydrilla* within subfamily Hydrilloideae of Hydrocharitaceae, either in proximity of *Nechamandra* and *Vallisneria* (e.g., Figure 1.8), or closer to *Najas*, depending on the data source and method of analysis implemented. A relationship to *Najas* has been suspected based on the shared occurrence of unusual abaxial midvein teeth in both genera, a morphological feature that occurs in no other alismatid genus. The genetic structure of *Hydrilla verticillata* has been studied quite extensively by analyses of various markers (e.g., isozymes, ISSRs, RAPDs) as well as by nuclear and plastid DNA sequence data. Isozyme data provided early genetic evidence for two independent origins of hydrilla plants in North America, which since have been characterized as dioecious and monoecious “biotypes” with respect to their corresponding sexual conditions. These two, distinct, nonindigenous North American strains have been confirmed subsequently by various genetic data; however, recent studies also have discovered a third strain (introduced to New England, USA) for which the sexual condition has not yet been determined (Figure 1.11). Although several *Hydrilla* haplotypes (5–9) have been described on the basis of plastid sequence data, analyses of nuclear sequence data have disclosed that substantially greater genetic diversity exists in the species due to extensive hybridization, which has occurred among all the strains throughout their Old World range. Even though the US dioecious and monoecious biotypes (Figure 1.11) represent specific haplotypes (i.e., H1/H2 and H5, respectively), both were derived initially through hybridization involving other Old World haplotypes. However, field studies and genetic analyses conducted at one North American reservoir indicate that hybridization between the dioecious and monoecious strains did not occur there, despite their sympatric occurrence. The basic chromosome

FIGURE 1.11 Genetic substructure in *Hydrilla verticillata* as illustrated by plastid *trnL-F* haplotype sequences (adapted from Tippery et al., 2020). Geographical affinities of coded haplotypes are as follows: H1/H2 (Brazil, Burundi, China, India, Nepal, Pakistan, the United States [dioecious strain], Vietnam); H3/H4 (Australia, China, New Zealand); H5 (China, Korea, the United States [monoecious strain]); H6/H7 (Australia, China, Indonesia, Malaysia, South Africa, Taiwan, Thailand, Vietnam); H8/H9 (China, Ireland, Japan, Korea, Latvia, Poland, the United States [Connecticut River]). The three nonindigenous US strains are highlighted in bold. Extensive hybridization has occurred among these basic strains throughout various portions of the Old World (see text).

number of *Hydrilla* is $x=8$. *Hydrilla verticillata* contains diploid, triploid, and tetraploid cytotypes ($2n=16, 24, 32$), with North American populations commonly being triploid. Chromosome variation in *Hydrilla* originates at least in part by endopolyploidy, which has been indicated by documentation of triploid plants at sites where only diploids had occurred previously, and moreover, by the observation of different polyploid cells ($2n=16, 24, 32$) found within single, clonal populations or even within individual root tips. *Hydrilla* occurrences recently have been detected successfully from environmental DNA (eDNA) samples.

Distribution: *Hydrilla verticillata* occurs in the eastern and western United States, with a southward extension into South America (Brazil).

References: Abdul-Alghaffar & Al-Dhamin, 2016; Adler et al., 2018; Balciunas & Minno, 1985; Baniszewski et al., 2016; Basiouny et al., 1978; Benoit, 2011; Benoit & Les, 2013; Benoit et al., 2019; Bianchini, Jr. et al., 2010; Bowes et al., 1977; 1979; Boyd, 1969; Canfield et al., 1985; Cook, 1982; 1996a; Cook & Lüönd, 1982a; Dodd et al., 2016; Easley & Shirley, 1974; Esler, 1990; Evans & Wilkie, 2010; Godfrey & Wooten, 1979; Grajczyk et al., 2009; Haller et al., 1976; Haug et al., 2019; Haynes, 2000b; Holaday & Bowes, 1980; Hoyer et al., 1996; Kanabkaew & Udomphon, 2004; King & Les, 2016; Lal & Gopal, 1993; Langeland, 1989; Langeland & Sutton, 1980; Langeland et al., 1992; Les et al., 1997c; Low et al., 1994; Madeira et al., 2000; Maki & Galatowitsch, 2008; Matsushashi et al., 2019; McDowell et al., 1990; Michel et al., 2004; Miller et al., 1993; Ming et al., 1994; Netherland, 1997; Nico & Muench, 2004; Osborne & Sassic, 1981; Owens et al., 2001; Pandi & Rajkumar, 2015; Pieterse, 1981; Posey et al., 1993; Promdee et al., 2018; Reiskind et al., 1997; Sable et al., 2012; Scott & Osborne, 1981; Simberloff & Leppanen, 2019; Sousa, 2011; Steward, 1991; 1993; Steward & Van, 1987; Stratman et al., 2013; Sutton et al., 1992; Tippery et al., 2020; True-Meadows et al., 2016; Van & Steward, 1990; Van et al., 1977; Verkleij et al., 1983; Williams et al., 2017; Wood & Netherland, 2017; Zhu et al., 2017.

2.3.6. Hydrocharis

Frog-bit; grenouillete, hydrocharide

Etymology: from the Greek *hydro chaeri*, meaning “water delight”

Synonyms: *Bootia* (in part); *Hydrochaeris*; *Monochoria* (in part); *Ottelia* (in part); *Pontederia* (in part)

Distribution: **global:** Africa, Australia, Eurasia, North America*; **North America:** northeastern

Diversity: **global:** 3 species; **North America:** 1 species

Indicators (USA): **obligate wetland (OBL):** *Hydrocharis morsus-ranae*

Habitat: freshwater; lacustrine, palustrine, riverine; **pH:** 6.5–7.8; **depth:** <1 m; **life-form(s):** floating-leaved or free-floating

Key morphology: plants floating freely or rooted in sediment; shoots contracted and rosulate or stoloniferous (to 20 cm), bearing simple or branched adventitious roots (to 50 cm), and terminating in summer buds (to 15 mm) or turions (to 9 mm); leaves aerenchymatous on underside, the blades (to 6.3 cm) orbicular, cordate at base, petioled (to 14 cm), with paired, free stipules (to 2.5 cm); flowers trimerous, unisexual, the plants dioecious or (rarely) monoecious; ♂ flowers (1–5) pedicelled (to 4 cm), arising from a peduncled (to 5.5 cm) spathe (to 1.2 cm); sepals (to 5.5 mm) greenish or white; petals (to 1.9 cm) white, obovate to orbicular; stamens (9–12) in 4 whorls; ♀ flowers solitary, pedicelled (to 9 cm); sepals (to 5 mm) greenish; petals (to 1.5 cm) white, obovate to orbicular, 3 staminodes present, styles (to 5 mm) 6, bifid (to ⅔ of length), ovary spherical, 6-carpelled; capsules (to 1 cm) berrylike, with numerous, bluntly papillate seeds (to 1.3 mm)

Life history: **duration:** perennial (stolons, turions); **asexual reproduction:** stolons, tubers, turions (stolons); **pollination:** insect; **sexual condition:** dioecious, monoecious; **fruit:** berrylike capsule (infrequent); **local dispersal:** seeds, turions (water); **long-distance dispersal:** whole plants or fragments (birds, humans [boating and fishing equipment]); seeds, turions (water, waterfowl)

Imperilment: 1. *Hydrocharis morsus-ranae* [GNR]

Ecology: general: All *Hydrocharis* species are perennial, floating-leaved aquatics. The plants grow either as free-floating rosettes on the water surface or can become rooted in the sediment when in shallower water. The flowers are unisexual and are arranged in a dioecious or monoecious condition; single rosettes mostly bear flowers of the same sex. The flowers of both sexes possess showy perianths, produce nectar (♀ only), and are pollinated primarily by insects. Vegetative reproduction can occur by the extension of stolons and also by the production of tubers during the summer, and by turions, which detach and overwinter. The characteristics of all three species are quite similar and are exemplified well by the following species.

2.3.6.1. *Hydrocharis morsus-ranae* L. is a nonindigenous species, which occupies shallow, mesotrophic North American waters (e.g., 0.5–0.6 m) associated with canals, channels, ditches, floodplains, impoundments, lagoons, lakes, marshes, ponds, rivers, streams, and swamps at elevations to 378 m (to 1500 m elsewhere). The plants have been observed in open and shaded sites (usually sheltered) and in clear to

turbid waters, which often are rich in organic matter. Shading has little influence on growth unless levels exceeding 50% are maintained. The plants have been described as favoring both calcium-poor waters and calcareous waters; North American sites represent circumneutral conditions (pH: 6.5–7.8). The plants do not appear to be well adapted to acidic, nutrient-poor (oligotrophic) conditions. They have been reported on substrates described as clay, detritus, mud, and rocky sandy silt. Flowering occurs from mid-June through August (North America). Floral sex expression is quite labile. Typically, the rosettes are unisexual (the plants being dioecious); however, a plant infrequently can produce both male and female rosettes (the plant then monoecious). Plants of a known sex also have been observed to produce plants of the opposite sex, which were derived vegetatively from their turions. The flowers open by early morning, become receptive by mid-day, and are pollinated by insects (see *Use by wildlife*). Despite the unisexual flowers and prevalent dioecy, genetic data (allozyme markers) have indicated low levels of variation and a relatively high degree of inbreeding. When formed, the maturing fruits are pushed beneath the water surface by a curving peduncle. Seed production often is uncommon (due in part to low pollinator visitation rates), but reportedly initiates in mid-August. It can be locally abundant (over 250 m⁻²), reaching 2,000–3,000 seeds m⁻² in some cases; however, few seedlings survive, even in such cases. An average of 26–42 seeds (to a maximum of 74 seeds) is produced per flower. Individual seed production generally is greater (e.g., 55–60 seeds) in high-density mats than in low density mats (e.g., 15–20 seeds). The seeds are enclosed in mucilage and are released when the capsules swell and burst after about 5 weeks following peduncle curvature. The seeds (averaging 0.17 g) float upon their release and are dispersed primarily by water currents, although the mucilaginous coating also is suspected to facilitate their attachment to the feet of waterfowl (Aves: Anatidae). The seeds germinate as the water temperatures rise above 15°C. A fairly high experimental seed germination rate (69%) has been achieved after 16 months of cold storage and subsequent exposure to high light levels. The seeds are known to retain viability after 2 months of storage at –20°C. The principal means of reproduction is vegetative through the production of stolons and turions. Individual plants can produce up to 150 turions. Between 15°C and 25°C, the turions are initiated by photoperiod, with higher temperatures requiring shorter photoperiods. No turions form below 10°C, but they develop readily at temperatures above 25°C regardless of photoperiod. Turions can remain dormant for at least 2 years, with greater dormancy characteristic of those that initiate at higher temperatures. Mature turions detach and sink to the bottom, where they remain for about 7 months; they cannot withstand prolonged periods of freezing (i.e., >10 days to several weeks). Turions require light for germination unless they have been thoroughly vernalized (i.e., cold stratified). The turions germinate from April to May and float to the surface. Individual turions can develop into fairly large plants (to 1 m²) within a single growing season. Great blue herons (Aves: Ardeidae: *Ardea herodias*) have been seen with whole,

entangled plants attached for significant distances (e.g., 2 km) and turions (of uncertain viability) have been recovered from the digestive tracts of American black ducks (Anatidae: *Anas rubripes*). **Reported associates (North America):** *Butomus umbellatus*, *Carex*, *Cephalanthus occidentalis*, *Equisetum fluviatile*, *Hottonia inflata*, *Lemna minor*, *Lythrum salicaria*, *Myriophyllum sibiricum*, *Myriophyllum spicatum*, *Nuphar variegata*, *Nymphaea odorata*, *Phalaris arundinacea*, *Phragmites australis*, *Pontederia cordata*, *Potamogeton crispus*, *Potamogeton epihydrus*, *Potamogeton pusillus*, *Potamogeton vaseyi*, *Sagittaria graminea*, *Sagittaria rigida*, *Salix*, *Scirpus*, *Sparganium*, *Spirodela polyrhiza*, *Trapa natans*, *Typha angustifolia*, *Typha latifolia*, *Utricularia macrorhiza*.

Use by wildlife: *Hydrocharis morsus-ranae* is eaten by various ducks (Aves: Anatidae), grass carp (Teleostei: Cyprinidae: *Ctenopharyngodon idella*), mice (Mammalia: Rodentia: Muridae), and snails (Mollusca: Gastropoda: Lymnaeidae: *Lymnaea*; Physidae: *Physa*; Planorbidae: *Helisoma*). The leaves also are eaten by larval moths (Insecta: Lepidoptera: Crambidae: *Elophila icciusalis*, *Synclita occidentalis*). In North America, the flowers are visited by numerous insects (Insecta) including aphids (Hemiptera: Aphididae) and flies (Diptera: Ephydriidae: *Hydrellia*, *Notiphila*), although the principal pollinators appear to be fairly specialized hover flies (Diptera: Syrphidae: *Toxomerus marginatus*) and solitary bees (Hymenoptera: Halictidae: *Lasioglossum*).

Economic importance: food: *Hydrocharis* plants contain from 22% to 24% crude protein, but have been described as “almost tasteless” and are of little culinary interest. They impart a reddish coloration to cooking water; **medicinal:** no uses reported; **cultivation:** *Hydrocharis morsus-ranae* is grown as an ornamental aquarium and water garden plant; **misc. products:** *Hydrocharis morsus-ranae* is easily cultivated and has been used as an experimental plant for physiological and developmental studies; **weeds:** *Hydrocharis morsus-ranae* can develop into dense floating mats and has been reported as a nuisance in Canada (Ontario and Quebec) and the United States (New York); **nonindigenous species:** In North America, *Hydrocharis morsus-ranae* was originally cultivated by an arboretum in Ottawa, Canada from material sent from Zürich, Switzerland in 1932; it was first observed as an escape in the region in 1939. The subsequent spread of plants through North America (at a rate of roughly 17 km year⁻¹) has been facilitated by their dispersal on boats and boat trailers. Plants also have been observed for sale at some local retail shops in the United States, and likely also have escaped from cultivation in water gardens.

Systematics: Analyses of DNA sequence data for two of the three *Hydrocharis* species indicate that the genus is related most closely to (but not necessarily distinct from) *Limnobium* (Figure 1.8). However, a simultaneous phylogenetic analysis of all three *Hydrocharis* species and both *Limnobium* species will be necessary to determine whether these two genera actually resolve as distinct sister clades, which appears to be the case when fewer exemplars are evaluated (Figure 1.12). Such an analysis also is necessary to determine the interspecific

FIGURE 1.12 Intergeneric relationships in Hydrocharitaceae based on analysis of complete cpDNA gene sequence data (adapted from Ross et al., 2016). Although only those taxa designated as OBL in North America are indicated in bold, the entire group shown comprises aquatic species.

relationships in *Hydrocharis*. DNA sequence data indicate that *Hydrocharis* and *Limnobium* have diverged approximately 11.7 million years before present (MYBP). The base chromosome number of *Hydrocharis* is $x=7$ or 8. *Hydrocharis morsus-ranae* ($2n=28$) presumably is tetraploid. No hybrids involving any member of the genus have been reported, due at least in part to the highly allopatric distributions of the three species.

Distribution: *Hydrocharis morsus-ranae* occurs in north-eastern North America.

References: Casper & Krausch, 1980; Catling & Dore, 1982; Catling & Porebski, 1995; Catling et al., 1988; 2003; Cook & Lüönd, 1982b; Dore, 1954; 1968; Haynes, 2000b; Lamoureux, 1987; Les & Tippery, 2013; Les et al., 2003; Mühlberg, 1982; Scribailo & Posluszny, 1983; 1984; 1985; Scribailo et al., 1984; Zhu, 2014; Zhu et al., 2014.

2.3.7. *Limnobium*

American frog-bit, American spongeplant

Etymology: from the Greek *limno bios* (“lake living”) in reference to the typical habitat

Synonyms: *Hydrocharella*; *Hydrocharis* (in part); *Hydromystria*; *Jalambicea*; *Rhizakenia*; *Trianea*

Distribution: **global:** New World (Americas); **North America:** southeastern United States

Diversity: **global:** 2 species; **North America:** 1 species

Indicators (USA): obligate wetland (OBL): *Limnobium spongia*

Habitat: freshwater; lacustrine, palustrine, riverine; **pH:** 5.6–8.6; **depth:** <1 m; **life-form(s):** emergent, floating-leaved, free-floating

Key morphology: plants floating freely or rooted in sediment; shoots dimorphic: contracted and rosulate, bearing branched adventitious roots (to 60 cm), or stoloniferous (to 15+ cm), terminating in new rosettes or compact winter buds; foliage dimorphic: aerial leaves with flat, leathery blades, and long, erect petioles (to 40 cm); floating leaves with thick spongy

pad of tissue on lower surface, and shorter petioles (0.8–12 cm); blades (to 10 cm), broadly ovate, apex acute, the base often cordate, stipules median, conspicuous (to 8 cm), longer on erect leaves; flowers trimerous, unisexual, the rosettes unisexual or monoecious; ♂ flowers (to 25), pedicelled (to 9 cm), arising from a peduncled (to 3.5 cm) spathe (to 6.3 cm); sepals (to 9 mm) greenish or yellowish, becoming reflexed; petals (to 9.4 mm) whitish, linear to lanceolate, stamens (3–16) inserted on a column, in 5–6 whorls, the latter three usually staminal; ♀ flowers (to 6) pedicelled (to 12 cm, but elongating further in fruit), arising from a peduncled (to 1.5 cm) spathe (to 5.5 cm); sepals (to 9.3 mm) elliptical, spreading; petals (to 14 mm) spreading, greenish-white; staminodes (to 3.3 mm) 2–6; ovary (to 8.5 mm) unilocular, styles (to 20 mm) 6–9, divided to ¼ their length; capsule (to 18 mm) oblong, berry-like; seeds (to 2.3 mm) numerous (to 200), covered by spike-like trichomes (to 0.4 mm)

Life history: **duration:** perennial (stolons, turions, whole plants); **asexual reproduction:** stolons, turions; **pollination:** wind; **sexual condition:** dioecious, monoecious; **fruit:** capsule (berrylike) (common); **local dispersal:** water (seeds, turions); **long-distance dispersal:** waterfowl (seeds, seedlings)

Imperilment: 1. *Limnobium spongia* [G4]; S1 (IL, IN, MD, NJ, WV); S2 (DE, KY, MO, NC); S3 (GA, VA)

Ecology: **general:** Both *Limnobium* species are perennial, emergent or floating-leaved aquatics. As in *Hydrocharis*, the plants can float freely as rosettes on the water surface (and grow in mats of other floating vegetation), or become rooted in the sediment when growing in sufficiently shallow water or on exposed substrates. Floating leaves develop on plants growing in more than 10 cm of water; the roots can anchor in the substratum when the water depth is below 60 cm. Vegetative plasticity (e.g., see above description) can be fairly extensive and represents an adaptive response to the various habitats (e.g., exposed sites vs. inundated sites) in which the plants may be found. The root caps are easily removed without damage, and are thought to facilitate the liberation of rooted plants from the sediment as water levels rise. The flowers are unisexual and although primarily of mixed sexes (the plants then monoecious), a single rosette also can be unisexual (individual plants, or at least separate ramets, then potentially dioecious). Unlike *Hydrocharis*, the flowers are not showy, lack nectar, and are pollinated abiotically by the wind.

2.3.7.1. *Limnobium spongia* (Bosc) Rich. ex Steud. grows in shallow (e.g., 0.5–100 cm), still or slowly moving waters, or on exposed, saturated substrates associated with baygalls, bayous, borrow pits, bottomlands, canals, channels (roadside), ditches (roadside), flats, floodplains, gravel bars, lakes, marshes (depression), meadows (flooded), mudflats, ponds, prairies, reservoirs, rivers, roadsides, shell pits, sinkholes, sloughs, springs (edges), streams, swales, and swamps at elevations to 204 m. Site exposures can range from full sun to shaded conditions. The substrates have been characterized as alluvium, clay, entisols (loamy), gravel, muck (Barbary, organic, Shenks), mud, Nittau (typic argiaquolls), peat, sand (coarse), silt, and silty clay. The plants are variable phenotypically, producing long-stalked, erect, coriaceous leaves

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