

Eleocharis compressa var. *compressa*

Flat-stem Spike-rush

Cyperaceae



Eleocharis compressa by Pat Deacon, 2020

Eleocharis compressa var. *compressa* Rare Plant Profile

New Jersey Department of Environmental Protection
State Parks, Forests & Historic Sites
State Forest Fire Service & Forestry
Office of Natural Lands Management
New Jersey Natural Heritage Program

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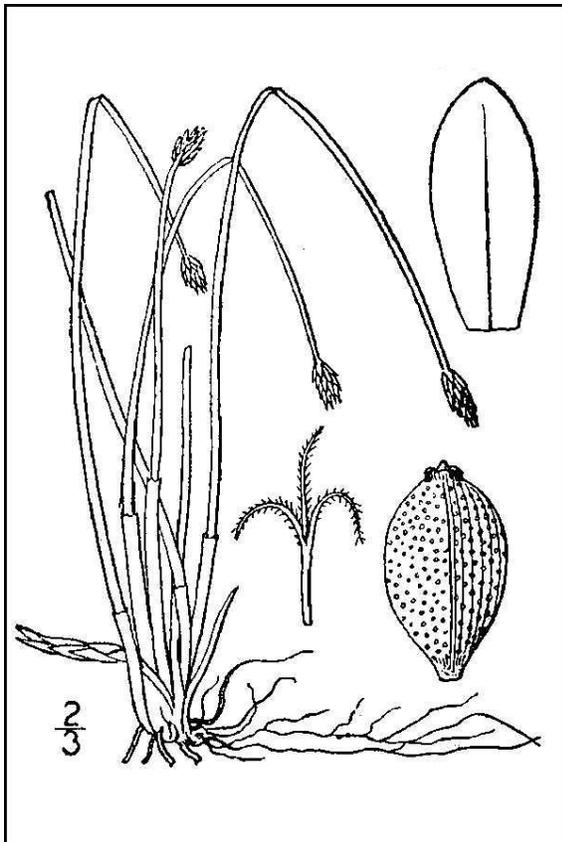
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Life History

Eleocharis compressa var. *compressa* (Flat-stem Spike-rush) is a rhizomatous perennial sedge. Vegetative propagation via the firm, stout (2–3 mm diameter) purplish rhizomes often results in a matted distribution of the plants. *Eleocharis* plants have leafless culms that are sheathed at the base and end in a single spikelet. The culms of *E. compressa* var. *compressa* are narrow, ranging from 0.8–1.5 mm in width, but they are distinctly flattened so their width is 2–5 times greater than their thickness. The flattened stems can be useful in distinguishing *E. compressa* var. *compressa* from some closely related species. The stems may be up to 50 cm tall and the sheaths are reddish at the base and green or straw-colored and papery near the top. The spikelets are ovoid, 4–8 mm long and half as wide, and have 20–60 floral scales that spread at maturity. The scales are chestnut brown with paler tips that often split, the three stamens have yellow-orange anthers, and the styles of the pistillate flowers are usually three-branched. The fruits are one-seeded achenes that are somewhat three-sided in cross-section and are topped with conic tubercles. The achenes have a rough surface and are yellow-brown or brown in color. When bristles are present there may be 1–5 and they are usually shorter than the achene. (See Britton and Brown 1913, Svensen 1932, Fernald 1950, Fassett 1957, Drapalik and Mohlenbrock 1960, Godfrey and Wooten 1981, Gleason and Cronquist 1991, Smith et al. 2020).



Left: Britton and Brown 1913, courtesy USDA NRCS 2023a. Right: John Hilty, undated.

Throughout its range, *Eleocharis compressa* var. *compressa* typically flowers in May or June (Weakley et al. 2022). Hough (1983) reported that New Jersey plants usually bloom and develop

fruit between mid-June and late July. However, fruit can be present from late spring through winter (Smith et al. 2020).



Flowering culms by Pat Deacon, 2019.



Basal sheaths by John Hilty, undated.

The other variety of *Eleocharis compressa*, *E. compressa* var. *acutisquamata*, is not found in New Jersey. Many of the sources cited in this profile discussed *Eleocharis compressa* without specifying a variety. However, the two varieties are very similar in both morphology and habitat requirements (Smith et al. 2020).

Pollinator Dynamics

Eleocharis compressa var. *compressa* is probably pollinated by wind. Wind is the predominant pollination mechanism for the majority of species in the Cyperaceae, although there are a few notable exceptions in scattered genera including *Eleocharis* (Goetghebeur 1998). Adaptations to wind pollination in the family include large anthers, long filaments, and prominent stigmas (Zomlefer 1994). The sedges that are fertilized by insects generally have other modifications to attract pollinators: For example, *Eleocharis elegans* has showy, scented floral spikes (Magalhães et al. 2005). Goetghebeur (1998) indicated that sedges with insect visitors were usually also pollinated by wind. Some insects obtain pollen from wind-pollinated plants without aiding in cross-fertilization—a topical review by Saunders (2018) found that almost half of the records of bee and syrphid fly species collecting pollen from wind-pollinated plant taxa were for graminoid species.

Cross-pollination is presumed for the majority of sedges, and most species improve the probability of cross-fertilization by developing female flowers in advance of male flowers and/or by achieving floral maturity in a bottom-to-top sequence (Goetghebeur 1998). However, the strategy may be less effective in clonal species. Observations of another clonal spike-rush (*Eleocharis mutata*) showed that the culms continued to elongate as they matured so that pollen from the later-developing staminate flowers was likely to fall on the stigmas of younger pistillate flowers in the same clump (Hill 1891). In some *Eleocharis* species, the transfer of pollen within clonal clusters has been identified as a possible cause of reduced seed viability (Demeda et al. 2018, Gudžinskas and Taura 2021).

Seed Dispersal and Establishment

Eleocharis achenes are likely to be dispersed by multiple means including gravity, animals, and water (Leck and Schütz 2005). The seeds of various *Eleocharis* species are consumed by ducks, geese, gulls, grouse, and shorebirds, often in large quantities (McAtee 1918, Martin and Uhler 1939, Fassett 1957, Morton and Hogg 1989). The dispersal of viable seeds following ingestion by waterfowl is well-documented, although results vary widely depending on both plant species and seed retention time (Soons et al. 2008, Wongsriphuek et al. 2008, Farmer et al. 2017). *Eleocharis* seeds may also be transported by birds that utilize plant stalks for nesting material or by adherence to feathers and feet (Morton and Hogg 1989, Leck and Schütz 2005). In water, *Eleocharis compressa* achenes have a relatively short flotation time and seldom maintain buoyancy for more than a day (Morton and Hogg 1989). However, even seeds that do not remain afloat can be transported by water movement or by attachment to floating vegetative matter (Leck and Schütz 2005).

Eleocharis compressa seeds that reach suitable locations may not sprout right away, as viable propagules have been found during multiple seed bank studies (eg. Abrams 1988, Beas et al. 2013, Zylka et al. 2016). The seeds of *E. compressa* are most likely to germinate in the spring, indicating that they are probably dormant at dispersal and require a period of low winter temperatures in order to finish ripening (Baskin and Baskin 1988). No information was found regarding the formation of fungal associations by *Eleocharis compressa* but it seems likely that they are not required for establishment. Some spike-rushes are mycorrhizal but many are not. Of the 14 *Eleocharis* species covered in a review by Wang and Qiu (2006) 21% were confirmed as mycorrhizal, 14% were sometimes mycorrhizal, and 64% were reported as non-mycorrhizal. Bohrer et al. (2004) reported that plants in wetlands can be colonized seasonally.

In aquatic settings, the movement of live vegetative matter such as root or rhizome fragments can be an effective and important means of dispersal (Boedeltje et al. 2004, Barrett 2015). While *Eleocharis compressa* seeds usually remain buoyant for less than a day its rhizomes can continue floating for more than a week (Morton and Hogg 1989). Vegetative propagules can also be relocated by nesting birds: Morton and Hogg found living rhizomes and rootstocks of numerous plant species in abandoned gull nests on an island in Lake Huron.

Habitat

Eleocharis compressa var. *compressa* has been found in a wide array of habitats ranging from rare and fragile communities to waste places. Flat-stem Spike-rush can occur at elevations of 0–2100 meters above sea level in shallow water, moist soil, or seasonally wet locations. The substrate is often calcareous but it may be composed of sand, gravel, rock, or peat. Reported habitats include grasslands, meadows, barrens, glades, fens, ditches, ponds, river shorelines, streambanks, tidal freshwater marshes, and intradunal pannes (Godfrey and Wooten 1981, Hough 1983, Hiebert et al. 1986, Rhoads and Block 2007, Tiner 2009, PANHP 2019, Smith et al. 2020, Weakley et al. 2022).

All of New Jersey's populations of *Eleocharis compressa* var. *compressa* are located along the shore of the Delaware River but three of the four are restricted to a very unusual community type that occurs on limestone ledges (NJNHP 2022). The association, *Deschampsia cespitosa* - *Carex viridula* Riverscour Wet Meadow, is critically imperiled globally (G1) because it is only known from three sites—all of which are in New Jersey. The sites are fed by groundwater seepage and the open communities are maintained by periodic flood scour. When large chunks of ice are transported down the river by spring snowmelt, most woody species are scraped off of the rocks but the herbaceous plants can rapidly regenerate from buried rootstocks and seeds. Vegetation is sparse where the rocks are smooth but denser in the crevices (Gawler 2006, Sneddon 2010, USNPS 2022).

Eleocharis compressa var. *compressa* can also be found in a similar kind of habitat, *Andropogon gerardii* - *Panicum virgatum* - *Baptisia australis* Riverscour Wet Meadow, that occurs elsewhere along the Delaware and other rivers in the east-central United States. The association is globally vulnerable (G3) due to fewer than 100 examples throughout its range. That community is also maintained by flood scour but it occurs on rapidly drained sandy soils and the typical dominant vegetation is an assortment of tall grasses such as *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and *Spartina pectinata* (Sneddon 2010, Sneddon et al. 2018).

There are several other types of highly specialized communities which develop over limestone substrate that have been known to support *Eleocharis compressa* var. *compressa*, including alvars and cedar glades. Alvars are dry grasslands that periodically become inundated or are sometimes seepage-fed. Flat-stem Spike-rush was noted as a characteristic species at an Ontario alvar (Catling 1977) and as an important component of the vegetation of an alvar on an island in Lake Erie (Belcher et al. 1992). The species is a primary component of the *Quercus muehlenbergii*/*Allium cernuum* - *Eleocharis compressa*/*Aulacomnium palustre* - *Bryum* spp. Wooded Grassland association which is globally critically imperiled (G1) and restricted to Ontario (NatureServe 2023). Two cedar glade communities in which *Eleocharis compressa* var. *compressa* is a defining species are also rare. The *Eleocharis (bifida, compressa)* - *Schoenolirion croceum* - *Carex crawei* - *Allium cernuum* Seep Grassland association is globally imperiled (G2) and the *Eleocharis (bifida, compressa)* - *Nothoscordum bivalve* Seep Grassland association is globally vulnerable (G3). The former association has been reported from Alabama, Georgia and Tennessee while the latter is restricted to Kentucky (NatureServe 2023). The frequency of *E. compressa* var. *compressa* has been known to vary considerably in these habitats (Baskin et al. 2007) but at one site the sedge became abundant enough to threaten the survival of another rare plant (Baskin and Baskin 1977).

Eleocharis compressa is often reported as a component of prairies and prairie remnants, particularly in poorly drained soils or depression wetlands (Klips 2003, Bried et al. 2019). Beas et al. (2013) assigned perennial prairie plants to five guilds based on their water depth preferences and placed *E. compressa* in the middle category (shallow emergent). Reemts and Belcher (2022) observed that *E. compressa* var. *compressa* was often found in microsites that held standing water for days or even weeks during the wetter parts of the year.

Bried et al. (2021) evaluated *Eleocharis compressa* for use as an indicator species of high floristic quality in wetlands but concluded that it was not well-suited to the purpose because it also frequently occurred in lower quality sites. The sedge has apparently persisted in places that were substantially altered by agricultural uses such as grazing and forage hay production (George and Nixon 1990, Reece et al. 1994), and Meissen et al. (2015) observed that the species seemed to benefit from frequent canopy removal in prairies that were regularly cleared with heavy machinery in order to obtain seeds for restoration projects at other locations. Mazanec (2020) successfully grew *E. compressa* on floating islands of vegetation to test its efficacy in removing excessive nutrients from aquatic systems (it was moderately effective).

Despite the fact that *Eleocharis compressa* appears to have multiple options for dispersal and can successfully establish and persist under so many different circumstances, reports of the species in restored prairie wetlands have been inconsistent. Zimmerman (1972) noted that the sedge was often missing from restored prairies and proposed the development of special techniques to promote its establishment in restorations. A comparative study of one undisturbed wetland complex and three wetland complexes that had undergone restoration 2–8 years earlier found that *E. compressa* was present in more than half of the wetlands sampled in the natural complex but was not in any restored sites (Mushet et al. 2002). In contrast, Beas et al. (2013) reported that *E. compressa* was abundant in restored wetlands that had been allowed to "self-design" after the substrate had been prepared. The colonization of a restored habitat by *E. compressa* may be governed by the proximity of a source population or by the random likelihood of a bird-dispersed propagule being transported to the site.

Wetland Indicator Status

The U. S. Army Corps of Engineers divided the country into a number of regions for use with the National Wetlands Plant List and portions of New Jersey fall into three different regions (Figure 1). *Eleocharis compressa* has more than one wetland indicator status within the state. In the Eastern Mountains and Piedmont region, *E. compressa* is listed as an obligate wetland species, meaning that it almost always occurs in wetlands. Throughout the rest of its range, *E. compressa* is considered a facultative wetland species, meaning that it usually occurs in wetlands but may occur in nonwetlands (U. S. Army Corps of Engineers 2020).

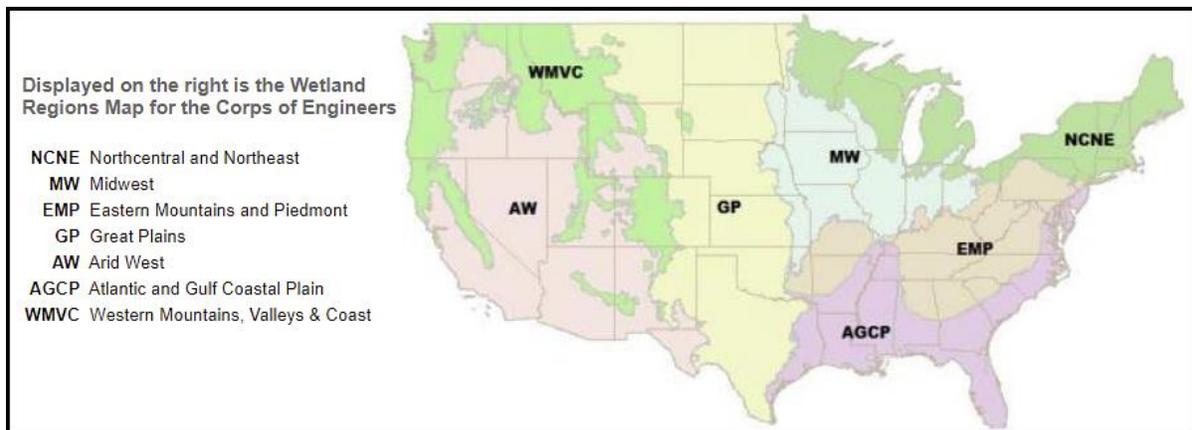


Figure 1. Mainland U. S. wetland regions, adapted from U. S. Army Corps of Engineers (2020).

USDA Plants Code (USDA, NRCS 2023b)

ELCOC2

Coefficient of Conservatism (Walz et al. 2018)

CoC = 10. Criteria for a value of 9 to 10: Native with a narrow range of ecological tolerances, high fidelity to particular habitat conditions, and sensitive to anthropogenic disturbance (Faber-Langendoen 2018).

Distribution and Range

The global extent of *Eleocharis compressa* var. *compressa* is limited to the central and eastern United States and Canada (POWO 2023). The map in Figure 2 shows the extent of *Eleocharis compressa* in North America without making a distinction between the two varieties. *E. compressa* var. *acutisquamata* does not occur east of Illinois (Smith et al. 2020).

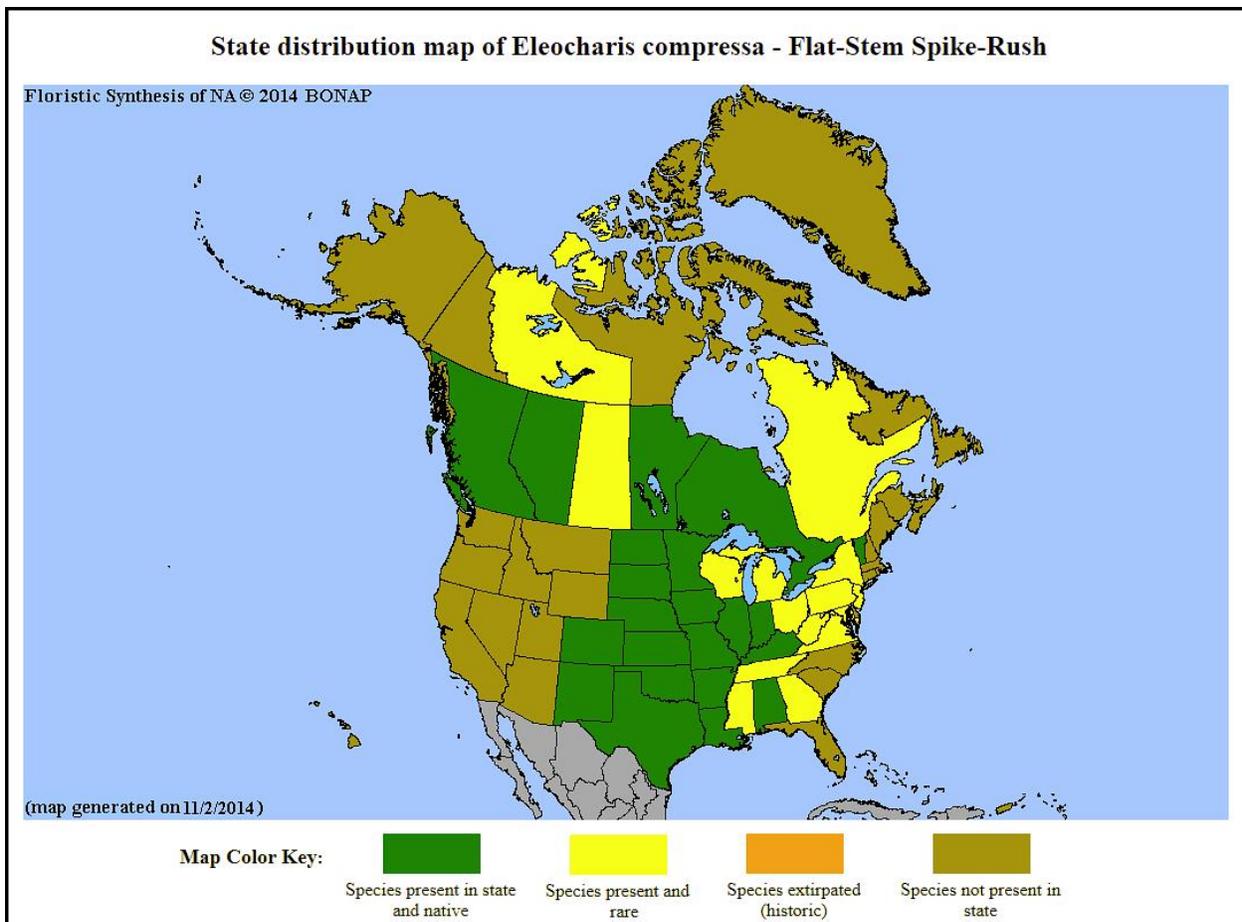


Figure 2. Distribution of *E. compressa* in North America, adapted from BONAP (Kartesz 2015).

The USDA PLANTS Database (2023b) shows records of *Eleocharis compressa* var. *compressa* in three New Jersey counties: Cape May, Sussex, and Warren (Figure 3). A number of specimens labeled as *E. compressa* also originated in Middlesex County (Mid-Atlantic Herbaria 2023). The data include historic observations and do not reflect the current distribution of the species. Hough (1983) particularly questioned the dependability of herbarium records for the species, noting that specimens of *Eleocharis tenuis* had sometimes been mislabeled as *E. compressa* because the two sedges had overlapping characteristics.

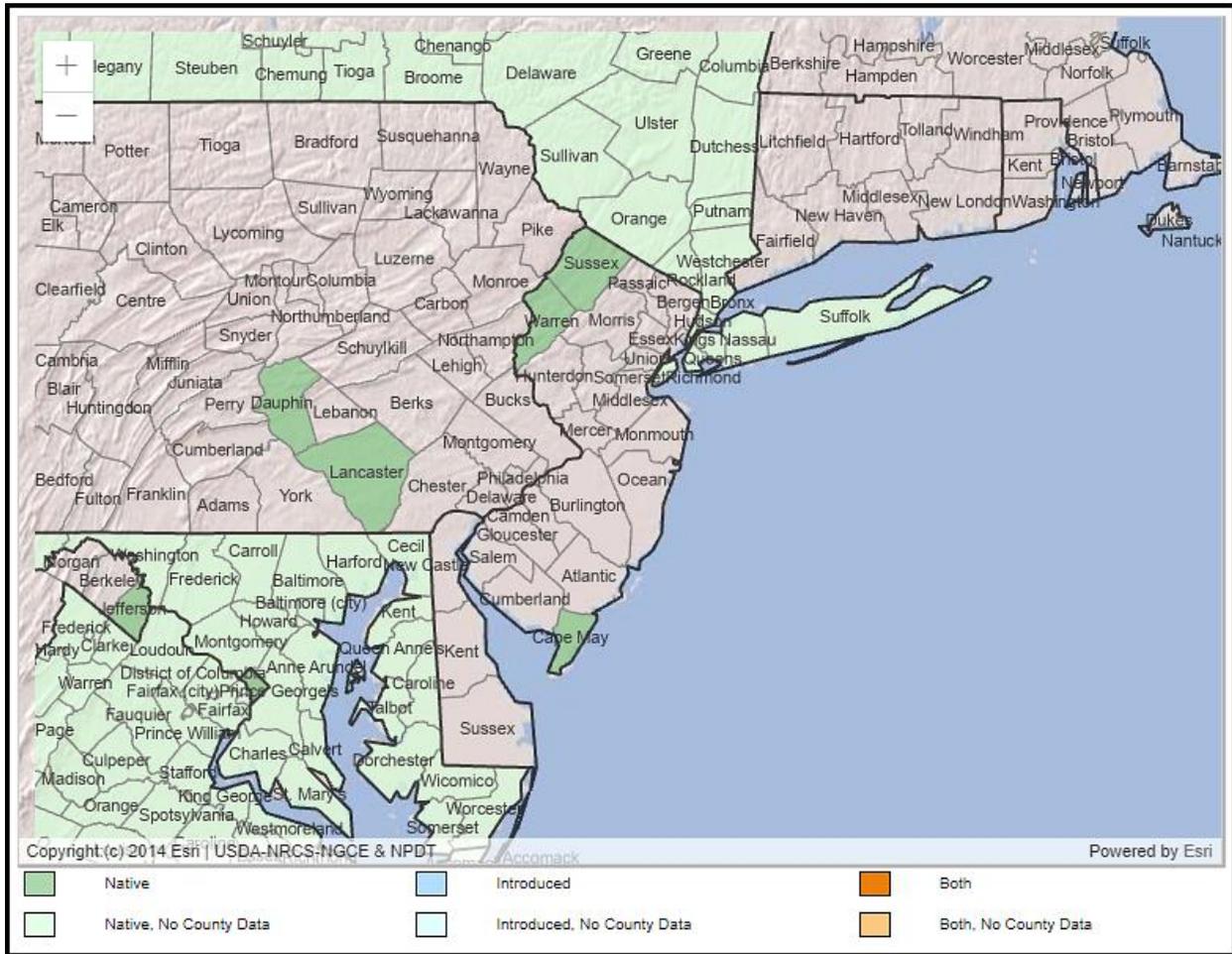


Figure 3. County records of *E. compressa* var. *compressa* in New Jersey and vicinity (USDA NRCS 2023b).

Conservation Status

Eleocharis compressa is apparently secure at a global scale. The G4 rank means the species is at fairly low risk of extinction or collapse due to an extensive range and/or many populations or occurrences, although there is some cause for concern as a result of recent local declines, threats, or other factors. The variety has not been ranked (NatureServe 2023). The map below (Figure 4) illustrates the conservation status of *Eleocharis compressa* throughout its range. Flat-stem Spike-rush is vulnerable (moderate risk of extinction) in four states, imperiled (high risk of

extinction) in seven states, critically imperiled (very high risk of extinction) in six states and two provinces, and possibly extirpated in Vermont. In other places where it occurs the species is secure, apparently secure, or unranked. In North America, *Eleocharis compressa* has also been identified as a plant species of highest conservation priority for the North Atlantic region, which includes four Canadian provinces and twelve U. S. states. The species has a regional rank of R3 (vulnerable), signifying a moderate risk of extinction in the region (Frances 2017).

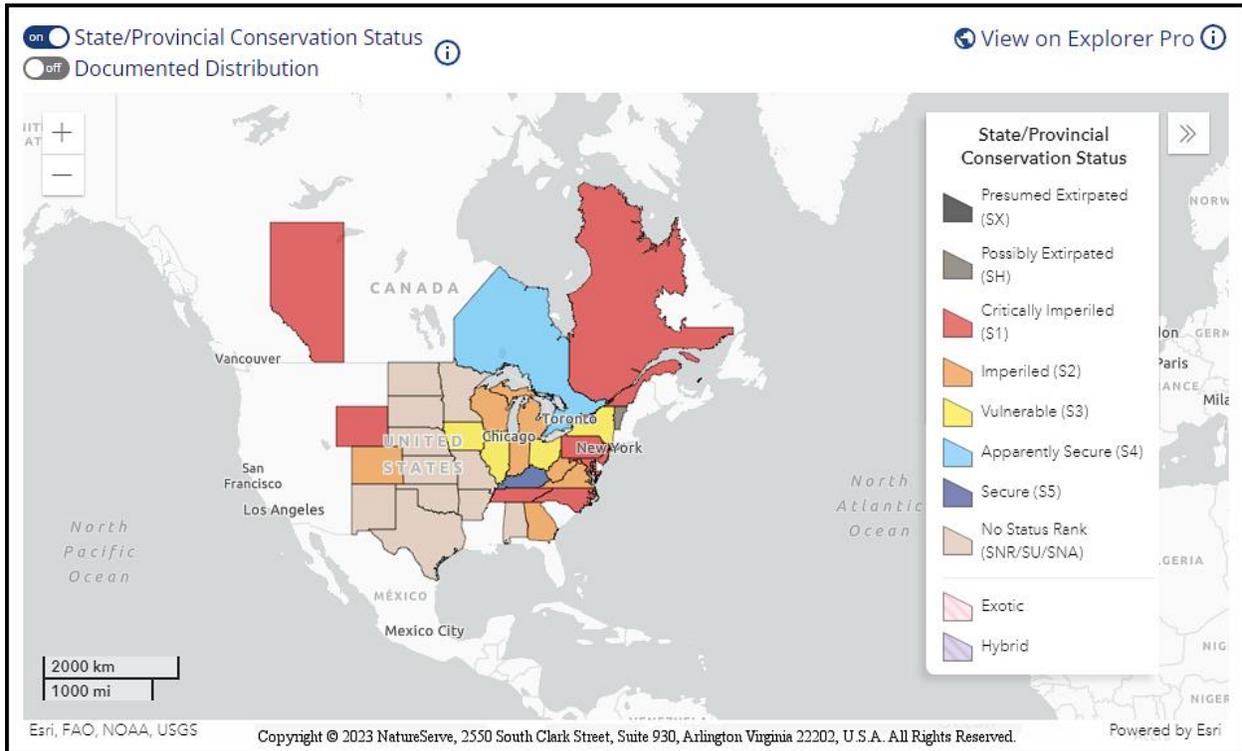


Figure 4. Conservation status of *E. compressa* in North America (NatureServe 2023).

Eleocharis compressa var. *compressa* is critically imperiled (S1) in New Jersey (NJNHP 2022). The rank signifies five or fewer occurrences in the state. A species with an S1 rank is typically either restricted to specialized habitats, geographically limited to a small area of the state, or significantly reduced in number from its previous status. Flat-stem Spike-rush is also listed as an endangered species (E) in New Jersey, meaning that without intervention it has a high likelihood of extinction in the state. Although the presence of endangered flora may restrict development in certain communities such as wetlands or coastal habitats, being listed does not currently provide broad statewide protection for the plants. Additional regional status codes assigned to the sedge signify that the species is eligible for protection under the jurisdictions of the Highlands Preservation Area (HL) and the New Jersey Pinelands (LP) (NJNHP 2010).

Eleocharis compressa var. *compressa* was first documented in New Jersey during the early 1920s, but it was not seen again for several decades until Vincent Abraitys discovered a population in Sussex County (Snyder 1984). Hough (1983) cited current records from both Sussex and Cape May counties. Breden et al. (2006) reported three populations in Sussex County and one in Warren. Although those four populations are still considered to be extant, several of them have experienced significant declines in recent years (NJNHP 2022).

Threats

The critically imperiled (G1) riverside communities in which the majority of New Jersey's populations of *Eleocharis compressa* var. *compressa* occur are severely threatened by nonindigenous plant species. Gawler (2006) initially noted that the sites were susceptible to invasion by Purple Loosestrife (*Lythrum salicaria*) and Stiltgrass (*Microstegium vimineum*) but in subsequent years the list of potentially threatening species in those habitats expanded considerably. Some of the introduced plants form dense monospecific stands and crowd out native species; examples include Common Wormwood (*Artemisia vulgaris*), Japanese Knotweed (*Reynoutria japonica*), and the invasive form of Reed Canarygrass (*Phalaris arundinacea*). Shrubby species like Autumn Olive (*Elaeagnus umbellata*), bush honeysuckles (eg. *Lonicera morrowii*), and Multiflora Rose (*Rosa multiflora*) form shady thickets where *E. compressa* var. *compressa* and other rare species cannot persist. Rapidly spreading vines including Japanese Honeysuckle (*Lonicera japonica*), Asian Bittersweet (*Celastrus orbiculatus*), and Mile-a-minute Vine (*Persicaria perfoliata*) have also been reported in the river shoreline communities (NJNHP 2022, USNPS 2022). When New Jersey's three G1 Riverscour Wet Meadow communities were observed during 2021 a nearly impenetrable cover of invasive plant species was found at all sites. Additional exotic species (*Sedum sarmentosum*, *Persicaria posumbu*) were noted as problematic at one location, and unusually high late-summer water levels were observed along the river for three consecutive years. No Flat-stem Spike-rush plants were seen during 2021, although some may have been present but submerged (NJNHP 2022). Invasive plant species pose a comparable threat to the globally vulnerable (G3) Riverscour Wet Meadow Communities in the mid-Atlantic region (Sneddon et al. 2018).

A number of *Eleocharis* species, including *E. compressa*, are susceptible to a fungal parasite (*Physoderma heleocharidis*). Sparrow and Johns (1965) documented the fungus on Flat-stem Spike-rush in Michigan, noting that it had caused some discoloration of the culms and basal sheaths. The presence of *Physoderma heliocharidis* can also result in the formation of stem galls (Smith 1907, Bioinfo UK 2023) but no extensive damage to *Eleocharis* plants has been reported. An investigation of the impact of a related fungus (*Physoderma dulichii*) on another sedge (*Dulichium arundinaceum*) found no apparent effect on vigor or reproduction in the host (Johns 1966).

The status of *Eleocharis compressa* var. *compressa* in New Jersey is likely to become more precarious as a result of changing climactic conditions. Shifting precipitation patterns and rising temperatures are leading to more frequent and prolonged droughts in New Jersey, as well as unpredictable flooding events (Hill et al. 2020). Both wetland drainage and inundation can threaten the sedge (NatureServe 2023). Extended periods of drought could reduce the seepage moisture that maintains the Riverscour Wet Meadow communities. The habitats are also particularly susceptible to changes in the seasonal flow patterns of the river. In the past, the communities have typically flooded during the spring as a result of local and upstream snowmelt. The spring floods often carried large blocks of ice that scoured the rocks and prevented woody species from establishing (USNPS 2022). Much of the snowmelt and ice originated upstream in New York, where the winters are now warming three times faster than the summers (NYDEC 2023). Reduced river ice and snowmelt can permit more growth of woody species, significantly altering light availability in shoreline communities. Additionally, severe storms that result in

excessive flooding during the growing season can further threaten rare species in those communities by hampering reproduction or dislodging plants.

Management Summary and Recommendations

Invasive species control and the maintenance of an open canopy should be top management priorities for *Eleocharis compressa* var. *compressa* in New Jersey. The National Park Service has already initiated efforts to address both issues. Biological controls are being used to reduce the spread of *Lythrum salicaria* and *Persicaria perfoliata*, while invasive shrub species are being removed by hand (USNPS 2022). Protection of the globally imperiled habitats is likely to directly benefit *E. compressa* var. *compressa*. Additional work will be needed to address other exotic plant species that have established in the communities, and shrub removal will have to be repeated periodically in the absence of ice scour.

In other parts of the sedge's range, one of the major management issues is likely to be maintenance of natural hydrologic conditions (PANHP 2019, NatureServe 2023). In prairie settings it is also important to keep the canopy open. There is presently insufficient information to determine which management strategy is most beneficial for prairie populations of *Eleocharis compressa*. At some locations the species has benefitted from mowing (Meissen et al. 2015) but in other places it barely persisted when sites were mowed but increased substantially after fire was employed to hamper succession (Rooney and Leach 2010). Reemts and Belcher (2022) reported that fire was a beneficial management tool for the tallgrass prairie community as a whole but the effects on individual species like *E. compressa* were not noted.

Despite the successful establishment of *Eleocharis compressa* in the restored wetlands studied by Beas et al. (2013), the authors would be likely to agree with Zimmerman (1972) that the species could benefit from additional efforts to re-introduce the sedge in prairie restorations. Beas et al. (2013) observed that restored sites were dominated by annual species but lacking in perennials and suggested that reseeding may be needed for the latter group due to a paucity of healthy prairie habitat in the landscape to serve as a source of propagules and also to relatively poor dispersal mechanisms.

Additional work is needed in order to clarify the relationship between the two varieties of *Eleocharis compressa*. Although they appear to share many characteristics there may be a significant difference that has not been detected. The conservation status map in Figure 4 does not make a distinction between the varieties but it shows *E. compressa* as vulnerable or imperiled in nearly all of the states east of Illinois where only var. *compressa* occurs. It is possible that the variety is equally rare in the central states but its scarcity has been masked by the presence of var. *acutisquamata* because the subtaxons are not distinguished. Resolution of the taxonomic question will determine the best direction for future research on the species or varieties.

Synonyms

The accepted botanical name of the species is *Eleocharis compressa* Sull. var. *compressa*. Orthographic variants, synonyms, and common names are listed below (ITIS 2023, POWO 2023, USDA NRCS 2023b). The other variety of *Eleocharis compressa*, *E. compressa* var. *acutisquamata*, differs mainly in culm width and cross-section shape (Smith 2001) and it does not occur in New Jersey (POWO 2023, USDA NRCS 2023b). Some sources (eg. Kartesz 2015, NatureServe 2023) do not treat *acutisquamata* as a distinct species or variety.

Botanical Synonyms

Eleocharis acuminata (Muhl.) Nees
Eleocharis acuminata var. *tenerrima* Boeckeler
Eleocharis compressa Sull. var. *atrata* Svens.
Eleocharis elliptica Kunth var. *atrata* (Svens.) S. G. Sm.
Eleocharis elliptica var. *compressa* (Sull.) Drapalik & Mohlenbr.
Eleocharis tenuis (Willd.) Schult. var. *atrata* (Svens.) B. Boivin
Trichophyllum acuminatum (Muhl.) House

Common Names

Flat-stem Spike-rush
Flatstemmed Spikerush

References

- Abrams, Marc D. 1988. Effects of burning regime on buried seed banks and canopy coverage in a Kansas tallgrass prairie. *The Southwestern Naturalist* 33(1): 65–70.
- Barrett, Spencer C. H. 2015. Influences of clonality on plant sexual reproduction. *Proceedings of the National Academy of Sciences* 112: 8859–8866.
- Baskin, Jerry M. and Carol C. Baskin. 1977. *Leavenworthia torulosa* Gray: An endangered plant species in Kentucky. *Castanea* 42(1): 15–17.
- Baskin, Carol C. and Jerry M. Baskin. 1988. Germination ecophysiology of herbaceous plant species in a temperate region. *American Journal of Botany* 75(2): 286–305.
- Baskin, J. M., E. Quarterman, and C. C. Baskin. 2007. Flow diagrams for plant succession in the middle Tennessee cedar glades. *Journal of the Botanical Research Institute of Texas* 1(2): 1131–1140.
- Beas, Benjamin J., Loren M. Smith, Karen R. Hickman, Theodore G. LaGrange, and Randy Stutheit. 2013. Seed bank responses to wetland restoration: Do restored wetlands resemble reference conditions following sediment removal? *Aquatic Botany* 108: 7–15.
- Belcher, J. W., P. A. Keddy, and P. M. Catling. 1992. Alvar vegetation in Canada: A multivariate description at two scales. *Canadian Journal of Botany* 70(6): 1279–1291.

Bioinfo UK. 2023. *Physoderma heleocharidis* (Fuckel) Schhroet. Accessed February 23, 2023 at https://www.bioinfo.org.uk/html/Physoderma_heleocharidis.htm

Boedeltje, Ger, Jan P. Bakker, Albert Ten Brinke, Jan M. Van Groenendael, and Martin Soesbergen. 2004. Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: The flood pulse concept supported. *Journal of Ecology* 92: 786–796.

Bohrer, Kelly E., Carl F. Friese, and James P. Amon. 2004. Seasonal dynamics of arbuscular mycorrhizal fungi in differing wetland habitats. *Mycorrhiza* 14(5): 329–337.

Breden, T. F., J. M. Hartman, M. Anzelone and J. F. Kelly. 2006. *Endangered Plant Species Populations in New Jersey: Health and Threats*. New Jersey Department of Environmental Protection, Division of Parks and Forestry, Office of Natural Lands Management, Natural Heritage Program, Trenton, NJ. 198 pp.

Bried, Jason T., Tommi S. Fouts, and Suneeti K. Jog. 2019. Enhanced indicator species performance with increasing contextualization. *Conservation Science and Practice* 1: e127. <https://doi.org/10.1111/csp2.127>

Bried, Jason T., Tommi S. Fouts, and Suneeti K. Jog. 2021. Searching for indicator species of high floristic quality depressional wetlands in the US southern plains. *Wetlands* 41(7): Article 96.

Britton, N. L. and A. Brown. 1913. *An Illustrated Flora of the Northern United States and Canada in three volumes: Volume I (Ferns to Buckwheat)*. Second Edition. Reissued (unabridged and unaltered) in 1970 by Dover Publications, New York, NY. 680 pp.

Catling, Paul M. 1977. On the occurrence of *Oarisma garita* (Reakirt) (Lepidoptera: Hesperiiidae) in Manitoulin District, Ontario. *The Great Lakes Entomologist* 10(2): 59–63.

Deacon, Pat. 2019. Photo of *Eleocharis compressa* from Ontario. Shared via iNaturalist at <https://www.inaturalist.org/observations/25916669>, licensed by <https://creativecommons.org/licenses/by-nc/4.0/>

Deacon, Pat. 2020. Cover photo of *Eleocharis compressa*. Shared via iNaturalist at <https://www.inaturalist.org/observations/49087067>, licensed by <https://creativecommons.org/licenses/by-nc/4.0/>

Demeda, Camila Luisa Bernhardt, Guilherme Dubal dos Santos Seger, Neusa Steiner, and Rafael Trevisan. 2018. Reproductive phenology and germination of *Eleocharis laevigulumis* R. Trevis. & Boldrini (Cyperaceae). *Acta Botanica Brasilica* 32(3): 487–492.

Drapalik, Donald J. and Robert H. Mohlenbrock. 1960. The taxonomic status of *Eleocharis elliptica*. *The American Midland Naturalist* 63(1): 143–148.

- Faber-Langendoen, D. 2018. Northeast Regional Floristic Quality Assessment Tools for Wetland Assessments. NatureServe, Arlington, VA. 52 pp.
- Farmer, Jaime A., Elisabeth B. Webb, Robert A. Pierce II, and Kevin W. Bradley. 2017. Evaluating the potential for weed seed dispersal based on waterfowl consumption and seed viability. *Pest Management Science* 73(12): 2592–2603.
- Fassett, Norman C. 1957. *A Manual of Aquatic Plants*. Second Edition. University of Wisconsin Press, Madison, WI. 405 pp.
- Fernald, M. L. 1950. *Gray's Manual of Botany*. Dioscorides Press, Portland, OR. 1632 pp.
- Frances, Anne (Principal Investigator). 2017. Prioritization and Conservation Status of Rare Plants in the North Atlantic - Final Report. Report prepared for NatureServe by the North Atlantic Landscape Conservation Cooperative, Hadley, MA. Available at <https://www.natureserve.org/publications/prioritization-and-conservation-status-rare-plants-north-atlantic-final-report>
- Gawler, S. C. 2006. *Deschampsia cespitosa* - *Carex viridula* Riverscour Wet Meadow conservation status factors. NatureServe, Arlington, VA. Accessed February 22, 2023 at https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.684522/Deschampsia_cespitosa_-_Carex_viridula_Riverscour_Wet_Meadow
- George, Robert J. and Elray S. Nixon. 1990. The herbaceous flora of three Weches formation outcrops in eastern Texas. *SIDA, Contributions to Botany* 14(1): 117–127.
- Gleason, H. A. and A. Cronquist. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. Second Edition. The New York Botanical Garden, Bronx, NY. 910 pp.
- Godfrey, R. K. and J. W. Wooten. 1981. *Aquatic and Wetland Plants of Southeastern United States: Monocotyledons*. The University of Georgia Press, Athens, GA. 728 pp.
- Goetghebeur, P. 1998. In Klaus Kubitzki and T. Stuzel (eds). *The Families and Genera of Vascular Plants, Volume 4: Flowering Plants. Monocotyledons: Alismatanae and Commelinanae (Except Gramineae)*. Springer-Verlag 521 pp.
- Gudžinskas, Zigmantas and Laurynas Taura. 2021. Confirmed occurrence of the native plant species *Eleocharis ovata* (Cyperaceae) in Lithuania. *Botanica* 27(1): 44–52.
- Hiebert, Ronald D., Douglas A. Wilcox, and Noel B. Pavlovic. 1986. Vegetation patterns in and among pannes (calcareous intradunal ponds) at the Indiana Dunes National Lakeshore, Indiana. *The American Midland Naturalist* 116(2): 276–281.
- Hill, E. G. 1891. The fertilization of three native plants. *Bulletin of the Torrey Botanical Club* 18(4): 111–118.

Hill, Rebecca, Megan M. Rutkowski, Lori A. Lester, Heather Genievich, and Nicholas A. Procopio (eds.). 2020. New Jersey Scientific Report on Climate Change, Version 1.0. New Jersey Department of Environmental Protection, Trenton, NJ. 184 pp.

Hilty, John. Two undated images of *Eleocharis compressa*. Photos from Illinois Wildflowers https://www.illinoiswildflowers.info/grasses/plants/fs_spikerush.htm, used with permission https://www.illinoiswildflowers.info/files/photo_use.html

Hough, Mary Y. 1983. New Jersey Wild Plants. Harmony Press, Harmony, NJ. 414 pp.

ITIS (Integrated Taxonomic Information System). Accessed February 22, 2023 at <http://www.itis.gov>

Johns, Robert S. 1966. Morphological and ecological study of *Physoderma dulichii*. American Journal of Botany 53(1): 34–45.

Kartesz, J. T. 2015. The Biota of North America Program (BONAP). Taxonomic Data Center. (<http://www.bonap.net/tdc>). Chapel Hill, NC. [Maps generated from Kartesz, J. T. 2015. Floristic Synthesis of North America, Version 1.0. Biota of North America Program (BONAP) (in press)].

Klips, Robert A. 2003. Vegetation of Claridon Railroad Prairie, a remnant of the Sandusky Plains of central Ohio. Castanea 68(2): 135–142.

Leck, M. A. and W. Schütz. 2005. Regeneration of Cyperaceae, with particular reference to seed ecology and seed banks. Perspectives in Plant Ecology, Evolution and Systematics 7: 95–133.

Magalhães, Aderbal F., Ana Lúcia T. G. Ruiz, Adriana Flach, Aparecida D. Faria, Eva G. Magalhães, and Maria do Carmo E. Amaral. 2005. Floral scent of *Eleocharis elegans* (Kunth) Roem. & Schult. (Cyperaceae). Biochemical Systematics and Ecology 33: 675–679.

Mazanec, Katherine May. 2020. Aquatic Plants and Their Application to Successful Floating Treatment Wetlands. Master's Thesis, Missouri University of Science and Technology, Rolla, MO. 54 pp.

Martin, A. C. and F. M. Uhler. 1939. Food of Game Ducks in United States and Canada. U. S. Department of Agriculture, Technical Bulletin 634. 156 pp.

McAtee, W. L. 1918. Food Habits of the Mallard Ducks of the United States. United States Department of Agriculture Bulletin No. 70. 36 pp.

Meissen, Justin C., Susan M. Galatowitsch, and Meredith W. Cornett. 2015. Risks of overharvesting seed from native tallgrass prairies. Restoration Ecology 23(6): 882–891.

Mid-Atlantic Herbaria. 2023. <https://midatlanticherbaria.org/portal/index.php>. Accessed on February 22, 2023.

Morton, J. K. and E. H. Hogg. 1989. Biogeography of island floras in the Great Lakes. II. Plant dispersal. *Canadian Journal of Botany* 67(6): 1803–1820.

Mushet, David M., Ned H. Euliss, and Terry L. Shaffer. 2002. Floristic quality assessment of one natural and three restored wetland complexes in North Dakota, USA. *Wetlands* 22(1): 126–138.

NatureServe. 2023. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed February 22, 2023 at <https://explorer.natureserve.org/>

NJNHP (New Jersey Natural Heritage Program). 2010. Special Plants of NJ - Appendix I - Categories & Definitions. Site updated March 22, 2010. Available at https://nj.gov/dep/parksandforests/natural/docs/nhpcodes_2010.pdf

NJNHP (New Jersey Natural Heritage Program). 2022. Biotics 5 Database. NatureServe, Arlington, VA. Accessed February 1, 2022.

NYDEC (New York Department of Environmental Conservation). 2023. Climate Change Effects and Impacts. Accessed February 25, 2023 at <https://www.dec.ny.gov/energy/94702.html#:~:text=The%20annual%20statewide%20average%20temperature,northern%20parts%20of%20the%20state.>

PANHP (Pennsylvania Natural Heritage Program). 2019. Species and Natural Features List. Fact sheet for *Eleocharis compressa* available at <https://www.naturalheritage.state.pa.us/SpeciesFeatures.aspx>

POWO. 2023. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Accessed February 22, 2023 at <http://www.plantsoftheworldonline.org/>

Reece, P. E., J. T. Nichols, J. E. Brummer, R. K. Engel, and K. M. Eskridge. 1994. Harvest date and fertilizer effects on native and interseeded wetland meadows. *Journal of Range Management* 47: 178–183.

Reemts, Charlotte and Brandon Belcher. 2022. Making a good prairie better: Plant diversity increased in a formerly hayed remnant prairie now managed with fire. *Natural Areas Journal* 42(1): 18–27.

Rhoads, Ann Fowler and Timothy A. Block. 2007. *The Plants of Pennsylvania*. University of Pennsylvania Press, Philadelphia, PA. 1042 pp.

Rooney, Thomas P. and Mark K. Leach. 2010. Replacing hay-mowing with prescribed fire restores species diversity and conservation value in a tallgrass prairie sampled thrice: A 59-year study. *The American Midland Naturalist* 164: 311–321.

Saunders, Manu E. 2018. Insect pollinators collect pollen from wind-pollinated plants: Implications for pollination ecology and sustainable agriculture. *Insect Conservation and Diversity* 11: 13–31.

Smith, A. Lorrain. 1907. New or rare microfungi. *Transactions of the British Mycological Society* 3(2): 111–123.

Smith, S. Galen. 2001. Taxonomic innovations in North American *Eleocharis* (Cyperaceae). *Novon* 11(2): 241–257.

Smith, S. Galen , Jeremy J. Bruhl, M. Socorro González-Elizondo, and Francis J. Menapace. Page updated November 5, 2020. *Eleocharis compressa* var. *compressa*. In: Flora of North America Editorial Committee, eds. 1993+. *Flora of North America North of Mexico* [Online]. 22+ vols. New York and Oxford. Accessed February 23, 2023 at http://floranorthamerica.org/Eleocharis_compressa_var.compressa

Sneddon, Lesley. 2010. Global Conservation Status Ranks of State-Rare Vegetation Associations in the Eastern Rivers and Mountains Network. Natural Resource Technical Report NPS/NER/ERMN/NRTR—2010/151 prepared for U. S. National Park Service, Northeast Region, Philadelphia, PA. 216 pp.

Sneddon, L. A., G. Fleming, P. Coulling, and S. C. Gawler. 2018. *Andropogon gerardii* - *Panicum virgatum* - *Baptisia australis* Riverscour Wet Meadow conservation status factors. NatureServe, Arlington, VA. Accessed February 24, 2023 at https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.688945/Andropogon_gerardii_-_Panicum_virgatum_-_Baptisia_australis_Riverscour_Wet_Meadow

Snyder, David B. 1984. Botanical discoveries of Vincent Abraitys. *Bartonia* 50: 54–56.

Soons, Merel B., Cornelius van der Vlugt, Barth van Lith, Gerrit W. Heil, and Marcel Klaassen. 2008. Small seed size increases the potential for dispersal of wetland plants by ducks. *Journal of Ecology* 96: 619–627.

Sparrow, F. K. and R. M. Johns. 1965. Observations on chytridiaceous parasites of phanerogams. *Archiv für Mikrobiologie* 51: 351–364.

Svenson, H. K. 1932. Monographic studies in the genus *Eleocharis* - II. *Rhodora* 34: 193–203 and 215–227.

Tiner, Ralph W. 2009. *Field Guide to Tidal Wetland Plants of the Northeastern United States and Neighboring Canada*. University of Massachusetts Press, Amherst, MA. 459 pp.

U. S. Army Corps of Engineers. 2020. National Wetland Plant List, version 3.5. https://cwbi-app.sec.usace.army.mil/nwpl_static/v34/home/home.html U. S. Army Corps of Engineers Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, NH.

USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2023a. *Eleocharis compressa* illustration from Britton, N. L. and A. Brown, 1913, An illustrated flora of the northern United States, Canada and the British Possessions, 3 vols., Kentucky Native Plant Society, New York, Scanned By Omnitek Inc. Image courtesy of The PLANTS Database (<http://plants.usda.gov>). National Plant Data Team, Greensboro, NC.

USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2023b. PLANTS profile for *Eleocharis compressa* var. *compressa* (Flatstem Spikerush). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed February 22, 2023 at <http://plants.usda.gov>

USNPS (United States National Park Service). 2022. Unique riverside habitat needs restoration. Article published online by National Park Service at <https://www.nps.gov/articles/rare-riparian-plant-communities.htm>

Walz, Kathleen S., Linda Kelly, Karl Anderson and Jason L. Hafstad. 2018. Floristic Quality Assessment Index for Vascular Plants of New Jersey: Coefficient of Conservatism (CoC) Values for Species and Genera. New Jersey Department of Environmental Protection, New Jersey Forest Service, Office of Natural Lands Management, Trenton, NJ. Submitted to United States Environmental Protection Agency, Region 2, for State Wetlands Protection Development Grant, Section 104(B)(3); CFDA No. 66.461, CD97225809.

Wang, B., and Y. L. Qiu. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* 16(5): 299–363.

Weakley, A. S. and Southeastern Flora Team. 2022. Flora of the Southeastern United States. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC. 2022 pp.

Wongsriphuek, Chanpen, Bruce D. Dugger, and Anne M. Bartuszevige. 2008. Dispersal of wetland plant seeds by Mallards: Influence of gut passage on recovery, retention, and germination. *Wetlands* 28(2): 290–299.

Zimmerman, James H. 1972. Propagation of spring prairie plants. *Proceedings of the 2nd Midwest Prairie Conference*: 153–161.

Zomlefer, Wendy B. 1994. *Guide to Flowering Plant Families*. University of North Carolina Press, Chapel Hill, North Carolina. 430 pp.

Zylka, Jason J., Christopher J. Whelan, and Brenda Molano-Flores. 2016. Restoration implications of land management legacy on aboveground and seed bank composition of North American grasslands. *The American Midland Naturalist* 176: 36–59.