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Wildrice (*Zizania palustris*; Manoomin) Biology, Functions and Values, and Soil Physiochemical Properties Affecting Production

A Review of Available Literature

Christine M. VanZomeren, Kevin D. Philley, Nia R. Hurst,
and Jacob F. Berkowitz

August 2023



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Final report

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Prepared for US Army Corps of Engineers, Detroit District
477 Michigan Ave Ste 700, Detroit, MI 48226
Under Project 478492, "Planning Assistance to States"

Abstract

Wildrice (*Zizania palustris* L.) is an annual aquatic emergent plant primarily distributed across portions of Minnesota, Wisconsin, Michigan, and Canada. Wildrice requires narrow environmental conditions that vary throughout its life cycle. Environmental conditions required include water levels between 15 and 90 cm, slow flowing water, anaerobic soil, and circum-neutral pH. Wildrice production and abundance is most often limited by nitrogen availability. Both short- and long-term changes in local conditions impact distribution and abundance of wildrice at local and regional scales. Reported declines in wildrice production have increased interest in evaluating changing environmental conditions, specifically within the Upper Peninsula of Michigan. Wildrice, or manoomin, is an important food and cultural resource, and remains important to native peoples throughout the region, including the Lac Vieux Desert Band of Lake Superior Chippewa Indians. This report provides a review of literature related to wildrice and examines potential factors affecting its production in the Upper Peninsula of Michigan. This report highlights cultural and traditional values, functions and values of wildrice, and unique chemical and physical aspects of the environment where wildrice grow. Additionally, this report synthesizes the data gathered in the literature review, identifies knowledge gaps, and provides research opportunities for improved wildrice production in the Great Lakes region.

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Preface

This study was conducted under the Wildrice Production Assessment: Hydrology, Water Column, and Sediment Conditions project, Planning Assistance to States and Tribes Project Number 478492. This project was a joint effort by the US Army Corps of Engineers (USACE) Detroit District, the US Army Research and Development Center, Environmental Laboratory (ERDC-EL), and the Lac Vieux Desert Band of Lake Superior Chippewa Indians.

Funding for the following report was provided by the Planning Assistance to States and Tribes Program through the USACE Detroit District. The program administrator was Mr. Gregory Masaulf of the USACE Detroit District.

The work was performed by the Wetlands and Coastal Ecology Branch, Ms. Patricia M. Tolley, chief, of ERDC-EL. At the time of publication, Mr. Mark Farr was chief of the Ecosystem Evaluation and Engineering Division of EL, and Dr. Jennifer Seiter-Moser was the EL technical director for Civil Works. The deputy director of EL was Dr. Brandon Lafferty, and the director was Dr. Edmond Russo. Ms. Kristina Sebastian and Ms. Sydney Bufkin provided a technical review of this report.

COL Christian Patterson was commander of ERDC, and Dr. David W. Pittman was the director.

1 Introduction

1.1 Background

Wildrice (*Zizania palustris* L.), also referred to as manoomin, is an annual plant that requires particular environmental conditions to germinate and mature. Specifically, seeds require wet and cold conditions for germination. Following germination, plants require a specific range of water levels and water quality conditions for successful production of wildrice grain. Both short- and long-term changes in local conditions can impact the distribution and abundance of wildrice at local and regional scales. For example, short-term impacts from weather may alter the density of rice in a given year, while longer term alterations of climate and water quantity/quality can impact harvestable wildrice across decadal timescales. Recently reported declines in wildrice production have increased interest in the effects of changing environmental conditions and associated implications of the sustainability of wildrice yields in the future.

Wildrice remains important to native peoples throughout the region. For example, the Lac Vieux Desert Band of Lake Superior Chippewa Indians relies on wildrice as an important food and cultural resource. Several lakes within the Upper Peninsula of Michigan previously produced wildrice, both with and without seeding efforts. However, tribal members report that production, abundance, and distribution has declined in recent years. Multiple lakes that previously supported productive beds of wildrice no longer contain harvestable quantities. Further, management efforts, including seeding, have failed to re-establish productive rice beds in these lakes.

A number of potential factors may be contributing to wildrice declines, including changes in water levels, water quality, increased water recreation, development, changing climatic conditions, invasive species, increased herbivory, or effects from disease and pests. Further assessment of environmental conditions is essential to understanding the relationships between these factors and their potential implications for wildrice production.

1.2 Objective

This report reviews available literature examining the biology and history of wildrice, and examines potential factors affecting the production of wildrice in the Great Lakes region. It highlights cultural and traditional values, functions and values of wildrice, and unique chemical and physical aspects of the environment where wildrice occurs. Additionally, this report synthesizes the data gathered in the literature review, identifies knowledge gaps, and describes research opportunities for improved wildrice production.

1.3 Approach

This report addresses topics related to wildrice based on a review of 111 peer-reviewed journal articles and published reports. Considerable research has been completed on biology of wildrice itself and on the influence of sulfur compounds on wildrice production, principally focused in Minnesota. However, data related to soil-nutrient interactions in wildrice remain limited, particularly in the Upper Peninsula of Michigan. Additionally, several published articles examine one aspect of wildrice production, for example hydrology or sulfur compound toxicity, yet few reports synthesize data across multiple studies and aspects of the ecosystem. As a result, this report focuses on wildrice, but also seeks to place it the context of multiple ecosystem processes related to wildrice production. Specific topics covered within this report include: (1) the biology and history of wildrice, (2) the functions, values, and economics of wildrice, (3) physicochemical factors affecting wildrice production, (4) synthesis of wildrice production challenges in an ecosystem context, and (5) identify knowledge gaps and opportunities for additional research.

2 Biology and History of Wildrice

The biology, ecology, and biohistory of wildrice has received considerable attention and study over the past few decades. Much of this was driven by the need to understand its response to environmental variables that may act as limiting factors on its establishment and management within the Great Lakes region. The advent of molecular techniques allowed for explorations into the origins of wildrice and its genetic relationship to other members of the Oryzeae tribe within Poaceae. Paleontological and archaeological studies have been integrated with these works, in conjunction with climatic data, to better understand spatial and temporal responses of wildrice at varying scales.

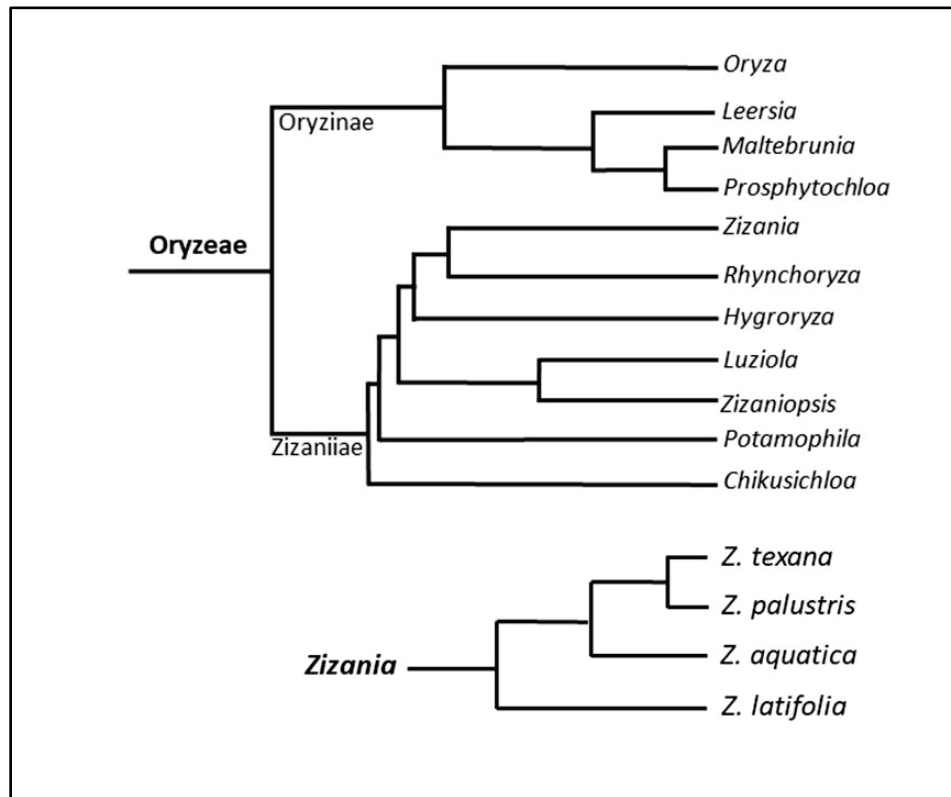
2.1 Phylogeny and biogeography of wildrice

Wildrice belongs to a monophyletic group comprised of four species with an intercontinental distribution in North America (*Zizania aquatica* L., *Z. palustris*, and *Z. texana* Hitchc.) and eastern Asia (*Z. latifolia* [Griseb.] Hance ex F.Muell.). *Zizania* resides within the Oryzeae tribe of the Poaceae family (Soreng et al. 2017). All genera within Oryzeae are restricted to wetland or aquatic habitats and distributed to every continent except Antarctica (Tang et al. 2010). Cultivated rice of both Africa (*Oryza glaberrima* Steud.) and Asia (*O. sativa* L.) are the most economically important species within Oryzeae, and among the principal cereal crops that have sustained significant portions of the human population (Xu et al. 2010). *Zizania latifolia* and *Z. palustris* are important food crops in Asia and North America, respectively.

Molecular DNA analysis from chloroplasts, genomes, and mitochondria has been used to determine ancestral areas of emergence and subsequent migration pathways of Oryzeae genera (Guo and Ge 2005; Tang et al. 2010; Xu et al. 2010). Xu et al. (2010) used dispersal-vicariance and relaxed molecular clock techniques to determine that Asia is the most likely ancestral origin of Oryzeae, diverging approximately 34.5 million years ago (MYA), with multiple long-distance dispersal events to Africa, the Americas, and Australia. Some dispersal events gave rise to genera that are restricted to specific continents while others such as *Leersia*, *Zizania*, and *Zizaniopsis* have intercontinental distributions.

Oryzeae is composed of 11 genera with approximately 70 species and divided into the Oryzinae and Zizaniiae subtribes (Figure 1). Tang et al. (2010) determined that the Zizaniiae subtribe containing *Zizania* began to diverge approximately 24.4 MYA at the end of the Oligocene, and rapidly evolved into five separate lineages by about 18 MYA. Xu et al. (2010) estimated divergence of this subtribe slightly later at about 18 MYA with the five lineages emerging by about 8 MYA. Either scenario would have occurred primarily during the Miocene epoch (23–5.3 MYA) which experienced explosive diversifications and adaptive radiations in grasses and other graminoids (Jacobs et al. 1999). This time period included major climatic shifts such as the Middle Miocene Disruption when temperatures dropped precipitously and the global climate became increasingly drier, resulting in a contraction of tropical biomes toward the equator while grasslands and temperate biomes expanded (Vincentini et al. 2008).

Figure 1. Phylogenetic tree of the Oryzeae tribe and *Zizania* (adapted from Xu et al. [2010]).

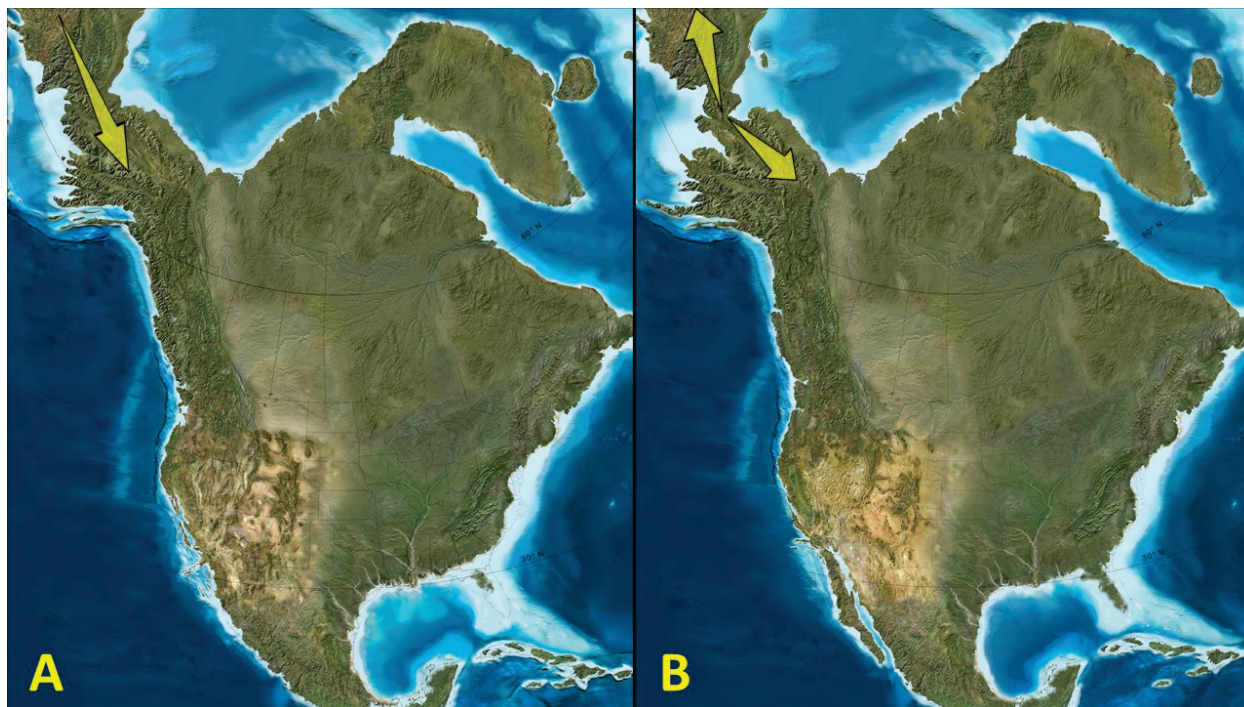


North America is the most probable area of ancestral emergence of *Zizania*, diverging between 17.5 to 10 MYA (Tang et al. 2010; Xu et al. 2010). The Bering land bridge (Beringia) is the most likely migration pathway for the ancestor of *Zizania* to arrive in North America during the early to middle Miocene (Figure 2). This feature is recognized as an important dispersal pathway for both terrestrial and wetland plants with intercontinental distributions in Asia and North America (Xu et al. 2010).

The American clade of *Zizania* and the Asian clade comprised solely of *Z. latifolia* diverged approximately 3.74 MYA during the Pliocene (Tang et al. 2010). The closing of Beringia and intrusion by the Bering Sea during that time may explain the disjunct isolation of *Zizania latifolia* (Xu et al. 2010). Haplotype distribution of *Z. latifolia* indicates a northeast to southwest migration path across Asia, lending support to the North America to Asia dispersal theory (Xu et al. 2008). The early divergence of these two clades is supported by differences in chromosome number and morphology. All North American species have a chromosome number of $n = 15$, versus $n = 17$ in *Zizania latifolia* (Duvall 1987; Terrell et al. 1997). Morphological differences are substantial with all North American taxa bearing segregated panicles with male spikelets on lower branches and female spikelets on upper branches, whereas panicle branches of *Zizania latifolia* are mixed (Xu et al. 2010). Segregation of staminate and pistillate flowers reduces self-fertilization and promotes genetic crossing (Hutchinson 2019).

The North American *Zizania* clade began to differentiate approximately 710,000 years ago during the middle Pleistocene (Tang et al. 2010; Xu et al. 2010). This time aligns with the peak of an interglacial period following the onset of the Brunhes glaciations. The Brunhes glaciations had ice sheets of greater extent and cooler global temperatures during glacial maximums compared to the previous Matuyama and Gauss glaciation eras (Barendregt and Duk-Rodkin 2011). Additionally, glacial-interglacial cycles at this time slowed to approximate 100,000 yr intervals, replacing the more rapid 41,000 yr intervals that defined most of the previous 1.8 million years.

Figure 2. (A) Hypothesized dispersal pathway of an ancestral *Oryzaeae* member into North America during the early to middle Miocene, subsequently giving rise to *Zizania*, and (B) separation of the Asian and North American clades during the Pliocene (© 2013 Colorado Plateau Geosystems Inc. <https://deeptimemaps.com/>).



Glacial cycling has been identified as an important driver of speciation through geographic isolation, gene flow disruption among fragmented populations, differential dispersal from refugia during glacial retreat, differential natural selection of genotypes, and localized adaptation (Hewitt 1995). Secondary contact among diverging taxa during range shifts or cohabitation of climate refugia can lead to introgression or intraspecific recombinations, thereby depressing or reversing the speciation process, or alternatively, speciation via hybridization (Nevado et al. 2018). Several of these factors are relevant to understanding both the distributions and relationships among the three North American species of *Zizania*.

The taxonomic recognition of *Zizania palustris* has not always been straightforward. *Zizania aquatica* (Southern wildrice, river-rice) is the type species of the genus and was first published by Linnaeus in 1753 based on specimens from J.F. Gronovious's 1743 *Flora Virginica* (Linnaeus 1753). In 1771, he described *Zizania palustris* from his own garden-cultivated specimens belonging to northern waters ("*septentrionalis aquifos*") with morphological traits that differed from the *Z. aquatica*

specimens (Linnaeus 1771). Because of range overlap among the two species and the discovery of plants with intermediate morphologies, *Zizania palustris* was eventually rejected in favor of a single species concept of *Z. aquatica* exhibiting broad gradients of morphological characters and high ecological adaptability to a diversity of wetland types including tidal flats, coastal marshes, freshwater lakes, and riverine environments.

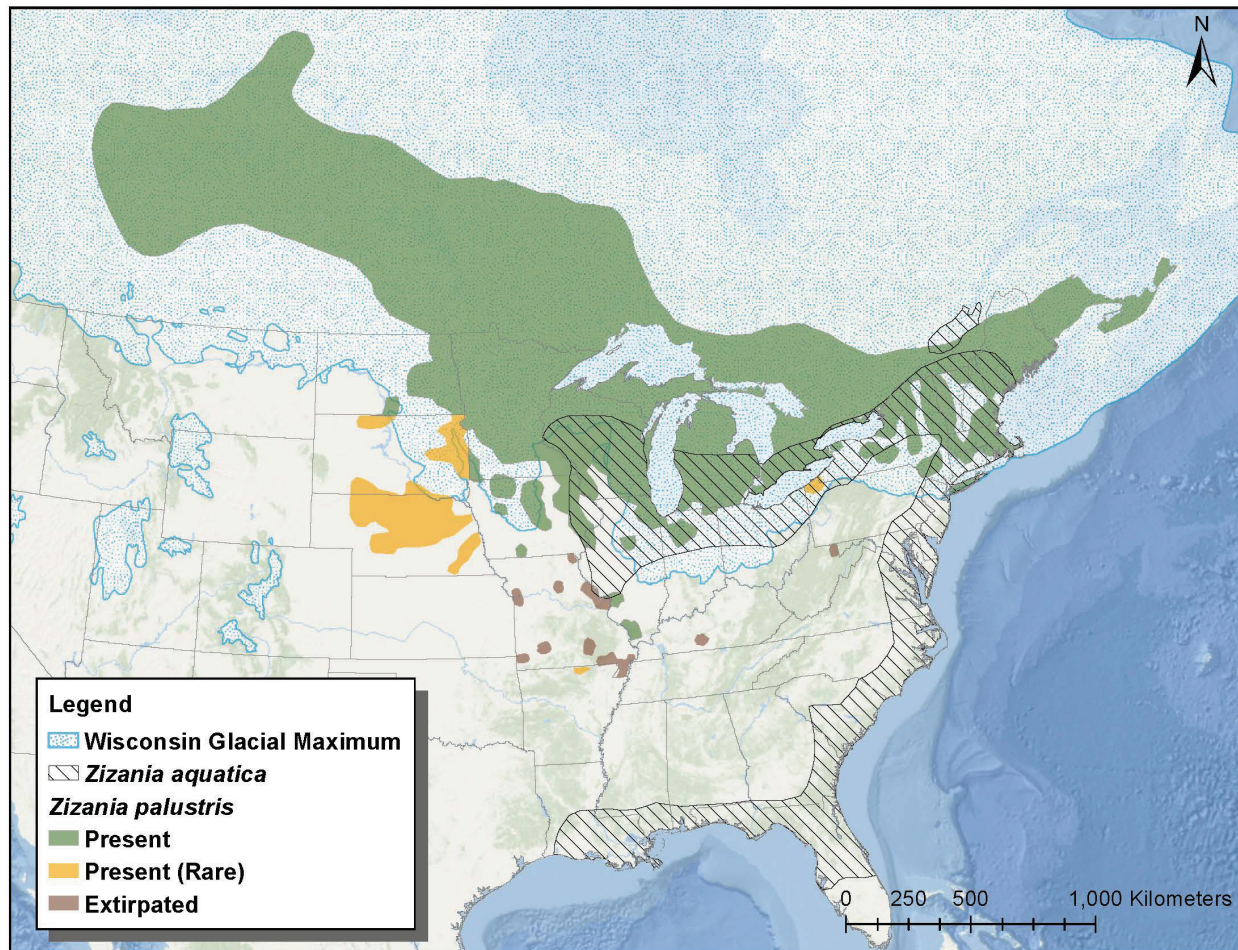
Hitchcock (1906) attempted to accommodate the two taxonomic descriptions published by Linnaeus through applying varietal status (*Zizania aquatica* var. *angustifolia*; “narrow-leaved”) to specimens previously recognized as *Z. palustris*. Fassett (1924) later proposed two additional varieties, one describing specimens from a distinct population restricted to rocky tidal flats of the St. Lawrence River estuary near Québec (*Zizania aquatica* var. *brevis*), and the other describing specimens with intermediate morphologies from the Midwest (*Zizania aquatica* var. *interior* [= *Z. palustris* var. *interior*]). Numerous taxonomic changes within the genus occurred from 1971 to 1990, including elevation of these recognized varieties to subspecific rank (Tropicos 2019). *Zizania palustris* was ultimately reinstated based on results from morphology, hybridization, and isozyme studies (Duvall and Biesboer 1988a, 1988b; Terrell and Wergin 1981; Warwick and Aiken 1986), leading to the present recognition of two annual species, each with two varieties (Terrell et al. 1997).

The phylogeography of the North American *Zizania* clade remains largely speculative despite range-wide comparative analysis by Xu et al. (2015). The onset of the Bruhnes glaciations with their more extensive ice sheets and slower oscillations would have forced the ancestor of *Zizania aquatica* farther south than the previous glacial cycles that occurred after its divergence from *Z. latifolia*. This climate-induced dispersal into lower latitudes may have given rise to *Zizania aquatica* through adaptation to tidal wetland ecosystems in either the Atlantic or Gulf coastal plain region. A subsequent isolation event acting on populations adapting to proglacial wetlands may have given rise to *Zizania palustris*.

The arcing distribution of *Zizania aquatica* shown in Figure 3 resembles that of several plants recognized as Atlantic and Gulf Coastal plain disjuncts found in the Great Lakes region (Reznicek 1994). It is not recognized as a disjunct in part because it occurs over a relatively uninterrupted range, including the Appalachian highlands province of the

northeastern US, but primarily because its dispersal pathways are not well understood and require additional study. Xu et al. (2015) found that haplotypes from the Midwest region did not appear to be derived from post glacial dispersal events out of the southeastern coastal plain populations. *Zizania aquatica* may have dispersed northward along the Atlantic coast and subsequently westward into the Great Lakes region along post-glacial wetlands and streams. This process may have occurred more than once given the numerous occurrences of interglacial periods since its divergence.

Figure 3. Wisconsin glacial maximum with the range of *Zizania palustris* based on Kartesz (2015) and Yost and Blinnikov (2011). Areas with known introductions and escapes not shown. Abundance ranking based on state-level designations in Kartesz (2015).



Much of the extant range of *Zizania palustris* has been tilled by multiple glaciation events since its estimated divergence from *Z. aquatica*. The last glacial maximum (25–21,000 years ago) during the Wisconsin Glacial

Period occupied nearly all of its current range where it is considered abundant or has high ecological and economic importance (Figure 3). Areas immediately south of the ice sheet were occupied by a relatively narrow band of tundra, followed by boreal and temperate-deciduous biomes positioned farther south. Multiple oscillations in the distribution of *Zizania palustris* would have occurred in response to these events but the extent of each movement, dispersal pathways, and areas of refugia are unknown (Hutchinson 2019).

Phylogenetic analysis of North American *Zizania* haplotypes by Xu et al. (2010) showed the clade can be subdivided into two groups, one group consisting entirely of *Zizania aquatica* haplotypes, and the other containing all haplotypes of *Z. palustris* and *Z. texana*, plus some haplotypes of *Z. aquatica*. The division of *Zizania aquatica* haplotypes across two groups suggests that incomplete lineage sorting or introgression has taken place (Xu et al. 2010). Warwick and Aiken (1986) found no evidence of interspecific gene flow during their isozyme studies of *Zizania*, and Duvall and Biesboer (1988b) revealed a unidirectional crossability barrier between *Zizania aquatica* and *Z. palustris* (low level hybridization only with female *Z. aquatica* + male *Z. palustris*) while conducting artificial hybridization studies. Prior to these findings, introgression was suspected of producing the morphologically intermediate variety described as *Zizania palustris* var. *interior* because it occurs primarily within the contact zone of the two species (Terrell et al. 1997). Terrell et al. (1997) suggested the morphological similarities between *Zizania aquatica* and *Z. palustris* var. *interior* may be explained by overlapping gradients of highly plastic traits rather than gene flow. Analysis by Xu et al. (2010) found that the *Zizania aquatica* haplotypes grouped with *Z. palustris* haplotypes were from localities outside their shared distribution, further diminishing support for introgression theories. Shared alleles derived from incomplete lineage sorting appears to be the strongest explanation for interspecific groups of *Zizania* haplotypes.

Zizania palustris and the evergreen perennial *Z. texana* are the most closely related of the three North American zizanids based on isozyme and nuclear sequence analysis (Horne and Kahn 1997; Xu et al. 2010). They are capable of hybridizing under artificial conditions (limited to *Zizania texana* x *Z. palustris* var. *interior*) although they are separated by more than 800 km and differ in life history and growth habit (Hutchinson 2019). The divergence of *Zizania texana* from *Z. palustris* occurred

relatively recently based on molecular DNA analysis (Xu et al. 2010). Horne and Kahn (1997) hypothesized that it was as recent as the Wisconsin glacial retreat (<18,000 years ago).

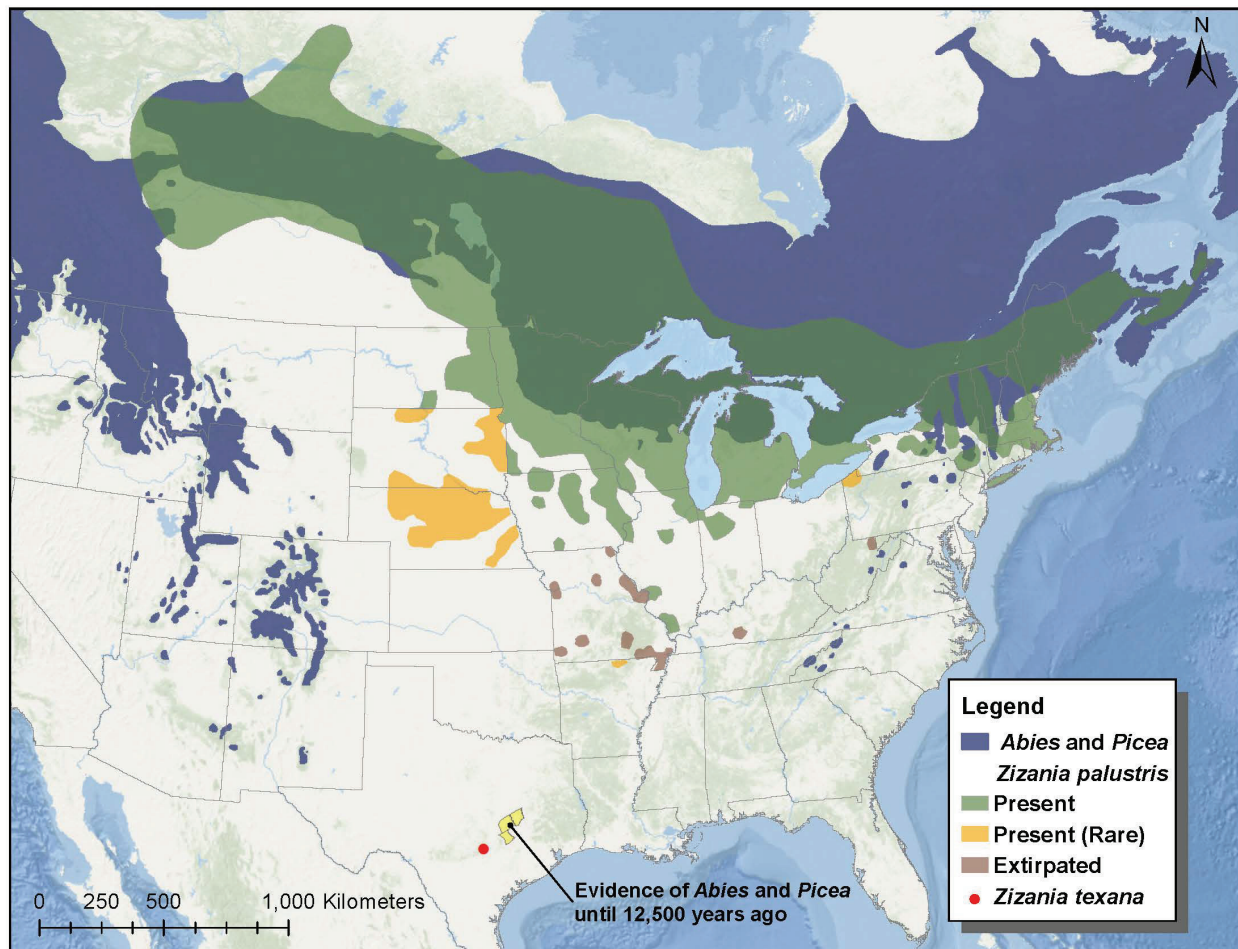
Zizania texana is restricted to spring-fed isothermic (20.4–25.5°C) waters along 5 km of the San Marcos River in Hays County, Texas, but believed to have been widespread in other spring-fed systems in the region prior to climatic events that extirpated it from all other locations (Hutchinson 2019). The remaining population is positioned in a discharge zone of the underlying aquifer that is considerably lower in elevation (approximately 14 m) than other springs along the Balcones escarpment. The spring that supports *Zizania texana* has demonstrated continuous discharge of >1,000 L per second during intense droughts while other major springs nearby stopped flowing (Horne and Kahn 1997).

The isolated distribution of *Zizania texana* suggests the range of *Z. palustris* oscillated southward during Pleistocene glacial cycles so that it occupied areas deep within the southern or southcentral US. Regional evidence of historic floristic elements closely associated with the contemporary presence of *Zizania palustris* gives additional support to this theory. Sediment core samples from peat deposits in three counties near *Zizania texana* revealed pollen grains derived from remnant stands of boreal floristic components such as *Abies* and *Picea* up until approximately 12,500 years ago (Bousman 1998; Graham and Heimsch 1960; Potzger and Tharp 1954). The primary distribution of *Zizania palustris* closely overlaps the contemporary sympatric range of these conifers (Figure 4). A warming regional climate following the Wisconsin glacial retreat caused northward range shifts for both *Abies* and *Picea*, with all populations extirpated from the southeastern and south-central US, except for the Appalachian highlands (Earle 2019; Kartesz 2015; Yost and Blinnikov 2011).

Common garden tests have demonstrated that *Zizania texana* does not maintain its unique growth habit (heterophyllous, leaves up to 2 m, culms mostly submerged, rooting at nodes) outside of the relatively stable temperatures and flowing waters of the San Marcos River, reverting to a growth form more like *Z. aquatica* and *Z. palustris* (Duvall 1987; Hutchinson 2019). Postflowering mortality was observed for some specimens during an *ex-situ* study by Hutchinson (2019), suggesting that its perennial lifecycle may be partially a function of its unique

environment but requires further study. The expression of overlapping phenotypic traits in *Zizania texana* combined with nearby evidence of historic flora elements now closely associated with *Z. palustris* strongly suggests that (1) the distribution of *Zizania palustris* historically occupied portions of the south-central US, and (2) speciation through local adaption and isolation is the most likely explanation for the peculiar disjunction of these two closely related taxa.

Figure 4. *Zizania palustris* and sympatric range of *Abies* and *Picea* with area of historic evidence of these conifers near *Zizania texana*. *Zizania palustris* range based on Kartesz (2015) and Yost and Blinnikov (2011). Sympatric range of *Abies* and *Picea* based on distribution data from Earle (2019).



2.2 Wildrice from paleo and archaeological contexts

The historical distribution and abundance of wildrice in North America remains uncertain, especially prior to European contact with indigenous people. Archaeological and paleontological evidence, oral testimonies, and written accounts provide data and descriptions about local settings but

often lack range-wide applicability. Buchner (1979), Rajnovich (1984), and Wright (1999) hypothesized that portions of its distribution outside the Great Lakes region resulted from dispersal events by indigenous people moving northward and westward, although no evidence has been found to support this (Boyd et al. 2013). Disturbance from logging, mining, dam building, and development beginning in the mid-1800's extirpated wildrice stands from numerous documented localities and potentially from many more that had no written records (Barton 2018). Intentional introductions, largely for wildlife habitat improvement or ecosystem restoration, have acted to further mask its natural distribution (Terrell et al. 1997). The following section describes investigative techniques used to establish the distribution and chronology of wildrice presence and abundance in the Great Lakes region.

Archeological research has confirmed that wildrice has been harvested and consumed by indigenous people for at least 2,300 years (Boyd et al. 2013). However, it rarely appears in archaeological settings largely due to the fragility of the grains and degradation of its discernible parts (Yost and Blinnikov 2011). Crawford and Smith (2003) documented 37 sites in North America where identifiable remains or residues from wildrice were recovered. They noted that evidence was mostly from after 300 AD, suggesting an increase in exploitation and/or dependence on wildrice as a primary food source. Dating some sites proved to be problematic because strategic landscape positions for wildrice collecting and processing, along with attendant features such as jiggling pits where the grain and chaff are separated, were used recurrently from prehistoric to modern times (Moffat and Arzigian 2000).

Indirect evidence of wildrice harvesting and processing is uncommon because the practices involved do not require specialized equipment other than wooden knockers used to dislodge the ripened grains (Boyd et al. 2013). Proximity of archaeological sites to areas that historically or currently have wildrice has been used to infer that other similar sites in the region may have supported productive wildrice beds (Johnson 1969; Salzer 1974). Lovis et al. (2001) argued that some of these sites may have been located on relatively low landscape positions such as floodplains and terraces near lakes to support maize agriculture, and not necessarily indicative of dependence on a local source of wildrice. Moffat and Arzigian (2000) noted that some sites occur at lakes with a rocky substrate and/or

depths that are not conducive to wildrice and were likely utilized for other resources.

Paleontological evidence of wildrice is relatively uncommon though increasing with the advent of emerging techniques. Wildrice apparently has a long-standing presence in the upper Midwest following the Wisconsin glacial retreat, with seeds dating to approximately 10,600 years ago found in sediment cores at Wolf Creek Bog, Minnesota by Birks (1976). Microfossils belonging to *Zizania* have been found in northwestern Ontario, in the northern portion of its range, dating back to approximately 5,300 years ago. This time period aligns with climate-driven lake-level increases that followed a more arid period during the middle Holocene which may have been a controlling mechanism on its broader establishment in the Great Lakes region (Boyd et al. 2013).

Paleoenvironments can be reconstructed through recovery of pollen inputs deposited in both aquatic and terrestrial settings. However, the analysis of pollen records can be constrained by low taxonomic resolution within some plant families such as Poaceae (Nurse et al. 2017). Grass pollen grains typically require detailed examination of surface morphology using scanning electron microscopy (SEM) to make species-level determinations (Lee et al. 2004). This method involves considerable inputs of time and labor that can be prohibitive for large-scale analysis and requires equipment that may be inaccessible.

Pollen grain size was investigated by Lee et al. (2004) to determine if it could be used to identify pollen belonging to wildrice. Their findings indicated that grain size alone is not indicative of wildrice due to high variability in size across time at individual sites and between populations. Inconsistent grain size produced considerable overlap with pollen from sympatric wetland grass species that also form dense monotypic stands such as *Glyceria* and *Phalaris arundinacea* L. Nurse et al. (2017) found that wildrice pollen could be separated from these potentially confounding effects when based on multiple morphological traits (i.e., annulus width, polar and equatorial length, and surface sculpturing) examined with standard microscopy techniques at 400x.

Relative abundance and grain size (collectively spectra) of grass pollen has been used to infer wildrice presence from paleolimnological records by comparing samples to known control sites with wildrice (Yost et al. 2013).

This method relies on the assumption that values for Poaceae exceeding 35–40% from lacustrine sediment cores in the upper Midwest are the result of localized inputs from dense monotypic stands of wildrice. Pollen spectra resulting from lower densities of wildrice would not be discernable from other grass-dominated communities in the region using this method. Accompanying inputs from co-occurring species with similar depth requirements such as *Nuphar* and *Nymphaea* indicate water levels at the site should have been appropriate for wildrice, while inputs from *Carex*, *Sagittaria*, and *Typha* indicate shallow water conditions where wildrice exhibits reduced competitiveness (Nurse et al. 2017).

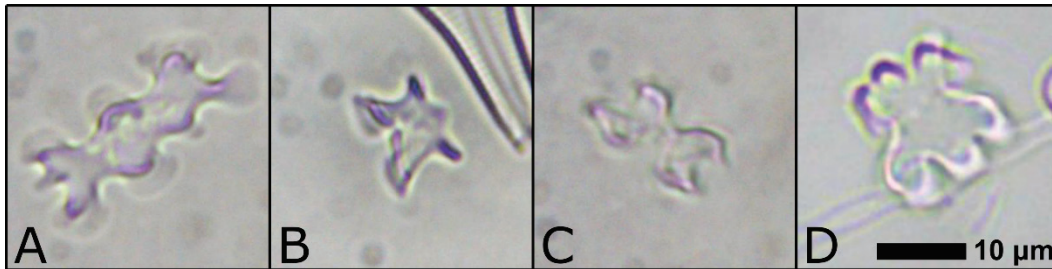
An emerging technique for detecting the historic presence of wildrice relies on examination of phytoliths extracted from sediment samples in conjunction with sediment layer chronology through isotopic dating. Phytoliths are microscopic silica bodies that form within cells, cell walls, and intercellular spaces of plants, and have been utilized for reconstructing paleoenvironments as well as examining archaeological contexts of vegetation resource utilization and landscape modification. These bodies form as soluble silica is absorbed from water as monosilicic acid, carried to various parts of the plant by vascular transport, and then converted to hydrogenated silicon dioxide precipitates (Nawaz et al. 2019).

Phytoliths are highly resistant to decay and can be ascribed based on morphology to family, tribe, genus, and species levels. Additionally, phytoliths may present a more localized representation of historic floras when compared to pollen which is highly susceptible to off-site transport by wind and water. Nurse et al. (2017) and Yost and Blinnikov (2011) reported rapid declines in wildrice phytolith abundance with increasing distance from known stands. Traditional paleolimnological studies allocate samples to deeper zones of waterbodies to maximize detection of pollen inputs from lacustrine floristic elements and to capture longer timescales of deposition. Apparent low off-site movement of wildrice phytoliths from stands could make detection and accurate sequence reconstruction highly sensitive to sampling location (Nurse et al. 2017).

Phytolith morphology studies of dominant wetland grasses in Minnesota indicated that wildrice phytoliths were regionally distinct and could be used to determine the presence of wildrice from both paleo and contemporary settings (Figure 5; Yost and Blinnikov 2011). These findings may not apply to areas outside the Great Lakes, especially the southern US

where *Zizania* is accompanied by closely related members of the Oryzeae tribe (i.e., *Luziola*, *Zizaniopsis*). Investigating phytolith morphology in the other North American members of Oryzeae may allow for studies in areas outside the Great Lakes region to determine wildrice migration pathways and refugia during prior glacial periods.

Figure 5. Micrographs of diagnostic wildrice (*Zizania palustris*) phytoliths. (A) Leaf phytolith from a floating leaf stage plant. (B) Inflorescence (lemma) phytolith. (C) Leaf phytolith from a mature plant. (D) Leaf sheath phytolith. Scale bar in D (10 microns) applies to all images (Photo Credit: Chad Yost).



Differential formation, deposition, and preservation of phytoliths complicates the interpretation of sample results. Some species are underrepresented in phytolith studies because they create few silica bodies or produce morphologies that are easily damaged beyond recognition by mechanical processes. Bioturbation and taphonomic processes such as erosion and sediment redistribution may affect both the abundance of phytoliths and the species composition represented in samples. Nurse et al. (2017) noted that strong winds, ice-out events, wave-action, and currents result in variable winnowing and redistribution of plant material (especially live versus decaying, and material that tends to float versus sink), and must be considered when interpreting phytolith samples.

Yost et al. (2013) found that rondels from the lemma and palea were the most encountered wildrice phytolith morphotype. These parts sink with the mature seed, as opposed to leaves, culms, and inflorescence branches that may be more susceptible to transport by wind or water after senescence and decomposition (Nurse et al. 2017). Routine and intensive harvesting of wildrice seeds would reduce the inputs of lemma and palea phytoliths deposited in situ. Therefore, wildrice phytolith loads are susceptible to differential deposition induced by both natural processes (e.g., riverine flows) and anthropogenic activities. Scouring and deposition of sediment in riverine environments may strongly reduce the applicability of these techniques outside of lacustrine wetlands.

Paleontological studies spanning the past 5,000 years have documented cyclical spikes in wildrice abundance as well as extended periods of site occupancy interrupted by long-lasting changes in community composition (Boyd et al. 2013; Keenlyside 1978; Lee et al. 2004; McAndrews 1994; Nurse et al. 2017). These data indicate both short-term oscillations in water levels and resultant wildrice abundance, and static hydrologic shifts not conducive to wildrice, leading to stand migration and/or succession to other species assemblages. Evidence of sedimentation events, charcoal inputs from wildfires, and influxes of pollutants captured with these data may allow for a better understanding of how these factors influence lacustrine plant community dynamics (Nurse et al. 2017).

3 Cultural, Wildlife, and Ecosystem Functions and Values of *Zizania palustris*

Wildrice is an integral part of both the native community and lacustrine wetland ecosystems, providing cultural, wildlife, and economic resources. Native communities rely on wildrice as an important food and cultural resource, while the healthy systems supporting wildrice production provides ecosystem services and values, such as providing habitat for fauna and nutrient cycling. As such, wildrice remains an important resource for humans and wildlife, and an indicator of ecosystem function, values, and services.

3.1 Cultural and traditional values

Wildrice, also referred to as “manoomin” in the Ojibwe language, has been an important food source for at least 2,000 years (Valppu 2000; Eule-Nashoba 2010). Wildrice is rich in minerals, vitamins, protein, dietary fiber, contains antioxidant phytochemicals, and is low in fat, with a nutritional quality comparable to other cereals (Oelke 1993; Surdendiran et al. 2014). Native communities harvest wildrice as a staple food rich in nutrients. Notably, it is also considered a sacred food source by many indigenous peoples (MNDNR 2008).

The process of harvesting wildrice is integral to native communities, and remains an important cultural practice conducted annually using traditional techniques. These traditional harvesting techniques result in food collection while considering the longevity and sustainability of wildrice stands. Utilizing a method sometimes referred to as “knocking the rice” intentionally scatters wildrice seeds both into the canoe for harvest and directly into the surrounding water body (Surdendiran et al. 2014), thereby seeding the lake bottom for germination the next season (Drewes and Silbernagel 2012). Harvesters also apply their knowledge of local lake conditions regarding the effects of harvesting levels and other ecosystem conditions influencing wildrice production to inform management decisions (Drewes and Silbernagel 2012). Unfortunately, interested harvesters, particularly younger harvesters, are in decline (Drewes and Silbernagel 2012).

The cultural and spiritual importance of wildrice to native communities is evident based on the language, traditions, and ceremonies applied to the

plant by the Ojibwe people and other communities in the Great Lakes region. Wildrice is considered a gift from the creator and is an important cultural resource to native communities (Vennum 1988; Drewes and Silbernagel 2012). Oral traditions of Ojibwe communities describe a historic migration west to the land where “food grows on the water” (Vennum 1988). Ojibwe communities migrated west to the Northern Great Lakes region in search of wildrice. The Ojibwe people consider wildrice as a foundation of their identity and considered themselves “people of the rice” (Vennum 1988).

Wildrice is intertwined with the cultural identities, traditional values, and food resources of native communities (Ackley 2000; Schlender 2000). Oral traditions and experienced harvesters communicate the cultural importance of wildrice through local knowledge transfer. For example, the Lac Vieux Desert Band of Lake Superior Chippewa Indians hold yearly “rice camps” to teach sustainable harvesting and traditional harvesting practices to tribal members and others. These tribal members represent repositories of ecological and cultural information related to wildrice. The importance of their indigenous knowledge highlights the need investigate reports that multiple lakes within the region have exhibited declining wildrice production in recent years and have rejected efforts to seed or otherwise manage areas to improve conditions for wildrice growth.

3.2 Wildlife values

Wildrice is an important energy source for wildlife, providing food for resident and migratory species, particularly aquatic and avian herbivores, and other seed consumers (Eule-Nashoba 2010; Pastor et al. 2017; Pollman et al. 2017; McAtee 1917; Hansen 2008). As an emergent aquatic plant, wildrice is also utilized by a variety of fish, invertebrates, and mammals, such as muskrats, providing shelter and a physical substrate for colonization of macroinvertebrates and other fauna (Drewes and Silbernagel 2012; Pastor et al. 2017). Reduction of wildrice is not only a concern as a cultural resource, but also the reduction can have a cascading effect on the larger ecosystem. A diverse aquatic food web is dependent on wildrice; declines in wildrice production can have a similar concomitant decline in wildlife dependent on energy rich wildrice seeds (Pastor et al. 2017).

3.3 Ecosystem services and values

Wildrice is found in riparian and fringe wetlands located along lakes and rivers in the Great Lakes region (Eule-Nashoba 2010). These wetlands provide several ecosystem functions and services. For example, riparian and fringe wetlands can dissipate the energy of unidirectional and multidirectional flow, leading to a reduction of sediment in the water column and the available sediment load available for offsite transport. The dissipation of wave and lentic energy also decreases as flood risk reduction and provides natural hydrologic control for receiving water bodies (Hildebrandt et al. 2012). Riparian and fringe wetlands also improve water quality through the detention of sediments, and the sequestration and transformation of a variety of elements and compounds ranging from metals to both naturally and anthropogenically derived organic and inorganic substances. Wetlands also contribute a significant amount of primary productivity to support the aquatic food chain (Wetzel and Howe 1999). These wetlands are important for nutrient cycling and play an important role in the organic carbon production and export. The wetlands in the region also provide floral and faunal habitat through establishment of physical structures used for cover and shelter; and the production of food sources for vertebrate and invertebrate consumers, and a variety of microbial populations including decomposers.

Wildrice is sensitive to ecosystem changes, particularly changes in hydrology and water quality that also alter the magnitude of the functions, values, and services that this unique plant community provides (Pastor et al. 2017; Pillsbury and McGuire 2009). The presence of large stands of wildrice indicate a healthy, functioning ecosystem, providing a high level of ecosystem services and values (Vennum 1988). A decline in wildrice production indicates a system change (Pillsbury and McGuire 2009) and is often associated with declines in ecosystem services and values (Vennum 1988). For example, waterfowl and other wildlife may not be present due to the loss of the high energy wildrice food source (Pastor et al. 2017).

3.4 Economics: Cultivation

There is limited information on the economics of wildrice. Most information is drawn from states (i.e., Minnesota and Wisconsin) with a permitting program for harvesting wildrice (Drewes and Silbernagel 2012). However, in this case permits likely underestimate true economics of wildrice in Minnesota and Wisconsin because, in most cases, tribal

members are not required to purchase permits within treaty-ceded lands (Drewes and Silbernagel 2012). In states such as Michigan where permits are not required to harvest wildrice, determining an economic value can be even more difficult. Additionally, the economic significance of wildrice extends past those who purchase a permit to harvest wildrice, but also to native and non-native populations who harvest and sell wildrice (Pollman et al. 2017; Drewes and Silbernagel 2012).

4 Chemical Factors Affecting *Zizania palustris*

Wildrice requires specific environmental conditions for germination, maturation, and growth. Ideal soil and water column conditions vary throughout the life stages of wildrice and changes in water column and/or soil chemistry can affect its production success variably across different life stages. This results in several complex soil-water-plant interactions. For example, wildrice seeds are particularly sensitive to soil porewater sulfide concentrations during germination, but plant growth and maturation following the floating leaf stage is primarily affected by nutrient availability and other water chemistry parameters. The following sections describe the environmental conditions conducive to wildrice success, and the resulting effects of changing water and soil chemistry on wildrice production.

4.1 Water column chemistry

Wildrice is adapted to tolerate a range of water column chemical compositions, but the productivity of the plant is maximized within a much narrower band of water quality characteristics. The chemical properties associated with wildrice production are discussed below in more detail, including a review of available information about pH, alkalinity, nutrients, and dissolved organic carbon (DOC). These properties collectively influence wildrice productivity directly (e.g., limit plant germination, growth, and fecundity) or indirectly (e.g., increasing potential competition for resources with other plants).

The optimal pH range for wildrice is circum-neutral (i.e., pH 6 to 8; Wild Rice in Minnesota 2008) based upon observations of healthy stands of wildrice in Minnesota and Wisconsin (Pillsbury and McGuire 2009). Changes in pH, either an increase or decrease in pH beyond this range, have been shown to decrease wildrice productivity. Notably, pH shifts result from a combination of factors including changes in the surrounding landscape that alter the pH of water entering the system or indirectly from changes in other water column parameters that subsequently effect pH (e.g., increased aquatic plant respiration).

Examples of direct shifts in pH include acidic conditions initiated by the introduction of sulfur bearing compounds or mine tailings from nearby

smelting operations into areas containing wildrice (MNDNR 2008). Acidic water reduces wildrice root mass (Pillsbury and McGuire 2009) and the acidification of surface waters because of anthropogenic activities has been documented in the Great Lakes region.

Indirect shifts in water column pH can be induced by enhanced anaerobic decomposition, where reduction of alternate electron acceptors decreases the hydrogen ion concentration (Reddy and DeLaune 2008). A decrease in hydrogen ion concentration increases the system pH. Anaerobic decomposition is triggered by the consumption of oxygen and is a normal process in wetland sediments driven by the availability of organic matter and alternative electron acceptors, the activity of microbial communities, and the rate of oxygen diffusion into the water column and sediment profile.

Once anaerobic conditions are induced, the potential accumulation of harmful sulfide compound concentrations can occur, especially in areas exhibiting sources of sulfur-bearing compounds (MNDNR 2008). As an example of the potential impact on soil and water column pH, Myrbo et al. (2017b) reported that a 44% decrease in hydrogen ion concentration and a pH increase from 7.57 to 7.81 was observed following anaerobic decomposition and enhanced sulfate reduction. Increases in nitrogen loading can also indirectly lead to increases in anaerobic respiration rates that influence pH. Wastewater discharges from septic tanks have been shown to increase ammonium availability in the region (Pillsbury and McGuire 2009).

Changes in hydrology that increase water residence times and decrease circulation can also trigger the onset of anaerobic conditions resulting in increased anaerobic decomposition and shift water column pH as described above. Lee and McNaughton (2004) documented microchemical changes in water column chemistries between wildrice and other aquatic macrophytes, particularly water-lily (*Nymphaea odorata* Aiton), which is a significant wildrice competitor (Figure 6). Water column chemistry within water-lily patches had higher pH, Fe, Mn, and Ca, and likely lower soil oxidation-reduction potentials when compared to areas with wildrice or open water.

Figure 6. Example of water-lily and wildrice competition in Lac Vieux Desert near Watersmeet, Michigan (Photo Credit: C. VanZomeren).



Alkalinity is a measure of the concentration of dissolved substances in the water column that can buffer shifts in pH by neutralizing acidity. Wildrice has an optimal alkalinity range above 40 ppm (Oelke et al. 1997; MNDNR 2008). Changes in alkalinity, typically increases, can alter aquatic plant community compositions, and result in conditions that favor other aquatic macrophytes over wildrice (Myrbo et al. 2017a; Lee and McNaughton 2004). A proportional increase in observed alkalinity from the anaerobic decomposition of sulfate has been documented in previous studies. Sulfate reduction consumes acidity, producing dissolved inorganic carbon (DIC) and increasing alkalinity (Myrbo et al. 2017b; Baker et al. 1986).

Dissolved organic carbon (DOC) is an important component of the system and a source of labile carbon (C). However, DOC also influences light availability for macrophyte growth, thermal stratification, and bioavailability of metals, Phosphorus (P), and C (Myrbo et al. 2017a). Anaerobic decomposition has been shown to increase DOC. For example, sulfate-driven enhanced mineralization of organic matter can release dissolved sulfides, nitrogen (N), P, DOC, and DIC, and increase alkalinity and pH of the system as described above (Myrbo et al. 2017b). Enhanced sulfate reduction during anaerobic decomposition can also trigger eutrophication associated with N and P release (Myrbo et al. 2017a). Low water transparency due to increases in colored DOC effects plant

establishment by increasing the energy needed during germination of wildrice seeds. Limited light availability from DOC can cause wildrice to exhaust their endosperm energy before achieving sufficient height to effectively photosynthesize, reducing production (Myrbo et al. 2017b; MNDNR 2008).

Myrbo et al. (2017b) and Baker and Brezonik (1988) point out that water residence time influences the impact of increased DOC, DIC, nutrients, and alkalinity/pH on water column effects and wildrice due to changes in soil decomposition and sulfate reduction. Changes in water column characteristics are more likely in lakes with >5 yr residence time than lakes with shorter residence times (e.g., <1 yr).

4.2 Soil chemistry

Soil chemistry has a significant influence on seed germination and wildrice development. For example, anaerobic conditions with oxidation-reduction potentials in the range of -150 mV are necessary for breaking seed dormancy and prompting germination. However, oxidation-reduction potentials below -200 mV (corrected for SHE) have been shown to restrict wildrice growth during later stages of its growth and reproduction. These findings suggest that wildrice requires narrow redox thresholds during different periods of its life cycle (Painchaud and Archibald 1990).

The chemical reduction of sulfate in anaerobic soils has been linked with decreases in wildrice productivity. Sulfate reduction produces hydrogen sulfide, a toxicant to rooted freshwater plants known to cause wildrice production declines (Myrbo et al. 2017a; Pastor et al. 2017). Soils exhibiting low oxidation-reduction potentials and sulfide production are thought to induce more significant declines in wildrice growth than soils exposed to depleted dissolved oxygen concentrations alone (Pastor et al. 2017). Additionally, increases in sulfide concentrations shifts vegetation community compositions, accelerates eutrophication, can induce benthic organism toxicity, can increase soil decomposition, and can inhibit vegetation uptake of ammonium (Johnson et al. 2019). Harmful sulfide concentrations and associated negative effects may be reduced in systems containing sufficient ferrous iron, which can react with free sulfides to form insoluble iron sulfide complexes that persist if anaerobic conditions are maintained (Myrbo et al. 2017a; Pollman et al. 2017).

Wildrice typically grows in systems with sulfate concentrations less than 10 mg/L (Moyle 1944). Sulfate availability can increase in freshwater systems due to several causes, such as introduction of salts from roadways, atmospheric deposition (Driscoll et al. 2001), wastewater inputs, groundwater source changes, shifts in wetting/drying cycles (Johnson et al. 2019), agricultural runoff, and mining of ores containing metallic sulfides (Pastor et al. 2017). Sulfate availability, and the resulting effects on wildrice, is particularly problematic in Minnesota (Pastor et al. 2017). Information regarding the degree of sulfate induced changes to wildrice in Michigan remains limited.

4.3 Litter decomposition and nutrient availability

Wildrice is an annual plant that does not store nutrients in rhizomes over the winter. Therefore, the nutrients required for wildrice growth are obtained primarily through soil and with limited nutrient uptake directly from the water column (Armstrong and Armstrong 2005; Pastor and Walker 2006; Grava and Raisanen 1978; Walker et al. 2010). Wildrice roots take up N and P from the soil and translocate nutrients to the rest of the plant (Sims et al. 2012a). Wildrice productivity is most often limited by N, followed by P (Pastor et al. 2017; Sims et al. 2012a). Nitrogen is limited early in the growing season but increases through plant maturity as the previous year's plant litter decomposes (Sims et al. 2012a; Walker et al. 2010). Sixty percent of annual N uptake occurs early in the growing season (Sims et al. 2012a), where wildrice is primarily allocating growth to its roots to take up nutrients and stabilize its above ground structures (Grava and Raisanen 1978). A second burst of nutrient uptake (N and P) occurs in August during seed filling and ripening (Sims et al. 2012a; Grava and Raisanen 1978; Grava 1982).

Immobilization of N can result in a delay in N availability, thus inducing N limitations early in the growing season (Walker et al. 2010). Availability of N drives growth, number of inflorescences, seed per inflorescence, and mean seed mass; and increased N availability accelerates growth and seed production (Sims et al. 2012b). Both timing and stage of wildrice litter decomposition are key drivers of wildrice production throughout the growing season (Walker et al. 2006). Nitrogen immobilized through microbial mineralization strongly influences production in subsequent years as N is not sufficiently mineralized until after the next growing season, reducing N availability for the following crop year (Sain 1983; Walker et al. 2006; Pastor and Walker 2006). Years with large wildrice

production abundances (colloquially described as bumper years) are thus often followed by years with decreased harvests (bust years) associated with N limitation (Moyle 1944; Archibald and Weichel 1985). Bust years are then succeeded by two to three fair years as adequate N mineralization occurs.

Walker et al. (2010) studied the effect of litter accumulation on wildrice production by measuring production rates and densities in wildrice mesocosms over 5 years. Both shoot and root litter immobilized N in the early stages of decay, effectively reducing the amount of N available in the subsequent year. Root litter immobilized almost twice as much N as shoot litter (Hildebrandt et al. 2012). The delay in N release from decaying litter is significant, as N is a major influencer of wildrice seed biomass and production, which both increase with N release from decomposition (Archibald et al. 1985; Walker et al. 2006; Sims et al. 2012b). Litter biomass and its immobilized N have been linked to the production oscillations seen in wildrice crops as described previously (Walker et al. 2006; Pastor and Walker 2006). This oscillation has additionally been associated with the lignin content of wild rice litter (Walker et al. 2010). The stimulatory nature of N on plant growth results in additional lignin content to provide physical stability of the plant (Hildebrandt et al. 2012; Berg and McClaugherty 2008). Lignin, however, is recalcitrant in nature and delays decomposition, providing nutrients for plant growth over longer timeframes.

Phosphorus limitation occurs less frequently in wildrice systems. Increases in P reduces P immobilization and enhances mineralization (Hildebrandt et al. 2012). However, unlike N, P enrichment often does not increase plant biomass when N levels are consistent (Walker et al. 2010; Sims et al. 2012a) but does have a stimulatory effect on N mineralization (White and Reddy 2000).

4.4 Summary of water and soil chemistry factors

Several chemical factors work in concert to determine the magnitude of wildrice production. The acceptable ranges of soil and water column constituents that promote the successful germination, growth, and reproduction of wildrice have been reported in other studies, providing a basis to evaluate the ecological conditions supporting wildrice. However, additional research is needed to effectively project the impact of changing environmental conditions on wildrice populations. In particular, changes

in chemical factors that directly or indirectly limit wildrice establishment and growth can occur during multiple phases of its life cycle. Changes in patterns of decomposition, accumulation of sulfides, hydrologic shifts, oxidation-reduction thresholds, and nutrient availability have all been identified as potential factors limiting wildrice productivity. The next phase of research will require linking these complex soil-plant-water interactions across spatial and temporal frameworks to gain a better understanding of the wildrice system.

5 Physical Factors Affecting *Zizania palustris*

Multiple physical factors influence wildrice production including soil substrate, hydrology, and water clarity. Soil characteristics drive many physical factors that promote wildrice growth. For example, root growth is driven by substrate type and bulk density conditions. Hydrology and water clarity impact the nutrient demands and physical stability of wildrice. For example, flowing water can provide nutrients to wildrice stands, but rapid water flow can uproot plants. Changes in the physical characteristics outside the limited tolerance range of wildrice can induce declines in production. The following sections describe the physical conditions that promote wildrice production and discuss the implications of changing physical characteristics for wildrice populations.

5.1 Soil characteristics

Wildrice can grow in a variety of substrates including flocculent sediment, sand, fractured bedrock, and gravel. However, it is found mostly in areas with soft, mucky, organic substrates at least 15 cm deep. The optimal depth for sufficient root anchorage is 46 cm (Figure 7; Archibald et al. 1985; Moyle 1944; Vennum 1988; Lee 1986; Fannucchi et al. 1986;). Day and Lee (1989) categorized the main types of bedforms that support wildrice growth, which were clay, organic, and flocculent substrates. Three hybrid types were also described as organic-floc, organic-clay, and organic over clay (Day and Lee 1989). Organic sediments containing adequate nutrients, are firmer, and more consolidated than flocculent sediments were ideal for wildrice growth and provided the best rooting support (Lee and Stewart 1984). Oelke et al. (1997) similarly suggested that organic soil materials are ideal, and in particular, organic soils containing 20% mineral matter and a C:N ratio <16.

Bulk density is related to sediment type, with clays and sands having increased bulk density in comparison to bedforms containing more organic or flocculent material. Bulk densities range from 0.07-0.31 g/cm³ (Eule-Nashoba 2210), with lower bulk densities reported in lake systems compared to riverine systems. Sediments with low bulk density, such as flocculent sediments, can result in uprooting, while sediments with high bulk densities can hamper the growth of wildrice root penetration. Moderate bulk densities are best for wildrice growth (Eule-Nashoba 2010).

Bulk density is generally higher in riverine systems than lake systems due to increased linear velocities and more turbulent flows capable of removing organic or flocculent soil particles and the translocation and deposition of mineral soil materials during high flows (Kincaid 2018).

Figure 7. Soil core profile of the organic, mucky substrate often associated with wildrice stands.



5.2 Litter accumulation

Excess litter accumulation (as senescent rice straw or other materials) that covers the sediment surface with thick layers of dead plant materials may hinder wildrice growth in the short term by physically suppressing seedlings and immobilizing nitrogen (N). However, biomass deposition can lead to increased harvests in the long-term through N release. Litter biomass can also reduce light penetration to wildrice sediment, shade out seedlings, create low oxygen conditions due to microbial respiration, and prevent wildrice stems from penetrating the water surface (Walker et al. 2006). Several studies have shown thinned wildrice stands to have increased seed viability and production, as well as larger plants (Aiken et al. 1988; Walker et al. 2006). However, senescent litter materials are often removed from stands gradually by wave action or uprooted by ice during spring thaw, minimizing the physical suppression effects (Walker et al. 2006).

5.3 Hydrology, water depth, and water clarity

Wildrice is most successful in areas with a moving but not turbulent water currents and, consequently, frequently occur alongside streams and near the inlets/outlets of rivers and lakes. Meeker (1996) found wildrice in nearshore stream environments with relatively slow velocities of $<0.025 \text{ m s}^{-1}$. It is important to note that presence or absence of wildrice, and wildrice growth stage, changes water velocities within vegetated areas (Meeker 1996). Water movement from wave action or flowing conditions is favorable to stagnant conditions as it can increase nutrient and sediment delivery while promoting aeration of the root zone (Vennum 1988; Meeker 1999). Although wildrice requires moving water for optimal growth, it is vulnerable to rapidly changing water levels. Slow flowing water with less than 15 cm of fluctuation during the growing season (or slightly declining levels) are ideal for wildrice (Moyle 1944).

Abundant wildrice stands are rarely found in stagnant waters, such as those located within the area of dams (both anthropogenic and beaver), because long term stable water levels tend to favor perennial plants rather than annual plants, such as wildrice (USDA 2004). Even when water is maintained at appropriate levels by dams for wildrice management, heavy precipitation and altered/reduced outlet flows can cause severe flooding and increase water levels rapidly, stressing wildrice stands (MNDNR 2008). Wildrice is most vulnerable to fluctuating water levels during its floating leaf stage, during which wildrice leaves float atop the water

surface (Figure 8). The plants are most buoyant during the floating leaf stage and can be easily uprooted, drowned, or washed away (Moyle 1944; Thomas and Stewart 1969; Dore 1969). Consequently, sudden increases in water levels, flooding events, and storms could easily remove and damage wildrice plants.

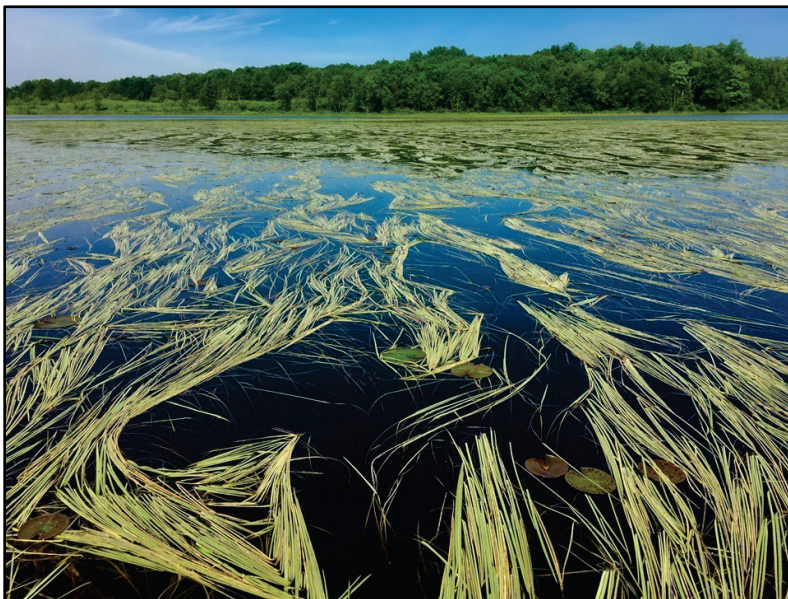
Water depth is another significant factor influencing wildrice due to its narrow tolerance range of inundation. Wildrice is usually found in water depths of 15-90 cm, with an optimal depth of 30-60 cm (USDA 2004; MNDNR 2008; Kjerland 2015). It is generally intolerable to depths beyond 90 cm, as evidenced by minimized seed production and eventual stand decline (MNDNR 2008). Weichel and Archibald (1989) evaluated 20 wildrice study sites in northern Saskatchewan, finding increased water depth negatively affected both seed and tiller production. Vennum (1988) observed similar results, documenting a relationship between increased water depths and a reduction in plant tillers, seed production, and overall plant biomass. Water depths beyond the tolerable range of wildrice can stress plants by limiting sunlight, drowning out growing stems, and making it difficult for wildrice to reach the surface, exhausting the energy reserves required for seed production (Meeker 1999; USDA 2004).

Increased water management can significantly alter wildrice production by maintaining water levels for prolonged periods either above or below its optimal range. High water levels often contribute to stand failure, especially in May and June when wildrice is in its vulnerable floating leaf stage (Figure 7). Conversely, low water levels provide a window for competing species introduction (ex. *Typha x glauca*) and enhanced competition by perennial emergent vegetation and submerged aquatic vegetation (SAV), which can often tolerate a greater variety of environmental and water conditions than wildrice. For example, lake drainages in Minnesota resulted in the loss of 344 ha of wildrice habitat due to invasion by competing species (Minnesota Tribal Wild Rice Task Force 2018).

Water transparency (i.e., turbidity) is also considered a primary criterion for suitable wildrice habitat since wildrice seeds need ample light and can be easily shaded out by perennial aquatic species, such as Giant Bur Reed, in the littoral zone (Mybro 2017). Low water clarity affects wildrice similarly to water depth, by reducing sunlight and subsequent photosynthesis by seedlings, discouraging plant development (Kjerland 2015; MNDNR 2008).

A secondary effect of hydrologic change is increased competition by other aquatic macrophytes (Pillsbury and McGuire 2009). Specifically, a shift from water levels that slowly recede over time to stable and persistent water levels due to installation of dams decreases circulation and oxygen availability, results in deleterious effects on wildrice production, and promotes the establishment of perennial aquatic vegetation that can outcompete wildrice (MNDNR 2008; Figure 5).

Figure 8. Floating leaf stage of wildrice. Stands are most vulnerable in this growth phase and are susceptible to being uprooted or drowned if water levels rise too quickly. Source: Fond du Lac Resource Management Division.



5.4 Temperature

MDNR (2008) cites climate change and its associated rising temperature as having “the potential for the greatest long-term impacts on natural wild rice.” Wildrice is sensitive to climatic changes because many stages of its germination and growth are strongly influenced by temperature. Wildrice seed germination only occurs after an extensive dormancy period, which requires being submerged in water for at least 90 days in cold, near freezing temperatures ($<1.6^{\circ}\text{C}$) (Kovach and Bradford 1992; Oelke 1993; MNDNR 2008). Afterwards, seed germination will begin when water reaches temperatures of at least 4°C (MNDNR 2008). Atkins et al. (1987) investigated wild rice germination under 100 combinations of temperature and after-ripening conditions, finding percent germination and germination rates increased with longer dormancy periods. The optimal temperature range required for germination also increased with after-

ripening. Seeds with five months of after-ripening saw greatest germination rates at average temperatures from 17.5-22.5°C; those with 7.5 months of after-ripening optimally germinated at a wider range of 12.5-32.5°C. Additionally, germination success rate increased from 29% to 66% when after-ripening period was extended from five to seven months.

The extensive after-ripening period required by wildrice is thought to increase the permeability of wild rice seed coats, with prolonged exposure to near-freezing temperatures increasing seed penetrability to water and gases. Higher winter temperatures would reduce the frequency of cold conditions necessary for seed germination, forcing the range of wildrice farther north where their thermal requirements will be met for successful germination (MNDNR 2008). While increased temperatures can accelerate wildrice plant growth, it is often accompanied by decreased floret numbers and stunted plant heights, resulting in an overall reduction in plant production (Oelke et al. 1997). Rising temperatures would also likely perpetuate the prevalence of invasive species, as wildrice is often in competition for space, light, and nutrients with several submerged aquatic, floating leaf, and emergent vegetation that can better adapt to rising temperatures (MNDNR 2008).

5.5 Summary of physical factors

Physical factors, in addition to the chemical factors described above, determine the success of wildrice production. Organic soils with moderate bulk densities are ideal soil characteristics as low bulk density does not provide a stable substrate for root structures and high bulk density physically hampers root penetration. Hydrologic characteristics also are important factors. Slow flowing water aerates the soil and provides a source of nutrients. Rapidly fluctuating water levels can uproot wildrice, while stagnant water encourages competition from other submerged aquatic vegetation. Shifts in the physical characteristics that lie outside the narrow tolerance range of wildrice can negatively impact production.

6 Summary and Identification of Knowledge Gaps

Wildrice grows in shallow (often <1 m) fringes of lakes and rivers predominantly in the upper Midwest region and adjacent portions of Canada where the period of cold winter temperatures provides favorable conditions for seed stratification. A healthy system that supports wildrice production also provides high levels of ecosystem function, as well as food sources for humans and wildlife. Wildrice is closely intertwined with cultural resources and traditional practices and remains important for subsistence and economic activities in indigenous communities (MNDNR 2008).

Specific environmental conditions are needed for wildrice seed production, germination, and growth. These environmental requirements are both physical (i.e., water depth) and chemical (i.e., pH, dissolved nutrients) in nature, and they change throughout the lifecycle of wildrice. For example, during early growth stages, water depth and clarity are critical for young plant development, as high water and turbidity reduces the success of seedlings reaching the surface before exhausting endosperm energy (Myrbo et al. 2017a; Aiken et al. 1988, MDNR 2008). Alternatively, water flow has a greater impact on wildrice production during the floating leaf stage when rapid changes in water level and velocity can uproot the plants and induce mortality (MNDNR 2008). Wildrice plants are also sensitive to changes in pH, alkalinity, sulfides, and other dissolved nutrient changes.

The narrow environmental thresholds varying across the lifecycle of wildrice can obscure underlying environmental changes that influence wildrice production. Several studies have elucidated some of the physical, chemical, and biological factors that limit wildrice productivity. For example, Myrbo et al. (2017a) sampled 108 different bodies of water with suitable wildrice habitat, both with and without wildrice, to assess the conditions indicative of wildrice presence. Porewater sulfide, water transparency, and water temperature were all found to be strong predictors of wildrice presence or absence. Further, wildrice density has been positively correlated with increases in alkalinity, and negatively correlated with increases in porewater sulfide concentrations (Myrbo et al. 2017a).

Pillsbury and McGuire (2009) similarly studied 60 historical wildrice beds with varying wildrice densities in Minnesota and Wisconsin to assess factors influencing wildrice abundance and distribution. Increased NH_4^+ , pH, and water depth were correlated with lower density wildrice populations, partially due to invasion by competing SAV and floating leaf species that can more rapidly consume N, decrease light penetration into the water column, and tolerate a wider range of environmental conditions than wildrice (Kjerland 2015). Pillsbury and McGuire (2009) also highlight potential declines in wildrice due to physical competition between SAV and wildrice, and the observation that SAV are more resilient to changing hydropatterns than wildrice, which are negatively impacted by hydrologic alterations.

Many previous studies focused on understanding the wildrice plant itself (Archibald and Weichel 1986; Xu et al. 2008), implications of hydrologic changes on wildrice productivity (Thomas and Stewart 1969), and the effects of sulfide toxicity and wildrice germination and growth (Myrbo et al. 2017a). Other less explored topics include the effects of altering the timing, volume, and intensity of precipitation events; changing temperatures (particularly winter temperatures); impacts of diseases or pests; SAV/invasive species; and secondary or synergistic effects of these topic areas.

Changes in climatic patterns, such as precipitation, temperature, or timing of events, will likely alter several of the environmental conditions key to successful wildrice production (MNDNR 2008). For example, changes in precipitation may induce rapid fluctuations of water levels and promote the uprooting of wildrice plants, particularly during the floating leaf stage (MNDNR 2008). Wildrice seeds require near freezing temperatures for an extended time to meet necessary physiological requirements for germination, thus warmer temperatures may inhibit seed germination (Kovach and Bradford 1992), either due to shorter periods of freezing temperature or extended warmer winter temperatures (Myrbo et al. 2017a).

Warmer temperatures during other parts of the year will likely increase decomposition rates and pore water nutrient concentrations, while decreasing oxidation-reduction potentials (Myrbo et al. 2017a). These factors have the capacity to impact wildrice production. Warmer temperatures can also increase the dispersion and impact of crop diseases. For example, brown spot disease (*Bipolaris oryzae*) thrives in humid

environments and would likely proliferate as rising temperatures are accompanied by increased humidity (Oelke 1993; MNDNR 2008). Brown spot disease, a fungal growth, contributed to the severely reduced 2007 wildrice harvest in Minnesota, resulting in 70-90% crop loss (Oelke 1993; MNDNR 2008). Additionally, warmer temperatures, higher humidity, and a reduction in the duration of freezing temperatures could lead to an establishment and proliferation of other diseases or pests such as soil nematodes (MNDNR 2008).

Healthy wildrice beds are largely monotypic, with some floating aquatic vegetation present (for example, water-lilies; MNDNR 2008; Mybro et. al. 2017a). However, an environmental shift, such as a change in hydrology (e.g., a dam installation), favors aquatic vegetation that is adapted to deeper water, and increases competitive advantage over wildrice (Pillsbury and McGuire 2009). Resource managers cite direct competition with other aquatic plants as a major factor driving decreases in wildrice; however, plant competition has not been extensively studied (Pillsbury and McGuire 2009).

Wildrice is predominately wind-pollinated, with its reproductive success linked to local weather patterns during anthesis. Extended periods of heavy rain or hot, dry weather with little wind are believed to greatly reduce pollen transfer (Moyle 1944). Anthesis in wildrice typically starts in late August and is protracted over several weeks, offering a buffer to these potential effects that may normally last several days. Effective dispersal distance of *Zizania palustris* pollen is unknown but assumed to be relatively low based on a study of *Z. texana* (approximately 1.5 m) by Oxley et al. (2008). However, dissimilarities in habitat type (riverine versus open lake) and dominant weather patterns could result in substantial differences. The wildrice pollination system is reinforced by dense stands without competing vegetation that can interfere with wind-driven transport.

Wildrice pollen may not disperse as far from source plants in years with high lake levels because the distance it can drift before encountering water is shorter, resulting in reduced pollination rates and seed production. Years with low water levels may allow wildrice pollen to drift farther, potentially reaching more pistillate flowers. Additional studies in effective pollen dispersal distance could inform our understanding of gene flow and population dynamics, as well as ecology and management of wildrice.

There is concern over potential gene transfer from cultivated varieties of wildrice to natural populations nearby with damaging environmental consequences. Assumptions that these concerns are unfounded are largely based on low pollen dispersal distance demonstrated by *Zizania texana*, and relative geographic isolation of most wildrice stands. Insect-derived pollen transfer in cultivated transgenic rice (*Oryza sativa*) has shown much higher rates and distances of dispersal than expected (>500 m), causing concern for both cultivated rice crops and their wild relatives in Asia (Pu et al. 2014). This could mean that pollen transfer to natural stands of wildrice from nearby cultivars is underestimated if relying on the estimates for wind-derived pollination alone. Insects are routinely observed visiting wildrice flowers but their contribution as effective pollinators and pollen dispersers is poorly understood.

Wildrice cultivars have selected traits that primarily enhance grain size uniformity and increased yields through shattering-resistance (retain more mature grains on the plant) and greater synchrony of flowering and grain maturation (Hayes et al. 1989). Shattering-resistance is a recessive trait that occurs naturally but in low levels, likely due to selection favoring higher seed dispersal and reduced availability to granivores. Asynchrony of flowering and resultant grain maturation is a trait that confers resilience to stochastic weather or flooding events that could otherwise eliminate effective pollen dispersal for the year or transport total seed output offsite to unfavorable locations. The desirable traits of wildrice cultivars may not offer fitness advantages in natural settings and would likely face high selection pressure.

Limited research on the physicochemical effect of vegetation shifts on wildrice is available. Pillsbury and McGuire (2009) attempted to elucidate environmental differences between submerged aquatic vegetation and wildrice with limited success. Other considerations on soil structure, nutrient flux and decomposition, dissolved organic carbon, and turbidity are needed in the context of vegetation shifts (Myrbo et al. 2017; Scheffer 1998). Walker et al. (2010) compared wildrice production with and without wildrice litter, and confirmed the importance of wildrice litter decomposition on available nutrients, primarily N. However, no studies have evaluated the effect of other types of litter material where decomposition rates and timing, nutrient content, or dissolved organic carbon may differ from the available data on wildrice straw.

The timing of N release to the water column and dissolved N concentrations are critical components of successful wildrice growth and reproduction (Painchaud and Archibald 1990; Walker et al. 2010). A shift in either of these is likely to result in declines in wildrice production. Wildrice N requirements are met through decomposition of the previous year's litter. Asynchrony or delay in nutrient supply (i.e., change in timing or rate of decomposition) with respect to timing of wildrice nutrient uptake will likely result in reduced productivity via nutrient limitation on growth or seed production (Pastor and Walker 2006). Changes in the spatial dynamics of litter accumulation, and therefore decomposition and available nutrient concentrations, is an important question for future research (Walker et al. 2006).

Water clarity is also critical for wildrice success (Sheffer 1998) and is influenced by DOC concentrations and turbidity (i.e., suspended sediment). Reduction in water clarity effectively excludes the emergence and success of rooted macrophytes (including wildrice), where endosperm energy is exhausted before the plants reach the water surface. Dissolved organic carbon increases with higher decomposition rates, which is likely to occur with warmer temperatures (Myrbo et al. 2017a). Turbidity may increase due to several factors, including increases in turbulent runoff events, changing land use patterns, and processes disturbing bedforms supporting wildrice populations. Turbidity can also increase because of storm events or recreational activities (e.g., boating; Pillsbury and McGuire 2009). Additionally, increased nutrient availability either from enhanced decomposition or new sources can support phytoplankton growth sufficiently to shade out wildrice (Myrbo et al. 2017a).

Finally, an interesting finding by Myrbo et al. (2017a) suggests the importance of phytoliths as a source of nutrients, particularly potassium. Elevated water temperature may enhance phytolith dissolution (Myrbo et al. 2017a). Accelerated phytolith dissolution, in addition to other factors reducing wildrice production, warrants additional research.

Wildrice is a unique and culturally important aquatic macrophyte in the Great Lakes regions. The complexity of the wildrice life cycle and narrow environmental thresholds required for successful wildrice production highlight the need for additional research in several areas. Previously completed research provides key information on the wildrice plant itself, hydrologic drivers of wildrice productivity, and the negative impacts of

sulfide toxicity on this species. Additional areas of research interest have also been identified. In particular, the effect of changing climate on precipitation events and winter temperatures needs greater attention. Issues related to competition from other aquatic macrophytes has been evaluated in several publications, yet there remains limited information on the long-term implications for wildrice populations. Further, indirect effects of changes in decomposition rates, nutrient availability, and other soil properties are other areas of research that require additional attention.

In summary, much additional work is needed to understand the drivers of wildrice productivity. Natural resource managers and indigenous communities require tools, approaches, and remedies to effectively manage wildrice habitat and improve conditions for its growth and reproduction. As the emphasis shifts from scientific studies to the development of actionable management strategies, individuals and communities need to incorporate the best available data driven decision making processes with sources of indigenous knowledge to ensure the sustainability of this ecological and cultural resource.

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REPORT DOCUMENTATION PAGE

1. REPORT DATE August 2023		2. REPORT TYPE Final report		3. DATES COVERED <table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="width: 50%; vertical-align: top;"> START DATE FY </td> <td style="width: 50%; vertical-align: top;"> END DATE FY </td> </tr> </table>		START DATE FY	END DATE FY				
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4. TITLE AND SUBTITLE Wildrice (<i>Zizania palustris</i> ; Manoomin) Biology, Functions and Values, and Soil Physiochemical Properties Affecting Production											
5a. CONTRACT NUMBER		5b. GRANT NUMBER		5c. PROGRAM ELEMENT							
5d. PROJECT NUMBER 478492		5e. TASK NUMBER		5f. WORK UNIT NUMBER							
6. AUTHOR(S) Christine M. VanZomeren, Kevin D. Philley, Nia R. Hurst, and Jacob F. Berkowitz											
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Environmental Laboratory US Army Engineer Research and Development Center 3909 Halls Ferry Road Vicksburg, MS 39180-6199					8. PERFORMING ORGANIZATION REPORT NUMBER ERDC/EL SR-23-3						
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) US Army Corps of Engineers, Detroit District 477 Michigan Ave Ste 700, Detroit, MI 48226				10. SPONSOR/MONITOR'S ACRONYM(S)	11. SPONSOR/MONITOR'S REPORT NUMBER(S)						
12. DISTRIBUTION/AVAILABILITY STATEMENT DISTRIBUTION STATEMENT A. Approved for public release; distribution is unlimited.											
13. SUPPLEMENTARY NOTES Planning Assistance to States											
14. ABSTRACT Wildrice (<i>Zizania palustris</i> L.) is an annual aquatic emergent plant primarily distributed across portions of Minnesota, Wisconsin, Michigan, and Canada. Wildrice requires narrow environmental conditions that vary throughout its life cycle. Environmental conditions required include water levels between 15 and 90 cm, slow flowing water, anaerobic soil, and circum-neutral pH. Wildrice production and abundance is most often limited by nitrogen availability. Both short- and long-term changes in local conditions impact distribution and abundance of wildrice at local and regional scales. Reported declines in wildrice production have increased interest in evaluating changing environmental conditions, specifically within the Upper Peninsula of Michigan. Wildrice, or manoomin, is an important food and cultural resource, and remains important to native peoples throughout the region, including the Lac Vieux Desert Band of Lake Superior Chippewa Indians. This report provides a review of literature related to wildrice and examines potential factors affecting its production in the Upper Peninsula of Michigan. This report highlights cultural and traditional values, functions and values of wildrice, and unique chemical and physical aspects of the environment where wildrice grow. Additionally, this report synthesizes the data gathered in the literature review, identifies knowledge gaps, and provides research opportunities for improved wildrice production in the Great Lakes region.											
15. SUBJECT TERMS <table style="width: 100%;"> <tr> <td style="width: 33%;">Wildrice</td> <td style="width: 33%;">Aquatic plants</td> <td style="width: 33%;">Plant-soil relationships</td> </tr> <tr> <td>Zizania palustris</td> <td>Great Lakes Region (North America)</td> <td></td> </tr> </table>						Wildrice	Aquatic plants	Plant-soil relationships	Zizania palustris	Great Lakes Region (North America)	
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16. SECURITY CLASSIFICATION OF: <table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="width: 33%; vertical-align: top;"> a. REPORT Unclassified </td> <td style="width: 33%; vertical-align: top;"> b. ABSTRACT Unclassified </td> <td style="width: 33%; vertical-align: top;"> c. THIS PAGE Unclassified </td> </tr> </table>				a. REPORT Unclassified	b. ABSTRACT Unclassified	c. THIS PAGE Unclassified	17. LIMITATION OF ABSTRACT SAR				
a. REPORT Unclassified	b. ABSTRACT Unclassified	c. THIS PAGE Unclassified									
18. NUMBER OF PAGES 56											
19a. NAME OF RESPONSIBLE PERSON				19b. TELEPHONE NUMBER (include area code)							

