Invasive Johnsongrass, a threat to native grasslands and agriculture

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Abstract

Among the weedy plant species, Johnsongrass (*Sorghum halepense*) is one of the most destructive. Johnsongrass has invaded new habitats beyond its native Eurasian origin by outcompeting native flora and cultivated crops. The Johnsongrass habitat is expanding continuously due to clonal and self-pollinating reproduction strategy, accelerated growth and the progressing climate change. As a result, Johnsongrass has reduced native plant diversity in grasslands and inflicted economic damage to agriculture on every continent. Johnsongrass is a growing threat to crop production, as it serves as a refuge for a variety of agricultural pests and plant viral diseases. Over the past decades, herbicides extensively applied to control Johnsongrass have boosted selection pressure, resulting in the independent evolution of herbicide-resistant ecotypes across multiple locations. The apparent threat to native flora and agriculture caused by the invasive Johnsongrass is a subject to a long and ongoing research. This review provides a historical and research overview on Johnsongrass expansion, its current as well future impact particularly on North American and European grasslands and agriculture.

Keywords Agricultural damage · Climate change · Habitat expansion · Herbicide resistance · Invasive species · Johnsongrass · Noxious weed · Perennial grass · Pest and plant virus host · Sorghum halepense · Threat to native flora

Introduction

Among the worldwide relevant weeds, Johnsongrass is one of the top 10 noxious global mild-latitude weeds. Johnsongrass was introduced to the U.S. separately, in South Carolina and Arizona (Sezen et al. 2016). The earliest introduction occurred around 1830 through contaminated cotton seeds from Egypt successfully invading agricultural pastures and natural plains in South Carolina (McWhorter 1971). Johnsongrass is classifies as weed in over 53 countries occurring in 30 different crops (Masood et al. 2017; Ryder et al. 2018). Dense Johnsongrass populations in crop fields have been shown to impact the yield quantity causing substantial damage to agriculture.

The narrow-leaved Johnsongrass seedlings exhibit a significant similarity to cultivated annual grain and can be misidentified as sorghum or maize plants. However, adult plants develop a distinct morphological phenotype reaching up to 2.5 m height and stems between 0.5 and 2.0 cm in diameter. The veined leaves with a prominent mid-vein expand up to 60 cm in length and 3.3 cm in width. In flowering, the panicle is erected and pyramidal gaining a size of up to 50 cm. Below ground Johnsongrass develops an extensive subterranean rhizome network that can resemble up to 70% of the entire plant dry weight (Paterson et al. 2020).

Johnsongrass naturally hybridizes with various *Sorghum* species resulting in new perennial and rhizomatous hybrids able to persist harsh environment and establish themselves in new habitats. For example, up to 72% of *S. bicolor* and *S. halepense* F_2 hybrid offsprings develop rhizomes and able to withstand sub-zero winter temperatures with a survival rate of up to 71%. Studies on *S. halepense* crossings with various other *Sorghum* species result also in rhizomatous progenies (Yim and Bayer 1997). For instance, *Sorghum almum* develops rhizomes and between $1050 - 43110$ seeds per plant. Its set of $2n = 40$ chromosomes resembled during hybridization between Johnsongrass and cultivated Sorghum. Alongside of Johnsongrass *S. almum* is also considered as weed spanning across five continents (North America, South America, Europe, Africa and Australia). However, in comparison to Johnsongrass *S. almum* rhizomes survive in warm climates but did not withstand the winter in colder regions resulting in lower invasiveness if compared to the noxious parent (Eberlein et al. 1988). Meanwhile, Johnsongrass established itself permanently in grasslands and

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agricultural fields not only in tropical and moderate climate regions but also demonstrates resilience in colder parts of the world such as Canada. Already in 1983 Johnsongrass was reported in Southern Ontario (Warwick and Black 1983). In that habitat Johnsongrass proves its toughness as one of the most noxious weeds by tolerating heat waves exceeding 32 °C and regular temperature plunges to -26 °C aboveground at the coldest time of the year (Smoyer et al. 2000; Coiner et al. 2018). This northward expansion of Johnsongrass might be associated with the progressing global climate change. The potential global average temperature rise up to 4.5 °C accompanied with doubled preindustrial atmospheric CO_2 levels by the end of the next century could expand the range of plant species between 500 and 1000 km to the north. For instance, those dramatic climate changes would disturb the diversity and distribution of the vegetation in North America creating favorable condition for Johnsongrass expansion throughout the continent (Overpeck et al. 1991).

Sorghum halepense origin and evolution

Currently, 25 taxonomically distinct species are recognized in the genus *Sorghum* which are dispersed throughout 5 subgenera: *Eusorghum*, *Chaetosorghum*, *Heterosorghum*, *Parasorghum* and *Stiposorghum* with chromosome counts of 2n = 10, 20, 30, 40 (Garber 1950; Lazarides et al. 1991). The *Sorghum* subclass *Eusorghum* harbors the species *Sorghum propinquum*, *Sorghum halepense* and *Sorghum bicolor*. The later resembles the only cultivated *Sorghum* varieties. Most of the *Sorghum* species are wild or weedy with varying inter and intraspecific compatibility ranging between 0 and 100% (Venkateswaran et al. 2019). However, *Sorghum halepense* ancestors *Sorghum bicolor* and *Sorghum propinquum* have been shown to have itself a common ancestor and an estimated divergence of around 2 million years (Guo et al. 2019). In contrast to *Sorghum propinquum* a substantial archaeological evidence suggests the cultivation and domestication of *Sorghum bicolor* in the central Sahara area 7500 − 7100 BC and its wide spread as an important crop in Asia and India between 4000 − 3500 BC (Winchell et al. 2018). The tetraploid *Sorghum halepense* (2n = 40) emerged less than 2 million years ago during a natural hybridization and chromosome duplication between diploid (2n = 20) *Sorghum bicolor*, a drought resistant crop native to tropical Africa, and rhizomatous southeast Asian *Sorghum propinquum* gaining the ability for vegetative reproduction by rhizomes (Warwick and Black 1983; Kong et al. 2013; Cox et al. 2018; Paterson et al. 2020). *S. halepense* origin has been established by protein sequence polymorphism studies resulting in 99.4% nucleotide match compared to *S. bicolor*, *S. propinquum* and outgroup *S. timorense*. Further, the remaining 0.6% of nucleotides match *S. bicolor* to 10.9% but deviate from *S. propinquum* and 6.6% vice versa (Paterson et al. 2020).

Johnsongrass as invasive plant species

One of the remarkable prosperity factors of Johnsongrass is self-pollination (Dweikat 2005). It blooms 46 days after emergence and produces up to 80000 seed per plant in a single season which remain viable for up to 10 years in the soil (McWhorter 1961; Ryder et al. 2018). Johnsongrass has a broad seed depth germination rate ranging from 64% at 1 cm to 30% at 20 cm depth. Up to 6% of its seeds are able to germinate from depths as low as 25 cm (Toth and Lehoczky 2006). The ability of Johnsongrass to produce modified subterranean stems, the rhizomes, enabling it to reproduce vegetatively by generating adventitious roots and new shoots as the main factor for its invasiveness similar to other rhizomatous weed species such as *Calystegia hederacea*, *Solanum eleaegnifolium* and *Cirsium* (Xiqing et al. 2016; Kariyat and Chavana 2018; Nunes and Kotanen 2018; Gu et al. 2019). The rhizome biomass allocation in Johnsongrass is with 31 − 37% significantly higher than in all sexual reproductive structures that ranges between 9 − 11% similar to other rhizomatous grass species, suggesting the clonal reproduction strategy as a sink for limited resources (Wilson and Thompson 1989; Benech Arnold et al. 1992). Rhizomes are essential organs in storing carbohydrates and minerals. Further, secondary metabolites produces in *S. halepense* root system have been shown to have a negative effect on popular medical plants grown in Iran such as *Ocimum basilicum*, *Nigella sativa*, *Cuminumcyminum*, *Foeniculum vulgare*, *Plantago ovata* and *Plantago psyllium* (Asgharipour and Armin 2010). Similar effects were observed in wheat. Wheat seed germination ration dropped by 30% exposed to *S. halepense* root extract. Further, it was demonstrated that *S. halepense* root tissue extracts have a negative impact on wheat seedling, radicle, and coleoptile development reducing the plant fresh weight significantly (Hamid et al. 2012). The rhizome multifunctionality combined with their allelopathic effects on competitor plants might contribute to the enhanced competitiveness and invasiveness of Johnsongrass (Anderson et al. 1960; Jang et al. 2009). A single plant can produce a rhizome network more than 60 m in in length in 152 days (McWhorter 1961). During early development, Johnsongrass plants gain up to 4-fold more biomass than North American prairie grasses *Panicum virgatum* L. (switchgrass), *Schizachyrium scoparium* (Michx) Nash (little bluestem) and *Andropogon gerardii* Vitman (big bluestem), due to increased leaf area, higher atmospheric carbon uptake and photosynthetic nitrogen-use efficiency (Reichmann et al. 2016). Greenhouse simulated seedling competition experiments between Johnsongrass and these same C_4 plant species resulted in a dramatic 95% biomass loss in the native species if grown along with Johnsongrass, which suffered a moderate 11% loss of non-root biomass (Schwinning et al. 2017). Transcriptome assembly analysis and annotation studies of Johnsongrass resulted in 6447 potential protein coding sequences. Its bioinformatic coding sequence analysis between *Thinopyrum intermedium*, a

rhizomatous and perennial grass, and the seasonal non-rhizomatous *S. bicolor* resulted in the identification of 98 candidate sequences involved in Johnsongrass rhizome development. Among these, the most expressed protein families belong to ZIM (zinc finger inflorescence meristem) family, DNA binding proteins, transcription factors and the Armadillo (ARM)-repeat superfamily which have been shown to play crucial roles in hormone signaling, development by exhibiting a differential expression pattern during environmental stress responses (Ryder et al. 2018). Similarly, the analysis of Johnsongrass ancestor *S. propinquum* promoter regions shows an enrichment of cis-regulatory elements involved in abscisic acid (ABA) and gibberellic acid (GA) responses, suggesting a cross-talk between those hormones in rhizomes. Both phytohormones are key regulators in rhizome development. In particular, promoter regions of differentially expressed genes in rhizome tip tissue are enriched with gibberellin regulated cis-elements such as pyrimidine box TATCAA and CAREs box (Jang et al. 2006). Additional genes enriched in rhizome tips are linked to hormone signaling pathways, sugar response and transport, cell cycle, cell division and development as well as splicing factors that enable biotic and abiotic stress tolerance.

Johnsongrass impacts on agriculture

The density of Johnsongrass plants is a critical factor that affects surrounding vegetation, and floral biomass loss accumulates drastically due to Johnsongrass density. A single Johnsongrass plant in an 8 m plant row decreased cotton yield by 7.12% and when densities increased to 32 plants/ 8 m plant row cotton yield dropped by 30% (Uludag et al. 2007). Similar results were observed in in the U. S. in Texas, where a single Johnsongrass plant/15 m cotton plant row reduced yield by 34$/hectare (Wood et al. 2002). Further studies demonstrated a significant cotton yield increase when treating Johnsongrass infested fields with herbicide fluazifop, where treating plots 3 weeks post-Johnsongrass emergence produced the same cotton quantity as weed-free lots. However, plot treatments delayed by 3, 5, 9 and 22 weeks reduced cotton yields by 20-, 60-, 80- and 90%, respectively (Keeley and Thullen 1989).

Soybean (*Glycine max*) is an important legume crop and was domesticated 3000 to 5000 years ago in Asia with a spread out of Asia 250 years ago (Lee et al. 2011; Liu et al. 2017). Due to its high protein and oil content and low carbohydrate content, it is widely used for animal feed and human consumption (Sedivy et al. 2017; Rizzo and Baroni 2018). Weeds such as Johnsongrass can drastically impact soybean production. Johnsongrass density of 32 culms / 10 m reduces soybean yield by 13- to 38% if it is allowed to compete uncontrolled for 6 weeks. The reduction increased up to 69% at a 7-week competition and reached 88% at full-season competition (Williams and Hayes 1984). In addition, field plot

experiments with soybean varieties heavily infested with Johnsongrass demonstrated yield reductions of between 23- and 42% over a 3-year period (McWhorter and Hartwig 1972). Similar effects were observed in corn (*Zea mays*), where uncontrolled 4-week competition between corn and Johnsongrass grown from rhizomes resulted in 10 – 14% less corn silage. A season-long competition between corn and Johnsongrass led to more than 80% corn seed loss compared to weed-free corn plots (Mitskas et al. 2003). In addition to crop yield losses from Johnsongrass competition, producers controlling Johnsongrass with herbicides incur expenses of between $12 to $20 per acre for herbicides and their application, establishing Johnsongrass as a serious threat to constantly increasing human demands for food (Paterson et al. 1995).

New habitat colonization and the role of climate change

In U.S. Great Plains as defined in 2000 are stretching throughout 475 counties and 11 states along the southern latitude of the 32nd degree spanning from the Midwest to Rocky mountains (east to west) and from northern Canada to central Texas (north to south) (Sylvester et al. 2013). The natural grassland ecosystem is shaped by the north-south temperature and the east-west precipitation gradient with annual rainfall between 1200 and 300 mm and temperatures from below 0 °C and above 20 °C (Gutmann et al. 2005). These ecoregions appear to be most suitable for invasive plant species including Johnsongrass. A large number of collected Johnsongrass populations in those regions suggests a permanent establishment, high climatic compatibility and suitable biotic and abiotic conditions. In computer models the Synthetic Ecoclimatic Index (EI) estimating the growth and stress factors was generated for Johnsongrass on the global scale. Predicted climate niche for Johnsongrass with suitable EI values > 20 stretches throughout all but Antarctic continents reaching habitats as north as Canada and Sweden, if water supply is available. According to computer models the wide niche range, Johnsongrass is able to colonize 62% of North American and 80% of U.S. ecoregions. In the continental US Johnsongrass showed a climate match between 50% – 90% in all 20 designated ecoregions excelling particularly in plains and prairies (Barney and DiTomaso 2011). Broad Johnsongrass dispersion predictions are confirmed in field studies where 939 out of 2077 visited sites resulted in the verified occurrence of Johnsongrass (Ohadi et al. 2018). Common North Americas C₄ prairie species such the big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*) and the little bluestem (*Schiachyrium scoparium*) are forced to compete with the perennial Johnsongrass belonging to the same functional group over territory and resources. The early grow schedule of invasive plant species is a key factor to gain the competition advantage. Faster seed germination, seedling growth and higher leafe area

have been shown as characteristic traits for invasiveness. In comparison to three native prairie species Johnsongrass seeds germinate faster and gain fourfold size advantage within first 17 days post germination compared to its competitors (Reichmann et al. 2016). A 13 – 30 fold higher Johnsongrass biomass production compared to three native species 50 days after seeding illustrates the potential threat to native flora (Schwinning et al. 2017). Under natural conditions prairie land is reigned by a high grass cover until woody species begin to dominate and drive it back proportionally. Undisturbed Oklahoma prairie plots showed the grass cover at 90% for a decade. The most dominant species such as *Schizaehyrium scoparium*, *Andropogon gerardii*, *Panicum virgatum*, and *Sorghastrum nutans* were pushed back to 38% during the rise of woody plants after 9 years, reaching maximal woody cover percentage of 58% after 32 years. A single plow however eliminates woody species and reduces the prairie grass cover opening the gate for pioneer invaders. In those areas the grass cover stagnates at 60% – 70% for almost 2 decades dominated by native perennial *Leptoloma cognatum* and invasive Johnsongrass. Similarly, annually plowed prairie was promptly populated by various weed species including Johnsongrass (Collins and Adams 1983). Johnsongrass has proven itself similarly successful in US Texas. The Fort Worth Prairie is populated by geographically characteristic native grass species such as *Schizachyrium*, *Bouteloua curtipendula*, *Sporobolus compositus*, *Bouteloua hirsuta*, *Sorghastrum nutans*, and *Andropogon gerardii*. However, over the past four decades a field study measured an overrun by Johnsongrass from the north, area previously used for agricultural purposes. The observed mean advancement of Johnsongrass in native prairie is 0.45 m per annum diminishing the native flora diversity by transforming the native grassland into transitional and subsequently into invaded prairie. The aerial cover Johnsongrass for each invasion stage reaches from 0% in native to 27% in transitional and 77% in invaded prairie pushing back the presence of native species by 47% while expanding the rhizomatous growth and altering the soil biochemistry during the invasion process (Rout and Chrzanowski 2009; Rout et al. 2013). The displacement rate of native grass species may vary depending on the geographic. For instance, various *Panicum virgatum* biotypes exhibit significant differences between age of first flowering, plant height, biomass, shots, and seed count per plant changing factors local flora modulation (Palik et al. 2016). Efforts to re-establish native flora on abandoned farmland have been proven to be difficult. A blunt native grass seed sowing effort does not alter the overall biomass of invasive grasses, including Johnsongrass. However, if combined with a physical removal the Johnsongrass biomass decreased by 63% while increasing the overall biomass by nearly 25% after 2 years of the experiment. Worth mentioning is that sowed grass species tend to form concentrated patches instead of a homogeneous distribution indicating a labor and time consuming recovery process (Tognetti

and Chaneton 2012). Delaying the grassland transition to later vegetation succession stages by grazing and above-ground burning slows down subsequently also the weed propagation, including Johnsongrass (Davidson 1993).

Furthermore, the globally progressing climate change has a positive effect on Johnsongrass propagation. Rising temperatures and change in precipitation could potentially unlock currently unreachable habitats. Long term studies affecting the weed propagation in Oklahoma U.S. under warming and precipitation conditions resulted in changed soil temperature as well the soil water content during experimental settings. On those plots the dominant C_3 biomass decreased and C_4 biomass increased over eight years constantly. Within the first three years a switch from 73% C_3 group biomass to 78% C_4 biomass was observed. The annual weedy grass and forbs community including species such as *Bromus japonicus* and *Ambrosia trifida* was transformed mostly to perennial bunchgrass *Tridens flavus* and *Sorghum halepense* (Shi et al. 2018). Similarly, increased territorial advancements of Johnsongrass due to the increasing global temperature are reported from Austria, Germany and other warm regions of Europe since the beginning of the 1990s. Depending on economy priorities and population growth in Germany and Austria in the next decades a conservatively forecasted average temperature increase between 0.9 °C − 2.9 °C due to global climate change is expected, if compared to the average reference temperature between 1961 and 1990 (Kleinbauer et al. 2010). The increase of temperature supports the current findings in Johnsongrass expansion trajectory. Between 1965 and 1999 in total 13 grids (33 km^2) clustered in the south-eastern crop fields and three in the northeastern part of Austria were colonized by Johnsongrass. Meanwhile, in years between 2000 and 2016 Johnsongrass populations were recorded in 42 grids concentrating in the south but with a clear expansion into northern crop fields (Follak et al. 2017). In 2010 the Johnsongrass records in fields increased to > 100 and > 190 outside of fields (Follak and Essl 2012). As of 2017 Johnsongrass is threatening to expand exponentially throughout 168000 ha agricultural area (Follak et al. 2017).

Further, the climate change associated high atmospheric CO_2 concentration stimulates the plant growth and the photosynthesis while simultaneously inhibiting the plant transpiration. Therefore, significant increase of air CO_2 content could have the potential to alter entire ecosystems (Tian et al. 2019). Those changes might level the field for invasive plant species, especially such as the broad niche compatible Johnsongrass.

Emerging herbicide resistance in Johnsongrass

Before the use of specialized herbicides for Johnsongrass, the species was controlled by repeated deep tilling and hoeing (Poienaru et al. 2005). Later, pre-emergent application of broad

range herbicides such as Guardian MAX, Merlin and Stromp 330 EC showed it to be highly effective against Johnsongrass infestations (Toth and Lehoczky 2007). Presently, susceptible Johnsongrass plants are controlled from 88- to 97% with quizalofop, glyphosate, imazethapyr plus imazapyr, nicosulfuron, and primisulfuron herbicides and 56% with glufosinate herbicide 3 weeks after treatment (Johnson et al. 2003). Over the past decades, however, glyphosate (N-(phosphonomethyl) glycine) has evolved as the most pre-ferred herbicide with more than 8.6 billion kg sold since 1974 (Benbrook 2016). Glyphosate controls systematically perennial weeds such as Johnsongrass (Baylis 2000). However, intensive world-wide glyphosate application has created glyphosate resis-tance in 35 known weed species, including Johnsongrass (Heap and Duke 2018). In Argentina, Johnsongrass has developed independent multiple types of resistance towards glyphosate re-quiring higher dosages for effective control (Vila-Aiub et al. 2007; Fernandez et al. 2013). Computer models accounting for complete plant life cycle including rhizomes and seeds were used to simulate decades of Johnsongrass resistance allele fre-quencies in populations exposed to glyphosate.

Recurrent nicosulfuron application to seedling- and rhizome-emerged Johnsongrass has also created resistant Johnsongrass biotypes with 33- to 46 times higher herbicide resistance than susceptible control plants (Hernández et al. 2015). Johnsongrass poses an exclusive threat to cultivated *S. bicolor* due to its close ancestry. In Texas and Nebraska, up to 32% of unique *S. bicolor* alleles were identified in Johnsongrass populations adjacent to long-term *Sorghum* production sites. The obtained evidence strongly suggests that engineered genes and herbicide resistance can potentially be transferred into Johnsongrass and widely dis-seminated (Morrell et al. 2005).

Johnsongrass, a pathogen source for cultivated plants

Over 25% of all existing flora is estimated to serve as host for more than 4000 phloem-feeding Aphidae (aphid) families (Dedryver et al. 2010; Jaouannet et al. 2014). Roughly 100 species of aphids are economically relevant species (Emden and Harrington 2007) which incur global agricultural crop losses of billions of dollars annually (Emden and Harrington 2007). Despite feeding-based biomass reductions due to significant chlorophyll and carotenoid removal from damaged plants (Riedell and Kieckhefer 1995; Ni and Quisenberry 2006; Ni et al. 2013), aphids also have the potential to vector at least 275 plant viruses. The potyviruses Maize Dwarf Mosaic Virus (MDMV), Sugarcane Mosaic Virus (SCMV), Johnsongrass Mosaic Virus (JGMV), and Sorghum Mosaic Virus (SrMV) are commonly found in corn, Johnsongrass and *Sorghum*, cause corn and sorghum yield losses of up to 70%, mostly by causing leaf necrosis and photosynthesis shutdown (Garrido 1993;

Wamaitha et al. 2018; Seifers et al. 2000). The severity potential of MDMV cross-contamination between Johnsongrass and crop plants was demonstrated in samples collected from Ohio (U. S.) which indicated that 20 of 33 Johnsongrass plants were infected with MDMV compared to 43 of 56 maize plants (Stewart et al. 2014). Virus identification studies on corn and Johnsongrass in cornfields suggest MDMV and SCMV viruses transfer from Johnsongrass to corn (Mohammadi et al. 2006), however, virus transmission strategies among and between plant species are highly diverse. Around 50% of all plant viruses are transmitted by aphids in a non-persistent mechanism (Hooks and Fereres 2006). To identify suitable host plants, aphids use their stylets to sample phloem sap. During this process, the stylets contact the plant cell content and included virons which if acquired, are transmitted by probing to healthy plants, and initiating the infec-tion process in the host plant (James and Falk 2006).

Conclusions

With the progressing global climate change the available habitat for the noxious weed Johnsongrass continues to expand. Due to predominantly clonal reproduction and speedy development Johnsongrass has already managed to colonize wide prairie stretches and infested farmland almost throughout the entire globe. Native grassland plant species are often subject to dis-placement if confronted with the broad niche invasive Johnsongrass. The destructive effect on agriculture could be not overstated. Significant crop yield losses are attributed to Johnsongrass itself competing for resources. Additionally, Johnsongrass serves an alternative host for a number of agricul-tural pest and vector-based plant diseases that are naturally trans-ferred to cultivated plants. The control of Johnsongrass has prov-en to be a challenging endeavor. Physical plant destruction by plowing results in fragmented rhizomes and subsequently more rapidly growing clones and extensive eradication efforts by her-bicides led to the evolution of herbicide resistant ecotypes hin-dering the management of this invasive species in the future.

Compliance with ethical standards

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