THE BIOLOGY OF CANADIAN WEEDS. 61. *Sorghum halepense* (L.) PERS.

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A review of biological information is provided for *Sorghum halepense* (L.) Pers., Johnson grass. A native of southern Eurasia to India, *S. halepense* occurs as a weed in most tropical and temperate areas of the world, and has recently become established in 10 counties in Southern Ontario. Listed as one of the world's worst weeds, *S. halepense* infestations result in severe crop losses either from competition or alleleopathic effects and/or by serving as an alternative host for several crop pests. The species is, however, an important forage crop in the southeastern United States and other areas of the world. Johnson grass has several features which contribute to its success as a weed, including the production of extensively creeping rhizomes and large numbers of seeds, rhizomes which regenerate easily if cut into small pieces in cultivation procedures, self-compatibility, seed longevity, seed dormancy and vigorous growth under a wide range of environmental conditions. To date, one population of *S. halepense* from Brant County, Ontario is known to produce rhizomes which successfully overwinter in Canada. This population would appear to be distinct from the other Ontario populations and is characterized by smaller seeds and seedlings and lower rates of germination. A combination of repeated tillage, proper herbicides and crop rotation will give the best control of Johnson grass.

Key words: *Sorghum halepense*, Johnson grass, biological review

[La biologie des mauvaises herbes du Canada. 61. *Sorghum halepense* (L.) Pers.]
Titre abrégé: Biologie de *Sorghum halepense* (sorgho d'Alep).

Cet article passe en revue les renseignements d'ordre biologique dont on dispose sur *Sorghum halepense* (L.) Pers., le sorgho d'Alep. Originaire du sud de l'Eurasie et de l'Inde, *S. halepense* est une mauvaise herbe que l'on rencontre dans la plupart des régions tropicales et tempérées du monde. Elle s'est récemment implantée dans dix comptés du sud de l'Ontario. Cette espèce, considérée comme une des pires mauvaises herbes du monde, occasionne des pertes importantes aux cultures, par la concurrence qu'elle exerce ses effets allélopathiques ou son rôle d'hôte secondaire à plusieurs parasites des cultures. Elle constitue cependant une importante culture fourragère dans le Sud-Est des États-Unis et dans d'autres régions du monde. Le sorgho d'Alep possède plusieurs caractéristiques qui contribuent à en faire une mauvaise herbe redoutable: la production d'abondants rhizomes rampants qui, s'ils sont coupés en petits morceaux lors du labour, se régénèrent facilement; un grand nombre des semences; l'auto-compatibilité; la longévité des semences; la possibilité des semences d'entrer en dormance et une croissance vigoureuse dans des milieux très variés. Jusqu'à maintenant, on n'a décelé qu'une population de *S. halepense*, dans le comté de Brant (Ontario), produisant des rhizomes capables de survivre à l'hiver canadien. Cette population semble être distincte des autres populations de l'Ontario et se caractérise par des semences et des pousses plus petites et un taux de germination plus faible. La

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combinaison de labours répétés, d'application d'herbicides appropriés et de rotation des cultures constitue le meilleur moyen de lutte contre sorgho d'Alep.

Mots clés: *Sorghum halepense*, sorgho d'Alep, revue biologique

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1. Name

Sorghum halepense (L.) Pers. — **Johnson grass, sorgho d'Alep** (Alex et al. 1980). Gramineae, grass family, Graminées.

2. Description and Account of Variation

A perennial grass with fleshy rhizomes to 1 cm in diameter and 2 m in length, often rooting from the nodes, internodes partially covered with brown scale-like sheaths. Culms (flowering stems) erect, usually unbranched, 0.5–2.5 m tall, 0.5–2.0 cm in diameter, often with basal adventitious prop roots, nodes sometimes with fine hairs. Leaves cauline; leaf sheaths often with a waxy secretion at the base, veins prominent, surface hairless and ribbed, margins open, overlapping; ligules membranous, with a hairy fringe, 2–5 mm long; auricles absent; blades rolled in bud, flat, bright green, or sometimes with purple pigments, 20–60 cm long, 1.0–3.3 cm wide, mid-vein conspicuous, everywhere hairless, with scabrous (small rough) projections on the lower surface and margins. Inflorescence a large, erect panicle, at first compact, later spreading and open, pyrimidal, purplish, hairy, up to 50 cm long and 20 cm wide. Branches in numerous whorls, slender, the lower up to 15 cm long, usually without spikelets for 2–5 cm from the base. Spikelets in pairs or at the end of each branch in threes, usually disarticulating as a unit. Spikelet units with one sessile and either one or two pedicelled spikelets. Sessile spikelet, 4–6 mm long, 1.8–2.5 mm wide, dorsiventrally compressed; perfect; green, almost glabrous to appressed silky; glumes becoming leather-like at maturity; lower glume flat across back, rounded on the margins against the upper glume, 7–11 veins, tip three-toothed; upper glume slightly boat-shaped, acute entire, 3–11 veins, margins inrolled around the lemma; lemma hyaline, ciliate, 3–5 mm long, one to three veins, usually with a 1.0- to 1.6-cm-long awn which generally develops after anthesis and is early deciduous as the seed ripens; palea hyaline, 3–4 mm long; two free lodicules about 0.5 mm long; three anthers 2.2–3.0 mm long; ovary apex glabrous; styles free to the base and yellow, pink, red, purple or black. Pedicelled spikelet, pedicels densely ciliate, 1.5–4.0 mm long; male or sterile; glumes green-purplish, lanceolate 4–6 mm long, 1.5–2.0 mm wide, lemma awnless, lemma and palea hyaline with 0–2 veins, shorter than the glumes. Grain remains enclosed by glumes 4.0–6.6 mm long, 2.0–2.6 mm wide, oblong-ovate, glumes reddish brown to shiny black, glossy, marked with fine lines on the surface.

Sorghum halepense has a chromosome number of either $2n = 20$ or 40, with the diploid races being described from Eurasian populations (Bolkhovskikh et al. 1969; de Wet 1978; Monoghan 1979). Chromosome counts for populations of *S. halepense* collected from nine counties in Ontario, two locations from New York state and one from Ohio were all $2n = 40$ (Crompton, Wojtas and Warwick 1982, unpubl. obs.). Plants with four to six accessory or B-chromosomes have been described in certain diploid populations from India (Raman et al. 1976). The latter plants have a similar morphology, but are more vigorous than diploid plants without accessory chromosomes, although 60% of the pollen is ill-formed and seed set is reduced by two-thirds.

Young plants of Johnson grass might be mistaken for very-narrow-leaved plants of maize, *Zea mays* L.; sudangrass, an annual forage sorghum, *Sorghum sudanense* (Piper) Stapf; or an annual grain sorghum, *S. bicolor* (L.) Moench. Separation from maize is only apparent by removing the seedling from the soil and observing the

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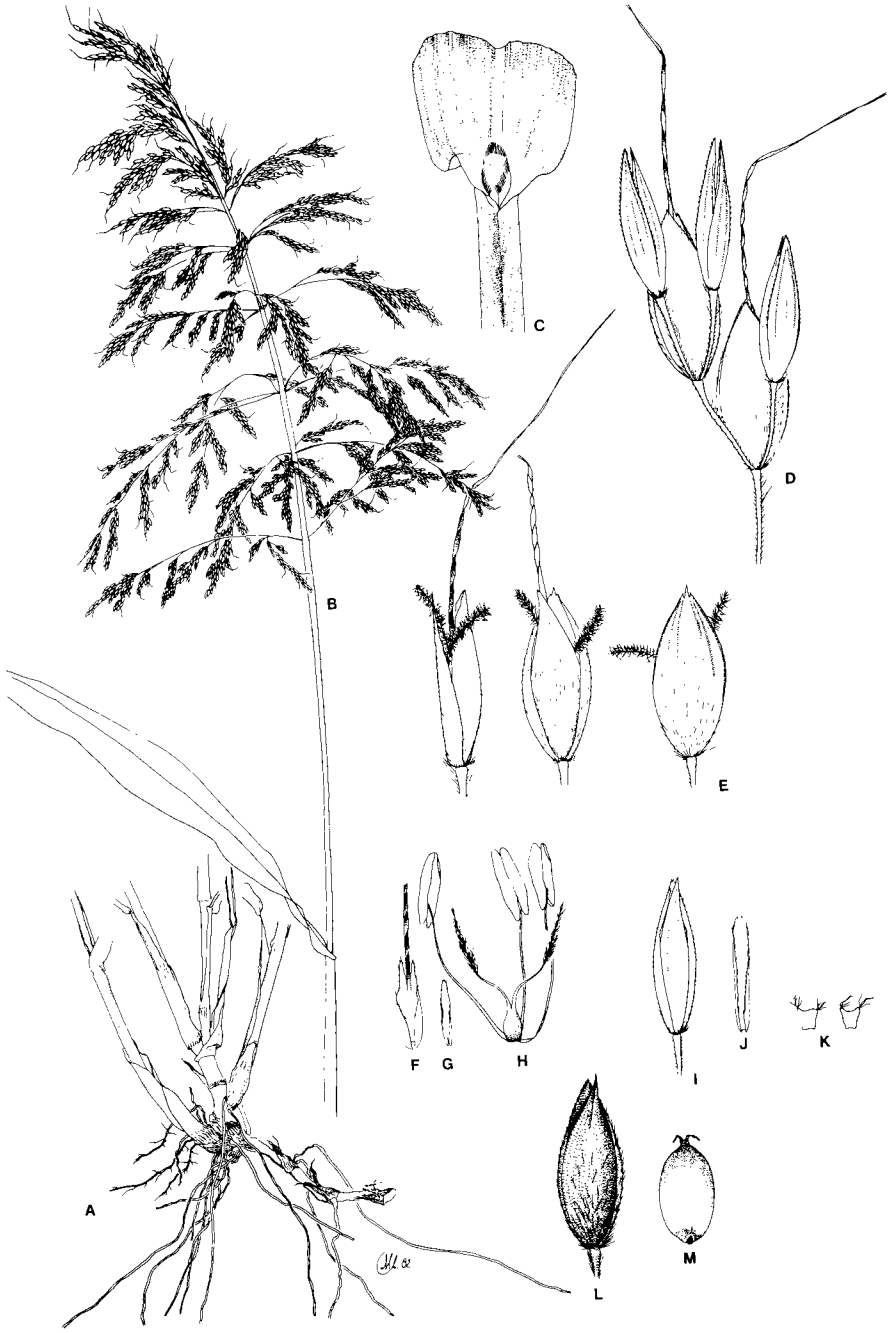


Fig. 1. *Sorghum halepense*. A, base of plant with rhizomes; B, inflorescence; C, ligule; D, terminal end of branch showing two sessile and three pedicellate spikelets; E–H, sessile spikelet; E, whole spikelet at anthesis, lateral ventral and dorsal view; F, lemma; G, palea; H, stamens and pistils; I, J, pedicellate spikelet; I, whole spikelet, ventral view; J, lemma; K, lodicules; L, sessile spikelet in fruit, grain enclosed by glumes; M, grain or caryopsis. Scale A and B × 1/2; C–M × 8.

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kernel of maize. Young plants of *S. halepense* cannot be distinguished from other *Sorghum* species, whereas older plants may be distinguished from annual sorghums by the presence of rhizomes and smaller seeds.

A detailed literature review on the taxonomic status of *Sorghum halepense* has been provided by Monaghan (1979). A native of southern Eurasia to India, the species belongs to the section *Sorghum*, which includes cultivated grain sorghum, a complex of closely related annual taxa from Africa, and a complex of perennial taxa from southern Europe and Asia. Varying taxonomic treatments of this section have been made by Snowden (1936), de Wet and Huckaby (1967), and de Wet (1978). The most current treatment (de Wet 1978) recognizes three species in the section *Sorghum*: two rhizomatous species, *S. halepense* and *S. propinquum* (Kunth) Hitchcock ($2n = 20$) and *S. bicolor* ($2n = 20$) to include all annual wild weedy and cultivated taxa. Several authors have suggested that *S. halepense* was established as a result of the spontaneous doubling of a natural hybrid between *S. bicolor* and *S. virgatum* (Hack.) Stapf (see review by Mouftah and Smith (1969)).

Morphological variants of *S. halepense* are associated with different areas of the distribution range (de Wet 1978). Plants occupying the western range of the species (i.e. the Mediterranean ecotype) are slender, with relatively small inflorescences and narrow leaf blades and are always tetraploid. Plants occupying the eastern half of the species range (i.e. the tropical ecotype) are more robust plants with large inflorescences and broader leaf blades and may also have diploid races. The tropical ecotype has often been referred to as *S. miliaceum* (Roxb.) Snowden. De Wet and Huckaby (1967) have suggested that the more robust tropical ecotype has originated as a result of introgression with cultivated sorghum.

S. halepense has been introduced as a weed to all warm-temperate regions of the world. Researchers believe that the Mediterranean ecotype was introduced into the new World and that it is this ecotype which is commonly referred to as Johnson grass (see review by Monaghan (1979)). Derivatives of an introgression of *S. halepense* with an unknown cultivated sorghum were first described from Argentina (Parodi 1943); these have been referred to as *S. almum* Parodi, Columbus grass or black sudangrass ($2n = 40$; Celarier (1958)).

Bennett (1949) reported on differences in disease resistance and yield variation in strains of Johnson grass. Ingle and Rogers (1961) indicated that rhizomes of Johnson grass collected from Michigan produced greater growth at low temperatures than did those from Indiana.

McWhorter (1971 a,b) compared 55 morphologically distinct strains of Johnson grass collected throughout the United States and other countries in a standard cultivation trial in Mississippi. He found strain differences in leaf and rhizome anatomy, leaf length and width, culm height and density, seed number, panicle and spikelet size, and the number and arrangement of branchlets within panicles. McWhorter also reported that plants of Johnson grass from Turkey, Ethiopia, and the Dominican Republic did not overwinter in Mississippi unlike American, Indian, Pakistani, Iranian and Israeli strains.

Burt and Wedderspoon (1971) Burt (1974) and Wedderspoon and Burt (1974) working in Maryland, described geographical ecotypes in clones of Johnson grass collected from different localities in the U.S.A. Their studies indicated that plants from more northern climates were earlier to flower, shorter and more highly branched, and produced less dry weight than plants obtained from a more southern latitude.

3. Economic Importance

Detrimental — In 1969, Johnson grass was considered to be one of the 10 worst weeds

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of field crops in the United States (Anderson 1969) and has been listed by Holm et al. (1977) as one of the world's 10 worst weeds. Occurring as a principal weed of corn, cotton and sugarcane in tropical to temperate climates, 53 countries have reported it as a weed in 30 different crops. Reported reductions in crop yields in the United States due to Johnson grass infestations include: 25–50% reduction in sugarcane (McWhorter 1972a), 12–33% reduction in maize (Holm et al. 1977), 23–42% reduction in soybean (McWhorter and Hartwig 1972). Johnson grass is also a major weed of soybeans in Argentina, causing losses of $300 million per year (Colbert 1979), and in southern Hungary, severe infestations have decreased maize production by 30–40% (Mikulas and Sule 1979).

Sorghum halepense serves as an alternate host for several insect, nematode and disease pests of sorghum and maize (see Section 13 for details).

The pollen of Johnson grass also contaminates sorghum grown for seed (Monaghan 1979) resulting in smaller seed and reduced yield of the grain (Youngclaus 1972).

Johnson grass sometimes produces cyanogenic compounds in sufficient abundance in the leaves and stems to cause prussic-acid poisoning in grazing animals (Findlay 1975; Looker 1981). This is particularly dangerous in secondary growth produced under adverse conditions such as frost, drought or high temperatures.

In Australia, Johnson grass constitutes a safety hazard along roadsides (Monaghan 1979) and in the United States, it is believed to be one of the causes of hayfever (Wodehouse 1971; Holm et al. 1977).

Allelopathic effects have been reported for Johnson grass (see Section 10 for details).

Beneficial — S. halepense was originally introduced into North America as a forage crop, and still forms an important forage in the southern United States and other areas of the world (Bennett 1973; Holm et al. 1977). Forage quality increases with plot fertility and decreases with plant maturity (Essig et al. 1977). Johnson grass is similar to alfalfa in protein content (14–17%) (Looker 1981), and to sudangrass and timothy in feeding value (Bennett 1973).

Because it forms extensive rhizome networks, Johnson grass has been used successfully in controlling soil erosion (Bennett 1973).

4. Geographical Distribution

Sorghum halepense occurs in all major agricultural areas of the world from latitude 55°N to 45°S (Holm et al. 1977). To date, the Canadian distribution of Johnson grass is limited to the following counties in southwestern Ontario: Essex, Kent, Middlesex, Bruce, Huron, Brant, Elgin, Waterloo, Peel and York (Fig. 2).

5. Habitat

(a) *Climatic requirements* — Although Johnson grass occurs as a weed in most of the tropical and temperate areas of the world, it seems best adapted to the warm, humid summer rainfall areas in the subtropics rather than areas which are strictly tropical (Holm et al. 1977; Monaghan 1979).

The extension of the range of Johnson grass into colder climates would appear to be limited by the lack of tolerance of rhizomes to freezing temperatures. In the laboratory rhizomes did not tolerate less than −3°C for a 24-h period (Hull 1970; McWhorter 1972a). Experiments conducted by Stoller (1977) indicated that Johnson grass rhizomes originating from Nebraska, Minnesota, Illinois and Mississippi survived winter in a field situation in Illinois at depths of 20 cm or more and were killed at temperatures below −9°C. Percent survival of rhizomes increased with increasing depths from 20 to 60 cm. Similarly Tadzhibaev (1977) working in the U.S.S.R. found increased rhizome survival at greater soil depths.

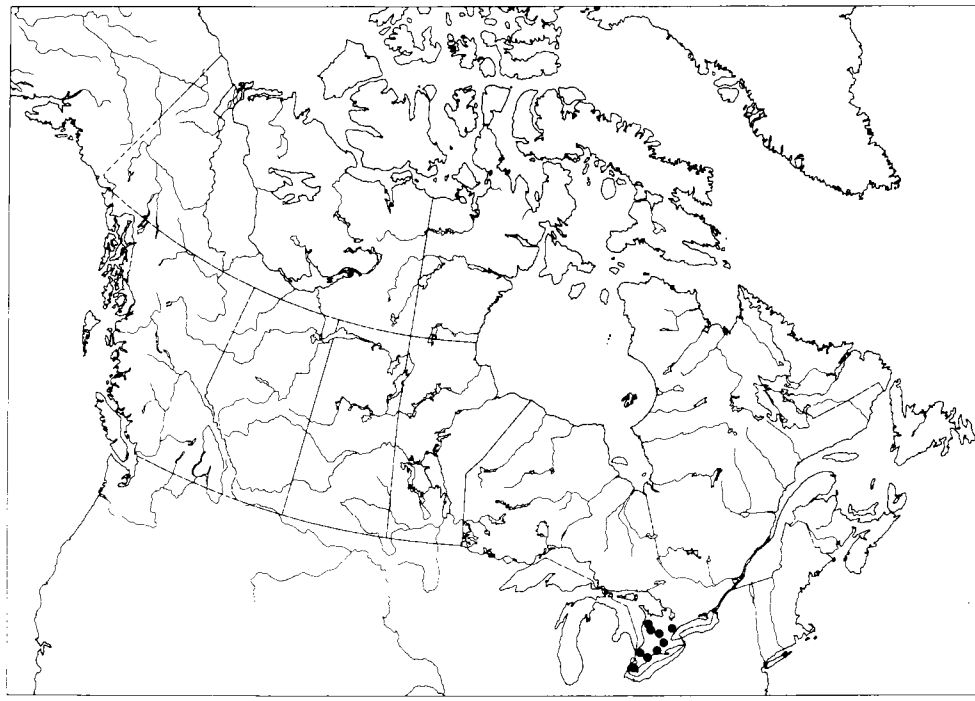


Fig. 2. Distribution of *Sorghum halepense* in Canada from specimens in DAO, OAC and TRT (herbarium abbreviations as in Holmgren and Keuken (1974)).

Rhizomes of Johnson grass are intolerant of high temperatures. Exposure of rhizomes to temperatures of 50–60°C at the soil surface killed buds within 1–3 days (McWhorter 1972a). Similar studies in the U.S.S.R. have indicated that exposure to 7 days of dessication at 30–35°C will result in rhizome death (Tadzhibaev 1977). Rhizomes are, however, able to withstand a high level of dehydration, with longer rhizome fragments exhibiting greater tolerance than shorter pieces (McWhorter and Hartwig 1965). Studies have indicated that dehydration below 5–25% of the original weight prevents sprouting (Anderson et al. 1960; McWhorter 1972a).

Johnson grass is tolerant of a certain degree of flooding. In Israel, Horowitz (1972a) obtained 80 and 35% sprouting in rhizome fragments of *S. halepense* which had been submerged for 1 and 4 wk, respectively. In Mississippi, McWhorter (1972b) found that flooding has a more severe effect at higher temperatures and on younger individuals. For example, flooding of rhizomes for 8 days at 40°C killed all the rhizomes, while 16 days of flooding were required to kill all the rhizomes at 30°C and at 10–20°C, few buds were killed but germination was delayed.

(b) *Substratum* — Johnson grass, adapted to a wide range of soil types, grows best on porous, fertile lowlands and least well on poorly drained clay soils (McWhorter 1973; Looker 1981). Plants tolerate pH of 5–7.5 (Looker 1981). Studies by McWhorter (1972a) indicated that rhizome production and depth is dependent on soil type, with greater production and depth on lighter-textured soil, for example, in clay 4.9 kg/m^3 of rhizome occurred at depths of 5–7 cm compared with 12.3 kg/m^3 to depths of 7–12 cm in sandy loam.

(c) *Communities in which the species oc-*

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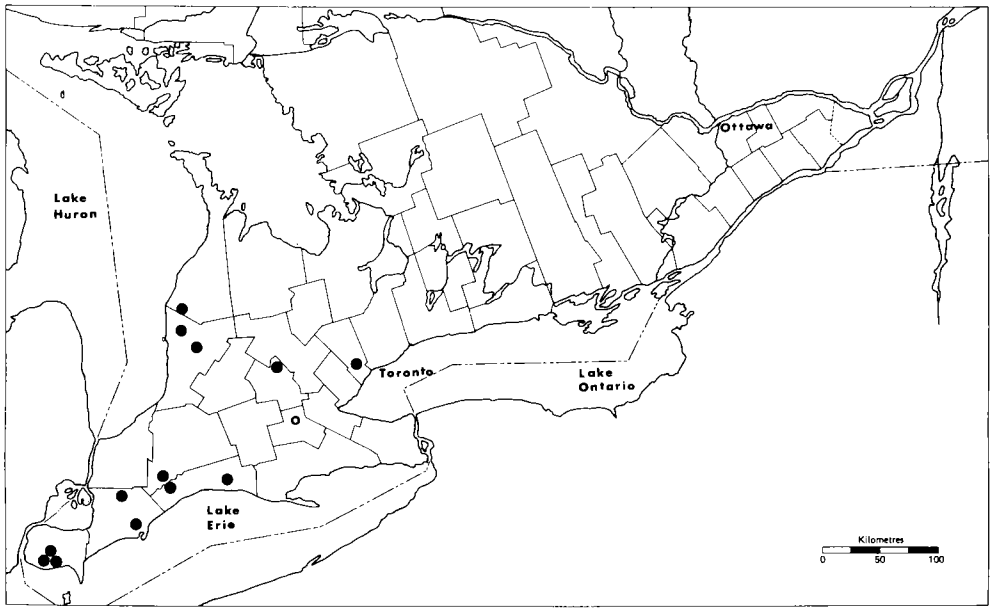


Fig. 3. Distribution of *Sorghum halepense* in southern Ontario from specimens as described in Fig. 2.

curs — In Ontario, stands of Johnson grass are found on arable land, particularly, maize and soybean fields, and on the edges of cultivated fields. In other areas of its range, Johnson grass occurs in orchards, vineyards, open waste ground, roadsides, pastures, arable land, along irrigated canals and at the edges of irrigated fields (Findlay 1975; Holm et al. 1977).

6. History

Sorghum halepense was probably introduced into the southeastern United States as a forage by the 1800s, and by the 1830s was commonly grown in that region (McWhorter 1971c). The common name, Johnson grass was generally accepted by 1870, named after the farmer who in the 1840s introduced the species into Alabama from South Carolina. By 1900, Johnson grass occurred as a serious weed throughout the United States, leading to the first U.S. federal appropriation specifically for weed control in 1900.

The earliest Canadian specimens of *S. halepense* would appear to have been made in 1959 from Lambton Co., Ontario (Alex et al. 1979). The first indication of field infestations occurred in Essex and Kent Counties, Ontario in 1971. By 1978, about 20 infestations of *S. halepense* were known to occur in Ontario in Brant, Elgin, Essex, Kent, Middlesex, Waterloo, and York Counties. Many of these first introductions are known to have been the result of separate introduction of seed. By 1980 more than 60 sites were reported from 10 counties (as listed above plus Huron, Bruce and Peel Counties).

7. Growth and Development

(a) *Morphology* — Johnson grass has several features which contribute to its success as a weed. These include the production of extensively creeping rhizomes and large numbers of seeds; rhizomes which if cut into small pieces in cultivation procedures regenerate easily; seed longevity; shattering of seed heads resulting in wider seed dispersal; seed dormancy; vigorous growth

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rate; plasticity under different environmental conditions, including a rapid rate of growth at low light levels (McWhorter and Jordan 1976a); and large variability which may contribute to the rapid adaptability of this species to more northern climates (Burt and Wedderspoon 1971).

(b) *Perennation* — Plants of Johnson grass overwinter either as seeds or as underground rhizomes. In 1926 Johnson grass rhizomes in North America were seldom reported to overwinter north of 38°N latitude. In 1971 they were reported as overwintering at 40°N latitude (Burt and Wedderspoon 1971) and in 1979 Alex et al. (1979) reported overwintering of rhizomes at 43°N (Brant Co., Ontario). Similarly, overwintering of rhizomes of Johnson grass have been reported at 43°N in New York State (R. Hahn, pers. commun. 1981).

Genecological studies by Warwick and Black (in prep.) have provided evidence for differences in populations of Johnson grass from Ontario which are not known to overwinter and populations from Brant County, Ontario, Ohio and New York state which overwinter as rhizomes (Table 1). Measurements made on specimens collected from fields in Ontario, New York and Ohio indicated that plants from nonoverwintering sites were taller, had wider culms, larger inflorescences, wider leaves and larger seeds. In a standard cultivation trial, individuals from nonoverwintering populations were characterized by greater germination, larger seedlings and greater rates of seedling growth. Studies comparing the growth of mature plants and the winter hardiness of these populations are currently in progress. The above results would suggest that the population from Brant Co., Ontario represents a special winter hardy genotype that is distinct from the other populations of Johnson grass in Ontario.

(c) *Physiological data* — McWhorter (1974) characterized the water-soluble carbohydrates in Johnson grass in the United States and found that glucose, fructose and sucrose were the major sugars in the leaves, culms and rhizomes. Sugar levels in the rhizomes were minimal at 10–30 days after plant emergence and were at a maximum in leaves within 30 days after emergence. At the bloom stage a rapid change occurs in the plant's metabolism (Bennett 1973; McWhorter 1974) and maximum sugar levels are recorded in the rhizomes. As the plant develops sucrose becomes the predominant storage carbohydrate and remains so in all parts of the plant (Bennett

Table 1. *S. halepense* overwintering populations (from Ontario, Ohio and New York) versus nonoverwintering populations (from Ontario)

Character†	Overwintering‡	Nonoverwintering§
1. Mean height of flowering culm (cm)	162 ± 17¶	186 ± 15
2. Mean culm width (cm)	0.58 ± 0.02	0.84 ± 0.04
3. Mean inflorescence length (cm)	23.8 ± 1.1	30.4 ± 1.5
4. Mean leaf width (cm)	1.90 ± 0.04	2.68 ± 0.18
5. Mean seed length (mm)	4.51 ± 0.11	5.60 ± 0.05
6. Mean seed width (mm)	1.84 ± 0.04	2.30 ± 0.03
7. Mean seed weight of 25 seeds (mg)	96 ± 6	211 ± 5
8. Germination (%)	38.0 ± 7.8	76.4 ± 3.3
9. Seedling height at 7 days (cm)	0.8 ± 0.3	2.7 ± 0.1
10. Seedling growth rate from 7-11 days (cm)	1.2 ± 0.2	3.4 ± 0.07
11. Seedling weight at 23 days (mg)	23.0 ± 6.3	72.0 ± 2.3

†1-7, data collected from field collections; 8-11, data collected from standard cultivation trial (Warwick and Black, in prep.)
‡Population size for characters 1-4 = 4 and for characters 5-11 = 80.
§Population size for characters 1-4 = 9 and for characters 5-11 = 180.
¶Mean ± standard error.

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1973; McWhorter 1974). Horowitz (1972b) working in Israel found that the water-soluble sugar content in rhizomes of Johnson grass was highest in early winter and also greater in the deeper rhizomes.

Evidence would suggest that Johnson grass flowers under short-day conditions. In Mississippi, Knight and Bennett (1953) studied the effects of 8-, 10.5-, 12-, 14- and 16-h photoperiods on flowering of Johnson grass. Flowering occurred during all photoperiods, but seedhead formation was inhibited at 16-h and limited at 14-h daylengths. The highest seed yields were obtained at 10.5- and 12-h photoperiods. Similar inhibition of flowering at 16-h photoperiods was obtained by Burt and Wedderspoon (1971) for populations of Johnson grass collected from Maryland and Louisiana.

McWhorter and Jordan (1976a) found that optimum temperature and light conditions for growth of Johnson grass varied with plant part. For example, overall maximum plant dry weight and leaf weight after 12 wk was obtained at 32°C and 19 and 9 klx, respectively. Primary culm height and weight were greater at 24°C regardless of the illumination, whereas root and rhizome development increased with increasing light intensity from 9 to 19 klx and was maximum at 32°C and minimum at 40°C.

(d) *Phenology* — The pattern of growth and development of Johnson grass seedlings and rhizome sprouts is similar, although in the field rhizome sprouts are thought to emerge earlier and to grow more rapidly than seedlings (see review by Monaghan (1979)). In Ontario, Johnson grass first emerges in May. Three to six weeks after emergence of seedlings and sprouts, when plants are in the five- to seven-leaf stage, a rhizome spur is formed and secondary tillers begin to develop (Keeley and Thullen 1979; Lolas and Coble 1980; Warwick and Black, pers. obs.). Flowering begins 6–9 weeks after emergence and continues for the rest of the growing season (Keeley and Thullen 1979; Monaghan 1979). Shoot growth predominates over rhizome growth at the beginning of the growing season, whereas nearly 90% of the annual rhizome production occurs after flowering (Bennett 1973; McWhorter 1973; Lolas and Coble 1980). Temperatures below 13–15°C tend to inhibit flowering and rhizome formation (Horowitz 1972c; Holm et al. 1977).

(e) *Mycorrhiza* — No information available.

8. Reproduction

(a) *Floral biology* — Members of the genus *Sorghum* are generally self-pollinated but there is no barrier to cross-fertilization between species (Tarr 1962). Up to 5% cross-fertilization has been reported in varieties of *Sorghum* grown next to one another; however, cross-fertilization was not evident at distances greater than 130 m apart (Tarr 1962).

(b) *Seed production and dispersal* — One seed is produced in each sessile spikelet. The number of sessile spikelets per panicle varies from 37 to 352 depending on ecotype (McWhorter 1971a). In Israel, Horowitz (1973a) found that after two seasons the mean seed production of plants grown in a garden trial was 84 g or 28 000 seeds per plant and in Mississippi, an average plant produces up to 1.1 kg of seed per season (Bennett 1973). Estimates of seed production of Johnson grass per hectare range from 540 to 1440 dm^3 of seed (Bennett 1973; McWhorter 1973).

Shattering greatly increases the chance for Johnson grass seed dispersal. McWhorter (1971a) found that the degree of shattering varied from 1 to 73%, depending on ecotype. Other methods include the spread of seed by water, wind, contaminated hay and grain, contaminated equipment shared by farmers, movement of stock and ingestion by birds and cattle (Holm et al. 1977; Youngclaus 1972).

(c) *Viability of seeds and germination* — In a seed burial study in Mississippi,

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60–75% of the seed remained viable after 2.5 yr burial in the soil (Egley and Chandler 1978). According to Looker (1981), studies in California have indicated that after 5 yr, viability is still 50%, although in one study in California viability had dropped to 2% after 6 yr in the soil. Johnson grass seeds have also remained viable after 7 yr in dry storage and after passing through the guts of animals (Holm et al. 1977).

Johnson grass seeds are dormant when first dispersed (Bennett 1973; Monaghan 1979). Taylorson and McWhorter (1969) found that, although seed dormancy among 43 ecotypes of Johnson grass varied, most were highly dormant exhibiting less than 10% germination at 20°C. Seed dormancy is largely imposed by mechanical restriction of the seed coat which contains tannin compounds responsible for its reduced permeability to water (Bennett 1973; Taylorson and McWhorter 1969). After-ripening for 4–5 mo in dry storage at room temperature overcomes most of this dormancy (Anderson 1968). Studies by Harrington (cf. Anderson 1968) have shown that freshly-harvested seed could be germinated at temperatures greater than 20°C, if the seed coat was removed or the seed treated with concentrated sulphuric acid for 2 min. In after-ripened seeds the presence of glumes was associated with residual seed dormancy (Harrington 1923, cf. Anderson 1968).

Germination response to temperature, potassium nitrate and light varies between Johnson grass ecotypes (see review Monaghan (1979)). Taylorson and McWhorter (1969) found that germination of after-ripened seed was highest after prechilling at 10°C for 20 days, with alternating temperatures of 24/40°C, continuous light and the addition of 0.2% KNO_3. Irradiation treatments with far-red and red light were able to reverse and simulate, respectively, the prechilling effects, indicating the importance of phytochrome control in germination of Johnson grass seeds (Taylorson 1975).

Emergence of Johnson grass seedlings was lower in a clay soil than in a fine sandy loam and declined with increasing depth of burial (McWhorter 1972a). Holm et al. (1977) indicated that seeds of Johnson grass can germinate from a depth of 15 cm, but most seedlings arise from the top 7 cm.

(d) *Vegetative reproduction* — Under favorable climatic conditions or in the case of hardier genotypes, the primary rhizome structures are alive at the beginning of the growing season, providing buds for renewed growth. Secondary extensions from the main rhizomes surface in early summer to form crowns and new plants. Tertiary rhizomes, formed after flowering, overwinter and produce new plants in the following season (Holm et al. 1977; Looker 1981).

In Mississippi, in both crop or waste-ground situations, a single plant of Johnson grass produced 60–90 m of rhizomes per season (Bennett 1973; McWhorter and Jordan 1976b) and 15–22 tonnes of rhizomes per hectare of pure Johnson grass (Stamper 1957; Looker 1981). Production of rhizome nodes varied from 94–229 nodes per plant after 10 wk (McWhorter and Jordan 1976a) and up to 5200 internodes after 18 wk (Anderson et al. 1960).

Keeley and Thullen (1979), studying growth and development of Johnson grass in California, found that for April to August sowings, rhizomes accounted for an average of 13%, 25%, and 40% of the total fresh weight 6, 9, and 12 wk after sowing, respectively, while roots accounted for 16%, 9%, and 6% of the total fresh weight and shoots 70%, 66% and 54% of the total fresh weight.

In studies of Johnson grass growth and development in Israel, Horowitz (1972b) found that rhizomes constituted more than 90% of the total subterranean weight. In a sward of pure Johnson grass 60%, 30% and 10% of the total subterranean weight was found in the 0–15 cm, 15–30 cm and 30–45 cm layers, respectively. Researchers have found Johnson grass rhizomes growing to a depth of 120 cm in cultivated soil (Looker

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1981). Rhizome depth and size may also be a function of the associated crop (see Section 12a), soil type (see Section 5b), and light intensity (see Section 7c).

Studies on growth and development of rhizome buds under a number of experimental conditions revealed the absence of physiological dormancy in field-collected, young or mature rhizomes (Hull 1970; Lolas and Coble 1980). However, some investigators refer to a winter dormancy of tertiary rhizomes until the following growing season (Anderson et al. 1960; McWhorter 1961). This could be low temperature suppression of bud sprouting (Monaghan 1979). However, even under favorable conditions some Johnson grass buds remain inactive ensuring the ability of the plant to re-establish after temporary adverse conditions (Monaghan 1979). Relatively high temperatures are required for rhizome bud sprouting and rapid shoot growth (McWhorter 1972a). Hull (1970) found that bud sprouting increased from an average of 14% at 15°C, to 82% at 23°C and to 92% at 30°C. Horowitz (1972c) found that rhizome sprouting was at a maximum at 28°C and nil at 10°C or lower. Johnson grass rhizomes are intolerant of both freezing temperatures and hot drying conditions (see Section 5a).

Lolas and Coble (1980) working in North Carolina examined the growth characteristics of Johnson grass grown in a field plot from rhizome pieces varying in length from 2.5 to 25 cm long and found that plant height and weight were increased significantly with the length of the planted rhizome up to 80 days after planting. Rhizomes 15–20 cm in length initiated new rhizome growth 20–30 days earlier than rhizomes 2.5–10 cm in length, as well as exhibiting more and faster growth. McWhorter and Hartwig (1965) and McWhorter (1972a) reported, however, that rhizomes 7.6 cm long produced more shoots than rhizomes 15.2 cm long when the planting depth was 7.5 cm, while the opposite was true for deeper planting.

Propogation by rhizomes is more important in sites where mechanical or combined mechanical and chemical weed control have not been practiced (McWhorter 1973).

9. Hybrids

Although incomplete isolation barriers do exist between the grain sorghums and *S. halepense*, including differences in flowering time, habitat preference and a small amount of cross incompatability (Raman et al. 1976), grain sorghums (all treated by de Wet (1978)) as conspecific with *S. bicolor* introgress with *S. halepense* in South Asia, and in other parts of the world where this species has become established, to form both annual diploid and perennial tetraploid weedy derivatives. Table 2 provides a summary of hybrid studies conducted on *S. halepense* and the grain sorghums. In hybrids derived from a cross between *S. almum* (see Section 2) and *S. halepense*, one had $2n = 39$ and 56% seed set and the other three had $2n = 40$ and 28–61% seed set (Endrizzi 1957).

Hybrids between *S. halepense* and the third member of the section *Sorghum, S. propinquum* ($2n = 20$), occur but are not fully fertile (De Wet 1978).

10. Population Dynamics

Johnson grass is an invasive weed, forming dense spreading patches which will completely smother other grasses (Findlay 1975). In a standard garden trial conducted in Israel, Horowitz (1973a) found that during the warm season, mean area increment of individuals equals 1.3 m^2 per month. After 2 yr of growth, patches extended up to 3.4 m, with a mean area of 17 m^2, shoot density was 190/m^2 and mean seed production was 28 000 seeds per plant. According to Holm et al. (1977), most Johnson grass strains quickly become sod bound, often within 3 yr, and the plants must be broken up to reestablish the stands. Studies conducted by Williams and Ingber (1977) demonstrated that increases in density of Johnson grass from one to eight plants per 20-cm pot resulted in a 3-wk delay in the

Table 2. Summary of hybrid studies of *S. halepense* and the grain sorghums (*S. bicolor* (de Wet 1978), including parents, hybrid chromosome number and fertility

S. halepense ($2n$ = 20 or 40)	Grain × sorghum ($2n$ = 20)	Chromosome no. Ratio	Hybrid fertility	Source
($2n$ = 40)	*S. vulgare* Pers.	$2n$ = 30: $2n$ = 40 7: 21	$2n$ = 30 highly sterile $2n$ = 40 highly fertile	Hadley (1953, 1958)
($2n$ = 40)	*S. vulgare* Pers.	$2n$ = 30: $2n$ = 40 1: 10	$2n$ = 30 1% seed set $2n$ = 40 37-38% seed set	Endrizzi (1957)
($2n$ = 40)	*S. bicolor*	$2n$ = 30: $2n$ = 40 0-22: 78-100	– –	Sengupta and Weibel (1971)
($2n$ = 20)	*S. nervosum* Bess. ex Schult.	$2n$ = 20	24-36% reduction in pollen fertility	Ramen et al. (1976)
	S. subglabrescens Schweinfand Aschers		52-58% seed set	
	S. roxburghii Stapf			
($2n$ = 20)	*S. subglabrescens* ($2n$ = 20 + 4–6 B-chromosomes)	$2n$ = 20 + 4, 4–6, 6–8, or 8–10 B-chromosomes	–	Ramen et al. (1976)

formation of rhizomes and panicles, reduced mean panicle, rhizome and shoot weight per plant, reduced percent dry weight allocation to rhizomes from 26% to 15%, but did not affect percent dry weight allocated to seedhead production (3–4%) or to shoots (41–54%).

Allelopathy may favor the presistence of Johnson grass. Several studies show that extracts of live and decaying leaves and rhizomes of Johnson grass as well as leachate from soil infested with Johnson grass have inhibited the germination and seedling development of many species including barley, clover, crown vetch, soybean, wheat and even Johnson grass itself (Abdul Wahab and Rice 1967; Friedman and Horowitz 1970). Kovacs (1972) identified an allelopath, dhurrin, in Johnson grass rhizomes. The competitive ability of Johnson grass may also be attributed to its rapid growth rate which depletes the soil of nutrients essential to other plants (Horowitz 1973).

11. Response to Herbicides and Other Chemicals

Several preplant-incorporated and preemergence herbicides have been developed to control seedlings of Johnson grass, whereas control of rhizomes in agronomic crops is more difficult. In the following discussion, the common names of the herbicides used are as described in Weed Abstracts.

Preplant-incorporated or preemergence control — In corn, seedlings of Johnson grass can be controlled with butylate at 4.4 kg/ha; butylate plus atrazine at 3.3 and 1.1 kg/ha, respectively; or alachlor at 3.3 kg/ha (McWhorter 1973). In soybean, seedlings of Johnson grass can be controlled with vernolate at 3.3 kg/ha; trifluralin at 3.3 kg/ha; nitralin at 1.1–1.4 kg/ha; alachor at 3.3 kg/ha; or chloramben at 3.3 kg/ha (McWhorter 1973). McWhorter (1972a) found that preplant incorporation of trifluralin and nitralin at 0.8 kg/ha reduced rhizome production. Jeffrey et al. (1981)

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indicate that several thiocarbamate and dinitroaniline herbicides can be preplant incorporated to control seedlings and rhizomes of Johnson grass.

Postemergence control — Excellent control of Johnson grass seedlings and rhizomes has been obtained with metriflufen (2-[4-(4-trifluoromethylphenoxy)phenoxy]-propanoic acid) applied at rates of 0.6–2.2 kg/ha (Azlin and McWhorter 1981); glyphosate applied in the fall at rates of 1.1–2.2 kg/ha (Jeffery et al. 1981); and dalapon applied at rates of 4.1–5.5 kg/ha.

Johnson grass collections have, however, been shown to vary in susceptibility to dalapon. Hamilton and Tucker (1964) found that five collections of Johnson grass from Arizona differed in the amount of regrowth after foliar treatment with dalapon in a greenhouse. McWhorter and Jordan (1976b) found that 5 wk after dalapon application at 11 kg/ha, control of Johnson grass varied from 36% for a Louisiana selection to 91% for a Georgia selection. They found that the more susceptible ecotypes produced more and shorter rhizome nodes, greater dry weights of culms and rhizomes and exhibited lower water content in culms and rhizomes as compared with the more resistant ecotypes.

12. Response to Other Human Manipulations

Johnson grass is extremely responsive to fertilizers, particularly nitrogen. For example, when grown as a crop, yield increases from 4700 to 9000 kg/ha were obtained with the addition of 54 kg of elemental N per ha (Bennett 1973).

Repeated and close mowing or grazing kills Johnson grass seedlings, reduces rhizome growth and regrowth of shoots and prevents seed production (Bennett 1973; Horowitz 1972d; Looker 1981; McWhorter 1973). McWhorter (1974) found that regrowth from clipped shoots of Johnson grass had significantly higher concentrations of glucose and sucrose and rhizomes of clipped plants had less sucrose but more glucose than unclipped plants.

Summer fallowing and repeated tillage prevents development of rhizomes and reduces a stand of Johnson grass (Looker 1981; McWhorter 1972a; Tadzhibaev 1977). McWhorter (1973) found that rhizome production was reduced by over 99% when a heavily infested area was thoroughly tilled six times at 2-wk intervals over the growing season. Repeated tillage exposes the smaller rhizome fragments to temperature extremes on the soil surface (McWhorter 1973; Tadzhibaev 1977). However, limited early season tillage will only encourage rhizome growth by redistributing relatively large pieces of rhizome and preparing an ideal seedbed for Johnson grass growth (McWhorter 1973; Lolas and Coble 1980).

Depth, size and overall production of Johnson grass rhizomes are affected by the associated crop. Rhizome production of Johnson grass is reduced in winter and late-summer-sown crops or in pastures (McWhorter 1973; Ghersa et al. 1976; Soriano et al. 1976). Mattioli (1978) working in Argentina found that rhizome production is greater in plants of Johnson grass growing in maize than in soybean.

A combination of repeated tillage, proper herbicides and crop rotation will give the best Johnson grass control (Looker 1981; Jeffrey et al. 1981).

13. Responses to Parasites

To date there is no published information on insects, fungi and viruses associated with Canadian populations of *Sorghum halepense*. Voucher collections made by the authors from Ontario populations were examined but did not show any fungal or viral infections (Shoemaker, unpubl. obs.).

(a) *Insects and other nondomestic animals – Sorghum halepense* serves as an alternative host for several pests of sorghum and maize. Records for North America include: (1) *Contarinia sorghicola* (Coquillett) (Diptera), the sorghum midge, re-

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ported to attack flower heads in California (Youngclaus 1972) and in Mississippi (Pitre and Gourley 1980); (2) *Graminella nigrifrons* (Forbes) (Homoptera), a leaf hopper, which is also a vector of corn stunt disease in South Carolina (Durant 1971) and of maize chlorotic dwarf virus (Bendixen et al. 1979); (3) *Rhopalosiphum maidis* (Fitch) (Homoptera), a corn leaf aphid, reported from New York (Onazi and Wilde 1974); and (4) *Schizaphis graminum* (Rondari) (Homoptera), greenbug, an aphid which is also a vector of sugarcane mosaic virus, reported in New York (Onazi and Wilde 1974) and California (Youngclaus 1972). Other insects are reported to attack Johnson grass from Australia, India and Pakistan (Bendixen et al. 1979, 1981; Chaudary 1970; Khan et al. 1979; Greber 1981).

Sorghum halepense serves as a host for the following nematode taxa in North America: *Helicotylenchus dihystera* (Cobb.) Sher, in Georgia; *Heterodera graminophila* Golden & Birchfield, in Louisiana; *Hoplolaimus columbus* Sher, in Georgia; *Meloidogyne incognita* (Kofoid & White) Chitwood, in Georgia; *Pratylenchus brachyurus* (Godfrey) Filipjev & Schuurmans Stekhoven, in Georgia; *P. hexincisus* Taylor & Jenkins, southern United States; *P. neglectus* (Rensch) Chitwood & Oteifa, in California; *P. thornei* Sher & Allen, in California; *P. zeae* Graham, in Louisiana; *Trichodorus christiei (Paratrichodorus christiei* (Allen) Siddiqi), in Georgia; and *Tylenchorhynchus martini* Fielding, in Louisiana (Hogger and Bird 1976; see reviews by Bendixen et al. 1979; Manuel et al. 1980).

(b) *Microorganisms and viruses* — The following fungi are reported to occur on *Sorghum halepense* in the United States (United States Department of Agriculture (USDA) 1960): *Ascochyta sorghina* Sacc., rough leaf spot; *Cercospora sorghi* Ell. & Ev., leaf spot; *Colletotrichum falcatum* Went; *C. graminicola* (Ces.) G. W. Wils., anthracnose; *Gibberella zeae* (Schw.) Petch, on culms; *Gloecercospora sorghi* D. Bain & Edg. ex Deighton, zonate leaf spot; *Helminthosporium sorghicola* Lefebvre Sherwin (= *Bipolaris cookei* (Sacc.) Shoemaker), leaf spot; *Helminthosporium turcicum* Pass (= *Setosphaeria turcica*) (Luttrel) Leonard & Suggs, leaf blight; *Ophiobolus implexus* (Ell. & Ev.) Ell & Ev., on adventitious roots; *Phyllosticta sorghina* Sacc. (= *Phoma sorghina* (Sacc.) Boerema, Dorenb. & V. Kest.), leaf spot; *Puccinia purpurea* Cooke, leaf rust; *Ramulispora sorghi* (Ell. & Ev.) L.S. Olive & Lefebvre, leaf spot; *Sclerophthora macrospora* (Sacc.) Thirum., Shaw & Naras., downy mildew (Tarr 1962); *Septoria pertusa* Heald & Wolf, leaf blight; *Sphacelotheca cruenta* (Kühn) Potter, loose kernel smut; *S. holci* Jackson; *S. sorghi* (Lk.) Clint., covered kernel smut; and *Uromyces andropogonis* Tracy, rust. Other fungi have been reported on *S. halepense* in central Asia, Argentina, Australia, Brazil, India, Israel, Philippines, Puerto Rico and South Africa (Levy and Cohen 1978; Liu and Ramirez-Oliveras 1980; Misra and Mishra 1971: Rawla et al. 1974; Singh 1977; Tarr 1962).

The following bacteria have been reported as occurring on *Sorghum halepense* in the United States (USDA 1960; Tarr 1962); *Pseudomonas andropogoni* (E.F. Sm.) Stapp., bacterial leaf stripe, *P. syringae* van Hall, bacterial leaf spot and *Zanthomonas holicola* (Elliott) Starr & Burkh., bacterial streak. Weaver et al. (1980) have suggested that Johnson grass is a reservoir of rickettsia-like bacteria associated with phony disease of peach. Mikulas and Sule (1979), working in Hungary, have indicated that *Pseudomonas syringae* pv. *syringae* van Hall is highly most-specific for *S. halepense* and may well be a useful tool for biological control.

Johnson grass serves as an alternate host for several viruses which attack crop species in North America. These include: corn stunt disease (CS), in South Carolina (Durant 1971); maize chlorotic dwarf virus

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(MCDV), in Ohio (Bendixen et al. 1979) and in Maryland (Damsteegt 1976); maize dwarf mosaic virus (MDMV), in Ohio (Bendixen et al. 1979; Knoke et al. 1981), in Pennsylvania (Gardner 1969), in Maryland (Damsteegt 1976), in Alabama (Canerday and Gudauskas 1970) and New York (Onazi and Wilde 1974); sugarcane mosaic virus (SCMV) in California (Gardner 1969; Youngclaus 1972). Other viruses are reported to infect Johnson grass in the Philippines, Japan, Hawaii, Australia, and India (Greber 1981; Holm et al. 1977; Penrose 1974; Teakle et al. 1970).

(c) *Higher plant parasites – Sorghum halepense* is reported to be parasitized by *Cuscuta* sp., dodder, in Texas (USDA 1960) and *Striga asiatica* (L.) O. Kuntze, witchweed, in Africa (Tarr 1962).

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