THE BIOLOGY OF CANADIAN WEEDS. 77.
Echinochloa crus-galli (L.) Beauv.

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Echinochloa crus-galli (L.) Beauv., barnyard grass (pied-de-coq), is an annual grass and a cosmopolitan weed with a range from 50°N to 40°S latitude. In Canada, it extends up to 53°N latitude in the prairies and is widely distributed along roadsides and in cultivated fields of all provinces. The success of this weed may be attributed to the production of large numbers of small, easily dispersed seeds per plant, possession of seed dormancy, rapid development and ability to flower under a wide range of photoperiods, and relative resistance of mature plants to herbicide sprays. In this review a summary of biological information on *E. crus-galli* is presented.

Key words: Barnyard grass, weed biology, *Echinochloa crus-galli*

[La biologie des mauvaises herbes canadiennes. 77. *Echinochloa crus-galli* (L.) Beauv.]
Titre abrégé: *Echinochloa crus-galli* (L.) Beauv.
Echinochloa crus-galli (L.) Beauv., communément appelée pied-de-coq (barnyard grass), est une mauvaise herbe annuelle cosmopolite dont l'aire de distribution s'étend du 50ᵉ parallèle nord au 40ᵉ parallèle sud. Au Canada, elle peut même atteindre le 53ᵉ parallèle dans les Prairies et on la trouve partout dans les fossés et dans les champs cultivés de toutes les provinces. Cette espèce doit sa réussite à sa capacité de produire de grandes quantités de petites semences qui se dispersent facilement et qui ont la faculté d'entrer en état dormance, à sa croissance rapide, à son aptitude à fleurir sous une grande variété de conditions de photopériode, ainsi qu'à sa résistance relative, à l'état mature, aux herbicides pulvérisés. Nous présentons un résumé des informations biologiques portant sur *E. crus-galli*.

Mots clés: Pied-de-coq, biologie des mauvaises herbes, *Echinochloa crus-galli*

1. Name

Echinochloa crus-galli (L.) Beauv. (Alex et al. 1980) – **barnyard grass, Echinochloa pied-de-coq** (Ferron and Cayouette 1971; Alex et al. 1980). Other common names: summergrass, watergrass, cockspur grass (Frankton and Mulligan 1970). A cultivated var. *frumentacea* is called Japanese millet or billion dollar grass. For other international names of this species refer to Holm et al. (1977). Poaceae (Gramineae, grass family, Graminées).

2. Description and Account of Variation

(a) Hitchcock and Chase (1951), Rahn et al. (1968), Dore and McNeill (1980), and Holm et al. (1977) presented the following description of the species. An annual, tufted, robust grass with fibrous roots, which reproduces by caryopses. Culms glabrous, stout, often branching and rooting from a decumbent base (Fig. 1f) up to 1.5 m tall; leaves glabrous and rolled at emergence, blades elongate with smooth or scabrous margins, 5–50 cm long, 5–20 mm wide with parallel hyaline veins and often a prominent and sharp midrib, leaf bases
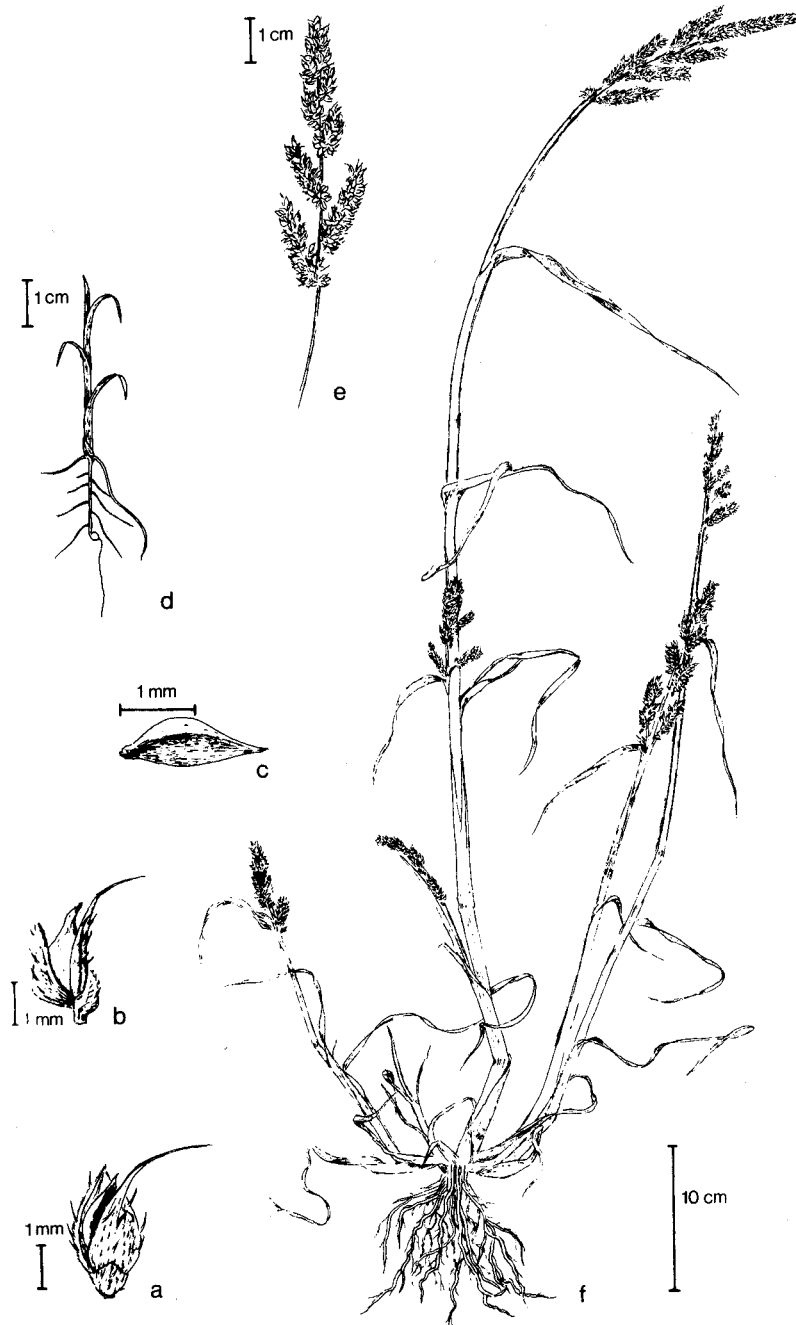
Fig. 1. (a) spikelet; (b) opened spikelet showing (left to right) second glume, fertile floret, awned sterile floret and first glume; (c) caryopsis; (d) seedling; (e) close-up of a part of the panicle; and (f) mature plant of *Echinochloa crus-galli* (L.) Beauv.

often with conspicuous anthocyanin (red) pigmentation; sheaths glabrous, compressed, keeled, split with overlapping hyaline margins, ligules and auricles absent (Fig. 1f); collar glabrous, broad, continuous; panicles erect or nodding, green or purple-tinged, 10–20 cm long; racemes numerous, 2–4 cm long, spreading, ascending or appressed, lower ones more distant than upper (Fig. 1f); spikelets 3–4 mm long crowded in 2–4 rows on each side of the rachis (Fig. 1e); awns when present variable, 0–10 mm long, sometimes as much as 30 mm long, oval unequal pointed and bristly glumes, first glume nearly half as long as the spikelet (Fig. 1a), second glume and sterile lemma equal in length, short hispid in nerves, hairs not papillose; spikelet contains one perfect and one sterile floret (Fig. 1a,b), fertile floret plano-convex; lemma smooth, hard and shiny, involute enclosing the similar textured palea; sterile lemma often drawn out into a long coarse awn; fertile lemma with a dull-colored and wrinkled tip marked off rather abruptly from the shiny body, minute setae present on the shiny portion of the fertile lemma just below the wrinkled tip; caryopses strongly convex on one side (Fig. 1c), flat on the other, broad below, narrow towards apex, orange-yellow to buckthorn brown, 2.5–3.5 mm long, obscurely three-veined.

The chromosome number of *E. crus-galli* is $2n = 54$ (Mulligan 1961) and the species is hexaploid with the basic chromosome number of the genus $n = 9$ (Brown 1948). As a result of taxonomic confusion with other *Echinochloa* spp., particularly the tetraploid *E. muricata*, earlier counts for *E. crus-galli* of $2n = 36$ are probably in error (e.g., Brown (1948) and see Gould (1968)).

(b) Alex and Switzer (1976) and Best et al. (1971) reported that plants can be distinguished from other genera of Canadian grass weeds by the absence of a ligule. Plants can be distinguished from *Setaria viridis* and *S. glauca* by several characters. *Setaria viridis* blades have serrulate scabrous margins while *S. glauca* blades have long twisted hair near base on upper surface.

(c) Taxonomic problems in *Echinochloa* are due to several intergrading polymorphic complexes of which *E. crus-galli* is the most widely distributed and difficult to classify. Lack of a comprehensive, worldwide, monographic treatment further exacerbates identification problems. Taxonomists working on regional floras have named countless intraspecific taxa within the *E. crus-galli* complex. The apparent diversity of forms is associated with high phenotypic plasticity coupled with a fluent adaptability to the wealth of habitats occurring in seasonally wet and ruderal sites. Variation patterns in North America are further complicated by multiple introductions of genetic material from different parts of the Old World followed by inbreeding (see below).

In North America, there are several conflicting taxonomic treatments of the *E. crus-galli* complex and related taxa (Hitchcock 1920; Wiegand 1921; Hitchcock and Chase 1951; Gould et al. 1972; Dore and McNeill 1980). Major sources of taxonomic disagreement concern the status of native and adventive taxa and intraspecific categories. Hitchcock and Chase (1951) and the majority of authors of these floras (e.g., Munz and Keck (1959), Radford et al. (1968), Correll and Johnston (1970), Scoggan (1978)) combine native and adventive taxa under *E. crus-galli* whereas Gould et al. (1972) following Wiegand (1921) separates native populations as *E. muricata*. Dore and McNeill (1980) further subdivide the native populations into three species, *E. muricata*, *E. microstachya* (Wieg.) Rydb., and *E. wiegandii* (Fassett) McNeill and Dore. Separation of native and adventive taxa is supported by chromosome studies. The introduced *E. crus-galli* is hexaploid, whereas *E. muricata* and allies are tetraploid. Gould et al. (1972) recognized three varieties of *E. crus-galli* in N. America,

var. *crus-galli*, var. *frumentacea* (Roxb.) Wight and var. *oryzicola* (Vasing.) Ohwi. The latter is a tetraploid crop-mimic and is probably best treated as a separate species (as either *E. oryzicola* Vasing. or *E. phyllopogon*, (Stapf.) (Koss.). See Barrett and Seaman (1980), Barrett and Wilson (1981), Barrett (1983) and Michael (1983) for further discussion of these taxa.

(d) Genetic variation — despite the high degree of phenotypic variation for morphological traits found in natural populations, there has been relatively little work on the genetics of *E. crus-galli*. Recently, S. C. H. Barrett and A. H. D. Brown (unpubl. data) examined the levels of genetic variation for isozymes (31 loci) and quantitative traits (e.g., flowering time, plant height, seed production, plant biomass) in 11 Californian populations of *E. crus-galli*, collected from in and around rice fields of the Central Valley. All populations contained significant amounts of genetic variation for most quantitative characters. With respect to the isozyme survey, the following conclusions were reached: (1) populations were relatively low in isozyme polymorphism but were moderately differentiated from one another. This pattern of variation most likely results from frequent colonizing episodes and predominant selfing. (2) Individual populations were composed of a number of highly homozygous multilocus genotypes. (3) Summary statistics for the electrophoretic data were as follows: (a) proportion of loci polymorphic = 0.52, mean number of alleles per polymorphic locus = 2.56, proportion of genetic diversity among populations = 0.33. A survey of isozyme variation in rice field populations of *E. crus-galli* for New South Wales, Australia also revealed similar results. Elsewhere, Gasquez and Compoint (1977) examined isozyme variation for peroxidase, esterase and acid phosphatase in populations of *E. crus-galli* from France. They report less isozyme variation in a population exposed to herbicide (atrazine)

sprays than in a population from an uncultivated area. Gasquez and Compoint (1976) reported differentiation of *E. crus-galli* populations in France in response to crop species with which they co-existed. Another cause of differentiation is herbicide usage (Roche and Muzik 1964).

3. Economic Importance

(a) *Detrimental — Echinochloa crus-galli* is a cosmopolitan weed in both temperate and tropical regions and is reported as a weed in 36 different crops in 61 countries (Holm et al. 1977). In N. America it is a troublesome weed in rice fields, grain crops, row crops, root crops, open disturbed habitats, gravel pits, roadsides, cultivated ground and well-manured soils (Best et al. 1971). Vengris (1953, 1965) found this annual species in 98% of all potato fields surveyed in the Connecticut river valley. As a weed, barnyard grass ranked first in potato fields, second in tobacco, third in onion and eighth in corn fields. Deschênes (1974) showed that in the St. Lawrence lowlands and the Gaspé peninsula, the principal cause of failure in the establishment of birdsfoot trefoil (*Lotus corniculatus* L.) was heavy competition from barnyard grass. According to Vengris (1966), seedling mortality of alfalfa was 80% if barnyard grass emerged within the first 2 wk of its life cycle. Barnyard grass causes considerable decreases in the yield of potatoes (Bayer 1965), snap beans (Rahn et al. 1968), sugar beets, green peas and melons (Roche and Muzik 1964). Heavy barnyard grass infestations make mechanical harvesting of row crops more difficult, increase labor costs in separating potatoes from barnyard grass clumps, and cause considerable breakage of machinery during lima bean and snap bean harvesting (Rahn et al. 1968). Experimental studies indicate that heavy stands of *E. crus-galli* may remove 60–80% of the nitrogen from the soil especially in the first half of the growing season (Holm et al. 1977). Under heavy competition, tillering in rice is reduced by

50% (Holm et al. 1977) and there is drastic reduction in the number of panicles, height of rice plants, weight of grains and number of grains per plant. It has been shown that one to five plants of *E. crus-galli* per square foot may reduce rice yields by 18–35% (Swain 1967) and 9 plants m^{-2} could reduce yield of low density rice by 57%. Further detailed information on the competitive effects of *E. crus-galli* on cultivated rice fields is available in Smith (1983).

(b) *Beneficial* — In North America, *E. crus-galli* var. *frumentacea* was advertised by seedsmen as a "billion dollar grass" and was recommended for forage as green feed, silage or hay (Wilkinson and Jacques 1972). However, it proved too succulent for hay and its use declined with the introduction of other high producing crops of greater value (Wheeler 1950). In Australia it was considered satisfactory in drought mitigation programs that required maintenance of large numbers of sheep in a small area (Wheeler and Hedges 1972). In tropical Asia and Africa, it is cultivated for its seeds which are eaten (Hitchcock and Chase 1951).

(c) *Legislation* — *E. crus-galli* is listed in class 5, other weed seeds, in the Canada Seeds Act and Regulations (Agriculture Canada 1967).

4. Geographic Distribution

The world distribution of *Echinochloa crus-galli* ranges from 50°N to 40°S latitude (Holm et al. 1977). In Canada, barnyard grass has been recorded in places situated above 50°N latitude, for example Edmonton (53°–33'N), Saskatoon (52°–07'N), Prince Albert (53°–12'N) and several others (Fig. 2). It occurs in all provinces of Canada but has not been reported from the Northern Territories (Fig. 2). Information gathered from herbarium sheets, floras and published accounts suggests that the species is abundant in Ontario, Quebec and the Maritime provinces (Fig. 2) but is rare in provinces west of Manitoba (Frankton and Mul-

ligan 1970). In Ontario, it has not been reported north of Lake Tamiskaming (Baldwin 1958). Until 1968 its range extended up to Abitibi in Quebec which, according to Rousseau (1968), must be considered its northern limit. Budd and Best (1964) reported that plants are common in eastern Manitoba and are extending their range westward. According to Moss (1974) and Best et al. (1971), barnyard grass is rare in Saskatchewan and Alberta but is abundant in British Columbia and Vancouver Island (Fig. 2). Boivin (1966, 1967) reported that the species is found on roadsides and fields in Newfoundland, and islands of St. Pierre and Miquelon. According to Erskine (1960) barnyard grass is distributed throughout Prince Edward Island. For a detailed distribution of barnyard grass in Quebec see map in Rousseau (1968).

5. Habitat

(a) *Climatic requirements* — *Echinochloa crus-galli* is a weed of warm regions and requires a frost-free period of 160–200 d per year, average July temperatures of 16–25°C and abundant moisture for plant growth and seed dispersal (Roche and Muzik 1964). Nishi (1981) showed that the dry matter production of *E. crus-galli* exceeded that of neighboring rice from 25.7 to 27°C but that below 25.7°C the situation reversed. Rahn et al. (1968) reported that barnyard grass grew best under wet conditions at about 35–65% soil moisture. The plants continued to grow in saturated soils or in partially submerged conditions but they became upright and produced lower yields. The increase in plant height of *E. crus-galli* was directly related to temperature. In spring, when temperatures are low, the growth is slow but the plants grow very rapidly in the heat of summer (Vengris et al. 1966a). In a study of habitat requirements of C_3 and C_4 plants, Takeda et al. (1977) reported that C_4 weeds (of which *E. crus-galli* is one) tended to have a higher summed dominance ratio (SDR) (in proportion to the total SDR) in upland than in lowland conditions. How-
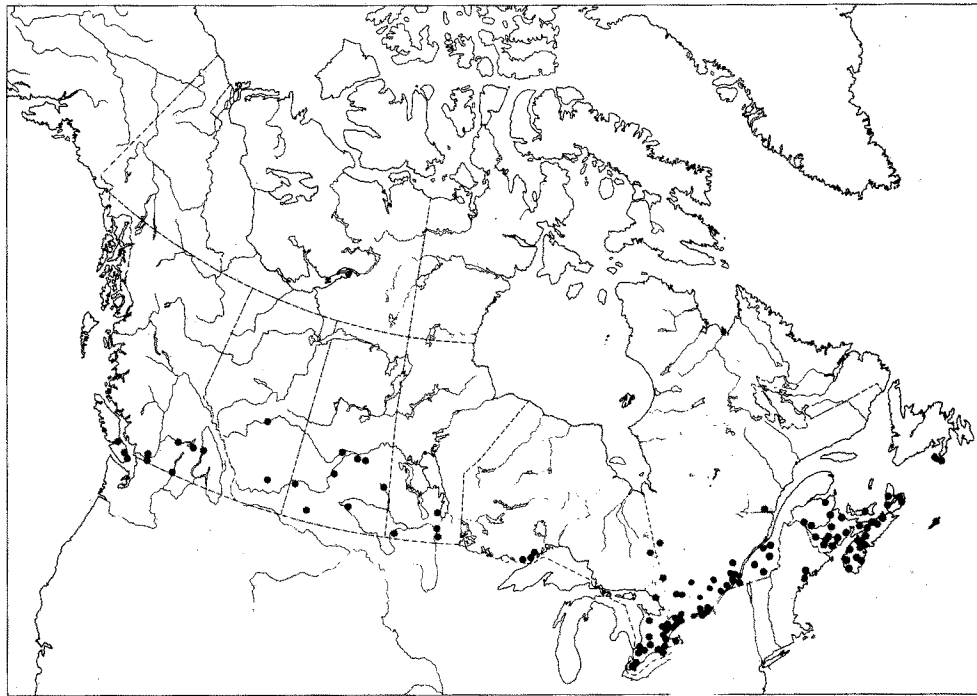
Fig. 2. Distribution of *Echinochloa crus-galli* (L.) Beauv. in Canada from specimens in the Plant Industry laboratory, Alberta Agriculture, Edmonton and the following herbaria: UAC, DAS, USAS, TRT, MTJB, CAN, SASK (Herbarium abbreviations as in Holmgren et al. (1981)).

ever, *E. crus-galli* grew better under wet conditions than other C_4 plants. *Echinochloa crus-galli* growing in wetland rice fields was unaffected by submergence under 90 cm of natural floodwater for 40 d (Singh et al. 1983).

(b) *Substratum — Echinochloa crus-galli* is found growing on a wide variety of soil types and textures from sandy loam or loamy sand to medium heavy soils (Brod 1968). Soils with relatively high water holding capacity and high fertility provide an ideal substrate. In Canada it is found most commonly in rich moist soils (Frankton and Mulligan 1970). Plants are indifferent to lime content in soil (Brod 1968). Bayer (1965) reported that addition of 50 to 100 lbs N per acre showed a significant linear increase in dry weight of barnyard grass on Howard gravelly loam and Eel silt loam

soils. Similar increases from phosphorus and potassium occurred only on Eel silt loam soils.

(c) *Communities in which the species occurs* — The habitat descriptions on herbarium sheets from Canada indicate that *E. crus-galli* occurs as a weed along roadsides, in ditches, mudbanks and wet shores of lakes and sloughs, river banks, waste places and dumps, railway embankments, gardens, gravel pits, and field crops. The species is capable of infesting a variety of crops such as wheat (Best et al. 1971), root crops (Brod 1968), potatoes (Rahn et al. 1968) forage crops, pastures, corn, soybeans, rice, cotton, and orchards (Muenscher 1980). Along roadsides in southwestern Ontario, it occurs in association with *Agropyron repens* (L.) Beauv., *Agrostis stolonifera* L., *Chrysanthemum*

leucanthemum L., *Cirsium vulgare* (L.) Scop., *Dactylis glomerata* L., *Poa pratensis* L., *P. compressa* L., *Prunella vulgaris* L., *Setaria glauca*, *S. viridis*, *Taraxacum officinale* Weber, *Trifolium repens* L. and *T. pratense* L. It also occurs with *E. muricata* thus causing much of the taxonomic confusion between the two. In field crops, barnyardgrass and other weeds associated with it vary with crop species, soil type, herbicides used and cultural practices of the farmers (M. A. Maun pers. obs.).

Echinochloa crus-galli is a troublesome weed of rice in the rice-growing regions of the world. Its ecological requirements are very similar to rice and certain races cannot be distinguished from it in the early stages of growth (Yabuno 1966). Like rice the seedlings of *E. crus-galli* are unpigmented (Kennedy et al. 1980). Barrett (1983) suggested that rice mimicry (weed resembles the rice plant at specific stages during its life cycle) arose through natural selection by handweeding practices conducted under the intensive systems of rice culture found in Asia. Comparative studies of growth, development and phenotypic variation of cultivated rice, *E. crus-galli* var. *crus-galli* and *E. crus-galli* var. *oryzicola* (4×) indicated that the crop mimic was more similar to rice in many morphological and phenological attributes than it was to its close relative. Barrett and Seaman (1980) showed that in California a hexaploid form of *E. crus-galli* var. *oryzicola* (= *E. oryzoides* (Ard.) Fritsch) has replaced *E. crus-galli* var. *crus-galli* as a weed in rice fields because the former can establish under the deep water conditions used for rice growing in the state.

6. History

Echinochloa crus-galli is native to Europe and Asia although the area of its origin is not known with any certainty. According to Good (1964), it is a tropical plant which has extended its range into the temperate zone. It was introduced in North America at an early date from Europe (Dore and McNeill

1980) and was recorded in California between 1825 and 1848 (Barrett and Seaman 1980). In Prince Edward Island its naturalization had occurred by 1888 (Erskine 1960). Rousseau (1968) reported that *E. crus-galli* was recorded in Nova Scotia in 1829 (Haliburton (1829) cited in Rousseau (1968)), in Boucherville (Quebec) in 1862 (Provancher (1862) cited in Rousseau (1968)) and in Quebec city in 1883.

7. Growth and Development

(a) *Morphology* — Kacperska-Palacz et al. (1963) described three phases (embryonic, vegetative, reproductive) in the developmental morphology of *E. crus-galli* plants. In the embryonic phase, the primary root is ensheathed by a coleorhiza and root cap while the plumule is enclosed with the coleoptile. The coleoptile is borne on a short axis. The vegetative phase consists of initiation and maturation of leaves (maximum of eight), development of tillers (up to 15) and adventitious root system (Kacperska-Palacz et al. 1963). The vegetative tillers of *E. crus-galli* arise in the axils of leaves by periclinal divisions in the third layer of cells of the embryonic internode just above the leaf primordium. As the primordium further enlarges, the apex turns upward between the inner surface of the leaf sheath and the stem forms an intravaginal shoot. Further development of this shoot repeats the pattern of the parent axis. Both the primary and secondary axes may form tillers from second, third, fourth, fifth and sixth internodes. During the reproductive phase, internodal elongation of tillers occurs and the growing point is transformed into a floral primordium (Rahn et al. 1968). Transformation from vegetative to reproductive phase depends in part on the date of seedling emergence; later seedlings initiate sooner in the cycle than earlier ones. The secondary root primordia of *E. crus-galli* originate from the pericycle. The stele is polyarch and the roots are white in color (Kacperska-Palacz et al. 1963). The root system of barnyard grass may extend down

to 116 cm in depth and 106 cm in lateral diameter in porous well aerated soils (Rahn et al. 1968) which enables the species to withstand drought conditions.

Kennedy et al. (1980) examined mitochondria from primary leaves of *E. crus-galli* var. *oryzicola* grown in aerobic and anaerobic conditions for 96 and 134 h. They found that anaerobically grown mitochondria are virtually indistinguishable in size and shape from those grown aerobically. Under these conditions the mitochondrial matrix was electron dense, the cristae were numerous and well developed and the mitochondrial envelope was clear. They suggest that the ability of mitochondria in *E. crus-galli* var. *oryzicola* to function under anaerobic conditions may explain why the species is capable of germinating in deep water and is a serious weed of flooded rice fields.

Barnyard grass is able to accumulate considerable amounts of macronutrients (Table 1) at the expense of crop plants thus reducing their yields especially when these elements are in short supply (Vengris et al. 1953). Barnyard grass had higher phosphorus content than onions and potatoes which may suggest that it is more efficient in phosphorus absorption from the soil (Vengris et al. 1953). Barnyard grass had lower nitrogen content than rice in the earlier stages of growth but closer to maturity, the percent nitrogen was the same in both species (Arai and Kawashima (1956), reported in Chisaka (1977)).

(b) *Perennation — Echinochloa crus-galli* is a caespitose therophyte (annual) which overwinters as seed on or under the soil surface. In Canada, the plants may be classified as summer-green which germinate in early summer, complete their life cycle during summer, and die after seed production in September and October.

(c) *Physiological data — Echinochloa crus-galli* (a C_4 species) normally appears to be a short day plant (Vengris et al. 1966a).

Table 1. The chemical composition of *Echinochloa crus-galli* of different ages growing in onions and potatoes (Vengris et al. 1953). The composition of crops is included for comparison

Growth Stage	Number of samples	Species name	N	P	K (% air dry weight)	Ca	Mg
					Mean composition ± standard deviation		
Bulb not developed	8	Onion	–	0.16±0.09	4.44±1.10	1.19±0.22	0.23±0.06
Before heading	9	Barnyard grass	3.64±0.83	0.42±0.15	5.76±0.76	0.55±0.12	0.48±0.12
Before maturity	11	Potato	2.98±0.44	0.22±0.04	6.42±1.0	1.24±0.17	0.37±0.18
After bloom (seeds not ripe)	10	Barnyard grass	2.20±0.40	0.39±0.06	3.44±0.36	0.32±0.05	0.36±0.08

However, the species is adapted to flower under a wide range of photoperiodic conditions and this adaptation may be a significant factor in the wide distribution of this cosmopolitan weed (Holm et al. 1977). Plants exposed to 8- to 13-h daylengths passed into the flowering stage very quickly when they were only 70 cm tall. In contrast the plants in long days (16 h) flower much later at about 150 cm plant height (Dickerson (1964) reported in Rahn et al. (1968)). Under long day conditions barnyard grass produces extremely large inflorescences with large seed output as compared with small inflorescences and low seed output under short day conditions (Vengris et al. 1966a; Barrett and Wilson 1981).

Light quality influenced growth and development of barnyard grass. Blue light significantly reduced the height and weight of barnyard grass as compared with white and red light; however, it did not reduce the number of tillers and panicles per plant (Dunn et al. 1968).

Barnyard grass plants are highly susceptible to shading. The number of tillers and panicles per plant were always greater in full sunlight than in heavy shade (Bayer 1965). The growth rate, leaf area and net assimilation rate also increased with increasing light intensity and temperature (Asano et al. 1981). The seedlings of *E. crus-galli* initiated flowering earlier in wet soil conditions than in dry soils; however, the date of maturity was not affected (Vengris et al. 1966a). The yield, height and numbers of tillers per plant were reduced under dry soil conditions.

On the basis of ultrastructure and ^{14}C labelling studies Kennedy et al. (1980) showed that anaerobically grown seedlings of *E. crus-galli* are highly active metabolically which may explain at least for var. *oryzicola* its ability to germinate and emerge from flooded rice fields. *Echinochloa crus-galli* var. *crus-galli* and var. *oryzicola* suffered inhibition of root (Kennedy et al. 1980) and plumule elongation and of

leaf greening when subjected to very low oxygen partial pressure (Kataoka and Kim 1978).

Robert et al. (1983) studied the thermal adaptation and acclimation of *E. crus-galli* at the enzyme level. They showed that the thermostability and thermodenaturation of phosphoenolpyruvate carboxylase (PEPC) have been modified in response to the selective thermal pressures of the environment in the region of their occurrence. For example, a Quebec population collected at the northern extreme of the latitudinal range showed reduced thermostability as compared with the other five populations from warmer southern locations. According to Simon et al. (1984) CO_2 enrichment elicited higher thermostability of PEPC. Potvin and Strain (1985) measured photosynthetic response of *E. crus-galli* plants to three thermoperiods (28/22, 24/18, 21/15°C) and two CO_2 concentrations (350 and 675 μL L^{-1}). They found that CO_2 enrichment increased the net photosynthesis and dark respiration for all populations but did not affect conductance, transpiration or transpiration/photosynthesis ratio. Plants exhibited higher rates of photosynthesis and dark respiration in warm temperature regimes.

(d) *Phenology* — In southwestern Ontario maximum emergence of *E. crus-galli* seedlings occurs in the beginning of June and continues intermittently throughout the summer (M. A. Maun, pers. obs.). Similarly, Vengris (1965) found that in potato fields barnyard grass seedlings emerged constantly from June to September. The seed germination is initiated by the appearance of primary root within about 24 h and first leaf within about 48 h of the imbibition of water by seeds (Rahn et al. 1968). The mesocotyle and first internode then elongate and the coleoptile and plumule emerge from the soil surface (Dawson and Bruns 1962). Within the next 5 d, adventitious roots are produced on the mesocotyle and first internode and coronal roots (Fig. 1d) emerge from the base of the coleoptile

(Rahn et al. 1968). Emergence of new leaves and vegetative growth of tillers and adventitious roots is profuse during the next 3 wk. Then the shoot apex starts to elongate, inflorescence primordia develop on tillers and internodes elongate upwards. The heading begins about 40 d after emergence. Seeds of barnyard grass mature about 20 d after heading and disperse in the autumn (Rahn et al. 1968).

Anderson and Richardson (1978) found that the phenological development of *E. crus-galli* is correlated with the accumulated growing degree-h temperature in the season. Specifically, Iwasaki et al. (1978) reported that the first leaf required over 200°C accumulated average temperature, the second about 300°C and the fifth about 500°C. An equation expressing the number of leaves at a given date as a function of the daily mean temperature, the sum of daily growing temperatures (starting from the final puddling date) and the previous year's emergence was formulated by Doi and Murakami (1977).

(e) *Mycorrhiza* — No mycorrhizal system has been reported for *E. crus-galli* although mycorrhizae have been reported for several members of Poaceae (Koske et al. 1975).

8. Reproduction

(a) *Floral biology* — *Echinochloa crus-galli* plants are self-compatible and highly autogamous. In common with many grasses cleistogamous flowers are produced late in the season when spikelets do not emerge from the surrounding leaf sheaths. Anthesis of individual spikelets occurs within a single day, but the flowering period of inflorescences can last for several days with spikelets at the top of the inflorescence entering anthesis before those at the base. The mating system of *E. crus-galli* involves a high degree of self-fertilization with occasional outcrossing mediated by wind. Predominant selfing results in a high degree of homozygosity within populations and relatively low levels of heterozygosity at polymorphic loci (S. C. H. Barrett and A. H. D. Brown, unpubl. data).

(b) *Seed production and dispersal* — Individual plants of *E. crus-galli* can vary enormously in their reproductive output (Table 2). Seed production values range from 2000 per plant in the Philippines to 40 000 in Lebanon (Holm et al. 1977). Seed output is a highly plastic character and is responsive to local growing conditions particularly nutrient availability, daylength and plant density. By growing plants under stressed and heavily fertilized conditions Barrett (1982) produced plants which varied by as much as 8537 times in aboveground biomass and 9410 times in seed production (range 1.0–17 880 seeds per plant). This type of environmentally induced variation enables genotypes of barnyard grass to survive and reproduce in the heterogeneous and unpredictable environments associated with seasonally flooded land.

Seed weight (caryopsis) in *E. crus-galli* var. *crus-galli* averages 1.73 mg (range

Table 2. Range of variation in four life history traits of barnyard grass taxa (*Echinochloa crus-galli* var. *crus-galli*, var. *frumentacea*, var. *oryzicola*, and *E. muricata*) grown in different environmental regimes under glasshouse conditions (Barrett and Wilson 1981)

	Range of taxon means in four environmental regimes			
	E. crus-galli			E. muricata
Life history trait	var. *crus-galli*	var. *frumentacea*	var. *oryzicola*	
Days to flowering	38.0-126.6	43.0-63.6	58.0-153.0	55.0-138.6
Net reproductive effort (%)	9.2- 33.7	11.5-31.3	0- 26.7	3.3- 29.2
Seed production	20.0-17880	37.4-7950	0-2890	29.2-8560
Total biomass (g)	0.5-320.8	0.5-235.1	0.5-251.8	0.6-408.0

1.66–2.11, $n = 10$ populations) and approximately 50% of seeds remained afloat after 4–5 d in water (Barrett and Wilson 1983) indicating that dispersal of seeds by water is likely, particularly in flooded habitats. Viable *E. crus-galli* seed has also been reported in irrigation water (Wilson 1979). In addition granivorous birds, especially blackbirds (*Agelaius* spp.) and waders are important dispersal agents, particularly in rice field habitats (Smith and Shaw 1966; Barrett and Seaman 1980). Probably the most important contemporary agent of long distance dispersal is man, since barnyard grass seed is a common contaminant of many seed crops and weed seeds are inadvertently introduced to fields during the sowing of the crop.

(c) *Viability of seeds and germination* — Freshly collected seeds of *E. crus-galli* exhibit innate dormancy, the duration of which varies considerably (Rahn et al. 1968; Barrett and Wilson 1983). The dormancy is due to the pericarp and epidermis (Arai and Miyahara 1963). Rahn et al. (1968) demonstrated that fresh seeds had only 0.3–1.4% germination. Storage of seeds for 4 and 8 mo increased germination to 19 and 44%, respectively. Of a sample of *E. crus-galli* seeds planted at various depths at the beginning of November, only 4.7% germinated over the first 2 mo, whereas 25.4% germinated during the sixth and seventh months after planting (Horng and Leu 1978). The most effective methods of breaking dormancy were removal of outer seed covering or pericarp, freezing and thawing for 4 d, exposing moist seeds to 120°F (49°C) for 5 h, soaking them in acetone for 20 min, in concentrated H_2SO_4 for 8 min, or in water for 4 d (Rahn et al. 1968). Use of 0.2% KNO_3 as a moistening agent gave slightly higher germination (Rahn et al. 1968). The optimum chilling temperature for breaking dormancy was 1–10°C for *E. crus-galli* var. *praticola* (Watanabe 1978). Miyahara (1975) concluded that primary dormancy was broken by low winter temperatures, alternating temperatures in spring, and spring flooding in paddy fields. Takabayashi and Nakayama (1981) found that germination of *E. crus-galli* var. *praticola* seeds buried 5 cm deep in sand was high in February and May but low in summer, a trend they attributed to secondary dormancy. Arai and Miyahara (1963) showed that storage of dormant seeds in submerged soil at 5°C overcame dormancy. Storage of seeds in nitrogen accelerated release of seeds from dormancy much faster at 30°C than at 5°C. Barrett and Wilson (1983) conducted germination tests on 9- and 18-mo-old seeds of 18 populations of *E. crus-galli* var. *crus-galli* and 11 populations of *E. crus-galli* var. *oryzicola*. They found that the decay of dormancy in var. *crus-galli* was less rapid than in var. *oryzicola* following dry storage and burial in soil.

The germination of *E. crus-galli* seeds was not reduced by exposure to 60 and 80°C temperatures for 1 h but exposure to 100, 120 and 130°C for the same length of time significantly lowered percent germination (Maun 1977a). The rate of germination was reduced only at 120 and 130°C.

The seeds of *E. crus-galli* germinate over a wide range of temperatures, from 13 to 40°C (Roche and Muzik 1964; Rahn et al. 1968). The optimum temperature for germination as reported by Watanabe (1981) was 5°C alternating with 30°C. The rate of germination of barnyard grass seed is markedly affected by temperature. Vengris et al. (1966a) showed that seeds germinated in only 5 d under high temperature conditions in mid-summer as compared to 11–12 d in early spring or fall when temperatures were relatively low. When temperature was not limiting (held at 20°C) the germination of *E. crus-galli* var. *praticola* seeds (wintered in soil) was entirely dependent on exposure to sunlight or to fluorescent light (Watanabe 1977). Under ideal germination conditions in a glasshouse, seeds of var. *oryzicola* from each of four locations in California germinated significantly faster

than those of var. *crus-galli* (Barrett and Wilson 1983).

The seeds may germinate at a rather wide soil pH range of 4.7–8.3 (Arai and Miyahara 1963) but the optimal for germination is around neutral (Brod 1968). Increasing moisture stress not only delayed initial germination but also slowed root and shoot elongation. The best germination occurs at about 70–90% field capacity of soil (Brod 1968; Arai and Miyahara 1963) and when oxygen content was lowered below 1% the percent germination decreased. Seeds in which dormancy had been broken (1 yr old) germinated best with continued exposure to light (60%) as compared with continuous dark (6%) (Rahn et al. 1968). More mature (dark grey or brownish and shiny) seeds produced significantly higher germination than immature (light grey) seeds (Rahn et al. 1968); however, some seeds harvested at milk or dough stage may be viable.

Percent germination of *E. crus-galli* seeds has been increased experimentally by various authors in the following ways: (a) exposure to approximately 440 W of 660.5 nm light for 5 min (Watanabe 1977); (b) chemical treatment with urea and potassium nitrate (Moursi et al. 1979a); (c) treatment with GA after storage of seeds at low temperature (Rizk et al. 1978); (d) physical scarification and H_2SO_4 or NaOH treatment (Yamasue et al. 1977); (e) sudden changes in temperature (Averkin 1978a); (f) exposure to freezing temperatures for 6 or 10 wk (Moursi et al. 1979b); and (g) ultrafreezing in liquid nitrogen to $-196°C$ for 5 min (Jordan et al. 1983). Conversely, percent germination was found to decrease when seeds were submerged under 20 cm of water (Panggabean 1976), exposed to freezing temperatures for 20 wk (Moursi et al. 1979b) or when the density of the soil in which they were sown reached 1.3 g cm^{-3} (Averkin 1978b).

Rahn et al. (1968) found no evidence of deterioration in viability of *E. crus-galli* seeds after storage for 3 yr in a glass jar in lab (dry) or loam soil at two depths (8 and 25 cm). Similarly, S. C. H. Barrett (unpubl. data) observed no reduction in viability of 6- to 8-yr-old seed of *E. crus-galli* var. *crus-galli* stored dry at room temperature. No reduction in germination of seeds buried in submerged soil for 30 mo was observed by Roche and Muzik (1964); however, seeds buried at 10- and 20-cm depths under normal soil conditions for the same period lost considerable viability. Dawson and Bruns (1975) buried seeds of *E. crus-galli* at 2.5-, 10-, and 20-cm depths in irrigated and nonirrigated sandy loam soil. They showed that seeds exhumed from 10- to 20-cm depths had highest germination in the second year after burial. The seeds buried for 13 yr had 3% viability but those buried for 15 yr were nonviable. Seeds buried at 20 cm remained viable for a longer period than at 10 cm probably because of greater induced dormancy (Roche and Muzik 1964). Germination was more rapid in sandy loam rather than loam soil and soil compacted by tamping and surface watering in a greenhouse produced higher germination (Rahn et al. 1968).

Dawson and Bruns (1962) buried seeds at depths ranging from 0 to 15 cm. The seeds germinated equally well at all depths but the maximum number of seedlings emerged from 1- to 2-cm depths. The maximum depth from which some seedling emergence occurred was 10 cm. The emergence occurred first from shallower depths. The surface-lying seeds germinated but produced few seedlings probably because of a lack of moisture. In saturated soils, however, seed burial caused a reduction in the rate of emergence even at 0.5- to 2-cm depths (Barrett and Wilson 1983). Seedling emergence was significantly greater at all burial depths (0, 0.5, 1.0, 2.0 cm) in var. *oryzicola* as compared to var. *crus-galli*. No seedling emergence in var. *crus-galli* occurred from 2-cm depth. Seedling emergence of var. *oryzicola* was also significantly greater than var. *crus-galli* from soil flooded to 9- and 18-cm water depth (Barrett 1983).

Wevers and Staas-Ebregt (1980) reported that emergence was positively correlated with soil water content up to the field capacity but negatively correlated with sowing depth. They associate emergence with the energy reserves of the seed in relation to the product of mechanical soil resistance and sowing depth.

(d) *Vegetative reproduction* — Reproduction is exclusively from seed and no regeneration has been reported through vegetative means.

9. Hybrids

No authenticated hybrids between *E. crus-galli* and other taxa in North America have been documented. Yabuno (1966, 1984) has artificially hybridized *E. crus-galli* with *E. oryzicola* (4 ×) and *E. oryzoides* (6 ×). In both cases, the F_1 hybrids were sterile.

10. Population Dynamics

Barrett and Wilson (1981) examined the repsonse of four taxa of barnyard grass to various growth regimes involving "stress" and "nonstress" conditions. They found striking developmental plasticity and differences in the timing of reproduction in response to sowing date and nutrient stress. Individuals germinating in August yielded less total biomass and allocated a smaller proportion to roots and a larger proportion to secondary tillers and seed than individuals germinating in April. In all taxa, except *E. crus-galli* var. *frumentacea*, a delay in flowering under long days resulted in larger vegetative biomass, lower reproductive effort, and where nutrients were limiting, inhibition of secondary tillers. Nutrient stress resulted in a delay in flowering, increased senescence rates, and a reduction in total biomass and reproductive effort. Although each taxon displayed a wide range of phenotypic plasticity (Table 3), certain fundamental differences in life history strategy among the taxa were maintained. For example, in all regimes *E. crus-galli* var. *crus-galli* flowered earlier, and exhib-

ited a greater seed production than the rice mimic (*E. crus-galli* var. *oryzicola*).

Potvin and Strain (1985) compared resource allocation for plants of *Echinochloa crus-galli* from Quebec, North Carolina and Mississippi grown in a common garden in Quebec. They showed that plants from Quebec allocated more energy to reproduction. Although resource allocation to flower and seed weight were relatively constant among individuals, seed number was extremely variable. Plants from Mississippi failed to flower altogether. There is a strong relationship between seed number and plant dry weight. Potvin and Strain (1985) also showed that the stage-specific selection coefficients of southern populations were increasingly selected against as the season progressed. At adult stage, plants from Quebec have a strong selective advantage.

Unfortunately, to date we have no data on the demography of populations and know of no other work on the subject. However, our own field observations indicate that populations can experience considerable seedling mortality as a result of the desiccation of temporarily wet sites, flooding, and herbicide use. Seedlings can germinate at any time since in agricultural sites irrigation time can vary throughout the growing season. Because of this, a wide range of demographic and life history patterns is evident. Seedlings emerging in spring usually grow to considerable size as a result of delayed flowering under long days. In contrast seedlings emerging in the fall often flower precociously from the stimulus of shorter days present during August and September (see Barrett and Wilson (1981)).

11. Response to Herbicides and Other Chemicals

Rahn et al. (1968) gave a partial list of many chemicals that are toxic to *E. crus-galli*. These include acetamides (CDAA and diphenamide), benzoics (amiben, dicamba, 2,3,6-TBA), thiocarbamates (EPTC, pebulate, vernolate), triazines (atrazine, simazine), substitute ureas (diuron, fenuron,

Table 3. Parasites of *Echinochloa crus-galli*

Species	Location and authority
INSECTA	
Coleoptera	
Dicladispa armigera (Oliv.)	India (Dhaliwal 1979)
Hyperodes humilis Gyll.	Mass. (USA) (Vengris et al. 1963)
Lissorhophrus oryzophilus Kuschl.	California (A. A. Grigarick 1981†)
Diptera	
Hydrelia griseola (Fallen)	California (A. A. Grigarick 1981†)
Hemiptera	
Crytorhinus lividipennis (Reuter)	Peninsular Malaysia (Sivapragasam 1983)
Homoptera	
Laodelphax striatella (Fall.)	Hunan, China (Lei et al. 1983)
Nilaparvata lugens (Stal.)	Hunan, China (Lei et al. 1983)
Sogatella furcifera (Horv.)	Hunan, China (Lei et al. 1983)
Sogatella panicola (Ishihara)	Hunan, China (Lei et al. 1983)
Lepidoptera	
Elasmopalpus lignosellus (Zeller)	Cuba (Perez and Lopez 1980)
Pseudaletia unipunctata (Haworth)	USA and Canada (Borror et al. 1981)
Orthoptera	
Euscyrtus concinnus (Haan)	Philippines (Barrion and Litsinger 1980)
Thysanoptera	
Haplothrips ganglbaueri (Schmutz)	India (Ananthakrishnan and Thangavelu 1976)
FUNGI	
Drechslera dictyoides	Ottawa (Shoemaker 1962)
(Drechs.) Shoem. f. sp. perenne	Ontario (Conners 1967)
Fusarium roseum f. sp. cerealis	Brazil (Reis 1982)
Rhizoctonia spp.	Brazil (Reis 1982)
Tolyposporium bullatum (Schroet)	Ontario, Nova Scotia, U.S.A. (Savile 1953; Conners 1967)
Ustilago crusgalli Tr. and Earle	Quebec, USA (Fischer 1953; Conners 1967)
Helminthosporium spp.	USA (Vengris et al. 1966a)
NEMATODA	
Pratylenchus spp.	Nebraska (USA) (Gast et al. 1984)
VIRUSES	
Tungro disease of rice	Rice growing regions (Wataneakul (1964) cited in Holm et al. (1977))
Dwarf disease of rice	Rice growing regions (Shinkai (1956) cited in Holm et al. (1977))
Maize dwarf mosaic	Rice growing regions (Conti 1981)
Barley stripe mosaic, lucerne dwarf, oat pseudo rosette, panicum mosaic, sugarcane mosaic, and white streak mosaic	Rice growing regions (Namba and Mitchell unpublished, cited in Holm et al. (1977)).

†Personal communication with A. A. Grigarick, Department of Entomology, University of California, Davis, Calif.

linuron), and several others (amitrole, CIPC, dalapon, DPA, DCPA, stoddard solvent trifluron). Since then, resistance to triazines has been reported (Morin and Gasquez 1981). Forms have also been found which are resistant to molinate and propanil (Sutisna and Guillerm 1980). Miele and Vannozzi (1977) found that resistance to atrazine began to appear after 4 consecutive years of treatment and thereupon increased steadily with each year of exposure.

As a result of the use of triazine herbicides in maize fields, *E. crus-galli* has become a major problem, even though it was of no importance in 1950, before the advent of chemical weeding (Mexner 1981). Heinzle (1981) reports that *E. crus-galli* has only now appeared in French vineyards after

several years of chemical weeding. For triazine resistant forms of *E. crus-galli*, 0.75 kg of atrazine ha^{-1} plus either 5.5 kg EPTC ha^{-1}, 6 kg vernolate ha^{-1}, or 1.98 kg metalochlor ha^{-1} has been recommended (Morin and Gasquez 1981). Rahn et al. (1968) emphasized that most herbicides are effective only when they come in contact with germinating seed or emerging coleoptile. Few herbicides kill established plants and still fewer selectively kill barnyard grass growing with cultivated crops.

Echinochloa crus-galli can be selectively controlled in several crops by using EPTC (ethyl N,N-di-n-propylthiol carbamate) which kills plants by injuring the seedlings after germination (Dawson 1963a). Exposing barnyard grass seeds to EPTC or EPTC vapors for extended periods of time did not reduce the germination of seeds (Dawson 1963b). Alley (1956) reported that dalapon (sodium 2,2-dichloro-propionate) at the rate of 5 lbs acid equivalent per acre was sufficient to control barnyard grass. The susceptibility of barnyard grass to dalapon also varied with the stage of plant development — younger stages of growth were significantly more susceptible than older ones. Butachlor applied pre-emergence inhibits amylase and protease activity in *E. crus-galli*, delays radicle emergence and inhibits emergence of the root and primary leaf from the coleoptile (Chen et al. 1981). Pre-emergence applications are the most effective in barnyard grass control (Rahn et al. 1968) because (i) few chemicals will kill established plants, (ii) most chemicals lack selectivity and (iii) plants are most vulnerable at seedling stage.

Of the selective herbicides in at least one (Simetryne) the selectivity is based on differences in the rate of absorption of the herbicide by *E. crus-galli* and the crop, and in the metabolic activity of the shoots (Matsumoto and Ishizuka 1983).

Several herbicides such as Dowco 221 (2,2,2-trichloroethyl) styrene (Geronimo and Hunter 1969), molinate (Swain 1974), chlorobromuron, simetryne (Hagimoto and

Yoshikawa 1972), metribuzin (Rioux 1974) are effective in controlling barnyard grass in rice. The best control of the weed was, however, obtained with pre-emergence and early postemergence applications and decreased rapidly with increase in age probably because of the growth dilution factor (Hagimoto and Yoshikawa 1972).

12. Response to Other Human Manipulations

Kacperska-Palacz et al. (1963) showed that clipping of shoot tips at the flowering and seed maturation stages stimulated the development of lateral buds whereas clipping prior to elongation did not have any effect on the number of tillers. Vengris et al. (1966b) concluded that clipping of barnyard grass was not an effective method of control because all plants recovered irrespective of frequency and height of clipping. However, exhaustion of plants may, of course, decrease the competitiveness of the weed and contribute indirectly to the effectiveness of herbicidal treatments (Vengris et al. 1966b).

The practice of fertilizing using liquid manure may contribute to the population of *E. crus-galli* in cropland. Schroder and Buart (1982) found that *E. crus-galli* seeds remained viable after passing through cattle, and that only ensilage for 8 wk resulted in complete loss of viability.

Ogg and Dawson (1984) demonstrated that emergence of *E. crus-galli* seedlings was significantly reduced by shallow tillage at monthly intervals, provided it was begun early enough in the spring. In no-till systems in a maize rotation, *E. crus-galli* was a predominant weed after 10 yr (Wrucke and Arnold 1982). However, Kutuzov et al. (1981) reported that *E. crus-galli* was completely eliminated after a rotation of maize-annual herbage spp./fodder beet/barley/barley and red clover/red clover for 2 yr/oats when all cultivation techniques were used at a high level and optimum time. Gawron'ska-Kulisza (1975) also found up to twice as much weed growth and a greater

proportion of *E. crus-galli* in monocultured plots than in plots in rotation. Flooding of soil continuously before emergence inhibited the germination of seeds from three depths (1.3, 2.5, 5.1 inches) (Smith and Fox 1973). An exposure of 40 d under clear mulch killed *E. crus-galli* seeds in the upper 3–4 cm of soil (Standifer et al. 1984). This includes the zone of maximum emergence (Dawson and Bruns 1962).

Kannaiyan et al. (1983) achieved a 47% decrease in *Echinochloa* spp. in 40 d after inoculation with 100 g m^{-2} *Azolla pinnata*. This increased to a 74% reduction when inoculation level was increased to 500 g m^{-2}. Seeding rice in water and repeated cultivations in spring at intervals of 1–3 wk before seeding reduces infestation (Shaw and Danielson 1961). Kust and Smith (1969) reported that decreased spacing in soybean rows increased crop yield and control of barnyard grass.

A practical measure for control of *E. crus-galli* is suggested by its response to photoperiod (Vengris et al. 1966a). As pointed out earlier (see Section 7c), seedlings emerging in spring and early summer in the temperate regions produce significantly higher dry matter than those emerging later in the season (Maun 1977b) because early in the season there is minimum shading and competition by the host crop, and nutrient and moisture supplies are optimal. These plants cause significant reductions in the yield of a crop (Maun 1977c) and produce large amounts of seed (Maun 1977b). In contrast seedlings emerging in mid- and late summer are stunted, produce few seeds and do minor damage to a crop. Maun (1977b,c) suggested that for high productivity of soybeans, barnyard grass plants must be controlled during the first 5–7 wk of its life cycle.

13. Response to Parasites

A list of parasites of *E. crus-galli* is presented in Table 3. Vengris et al. (1963) reported that the larvae of a weevil (*Hyperodes humilus* Gyll.) attacked the growing points of *E. crus-galli* seedlings, the young tissue around the growing points, and the new shoots of intercalary growth. The insects caused infestations of up to 50% of all plants and plants infested at a young stage were often killed (Vengris et al. 1963). The authors suggested that this weevil could be of interest as a biological control agent. The adults of rice water weevil (*Lissorhophrus oryzophilus* Kuschl.) feed on leaves while larvae consume roots of *E. crus-galli* (A. A. Grigarick, pers. commun.). The rice leaf miner (*Hydrallia griseola* (Fallén)) feeds on leaves of *E. crus-galli* as larva (A. A. Grigarick, pers. commun.). Larvae of army-worm (*Pseudaletia unipunctata* (Haworth)) feed and develop on *E. crus-galli* plants and then infest corn and wheat.

Echinochloa crus-galli has also been shown to support adult beetles of the rice hispa (*Dicladispa armigera* (Oliv.)) (Dhaliwal 1979). Lei et al. (1983) collected the eggs of four plant hoppers on *E. crus-galli* plants in rice fields in China: *Sogatella panicola* (Ishihara), *S. furcifera* (Horv.), *Nilaparvata lugens* (Stal.) and *Laodelphax striatella* (Fall.). Of these *S. panicola* preferred *E. crus-galli* to rice and survived better on the weed than on rice, whereas *N. lugens* (Stal.) preferred rice (Lei et al. 1983). *Nilaparvata lugens* (Stal.) is preyed upon by *Cyrtorhinus lividipennis* (Reuter) which has been shown in glasshouse studies to deposit more eggs on *E. crus-galli* than on rice or on other weeds of rice (Sivapragasam 1983).

Echinochloa crus-galli is an alternate host of several plant diseases and viruses (Table 3).

ACKNOWLEDGMENTS

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