THE BIOLOGY OF CANADIAN WEEDS. 24.
AGROPYRON REPENS (L.) BEAUV.

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Agropyron repens (L.) Beauv., quack grass, is an introduced perennial grass found in all provinces of Canada and the Northwest Territories. In most agricultural areas it is a serious weed of cultivated crops; alternately it can be used as pasture or hay. A summary of the biology of quack grass is presented as part of a series of the biology of Canadian weeds.

Le chiendent, Agropyron repens (L.) Beauv., est une graminee vivace introduite qu'on retrouve dans toutes les provinces du Canada et dans les Territoires du Nord-Ouest. C'est une mauvaise herbe importante des cultures de la plupart des régions agricoles; cependant elle peut aussi être utilisée comme plante à pâturage ou à foin. Dans le cadre de la série d'articles sur la biologie des mauvaises herbes du Canada, cette contribution résume les données de la biologie du chiendent.

[Traduit par les auteurs]

1. Name
Agropyron repens (L.) Beauv. — quack grass, couch grass (Canada Weed Committee 1969); chiendent (Ferron et Cayouette 1975). Poaceae (Gramineae), grass family, Graminees. The species has also been listed as Elytrigia repens (L.) Nevski or Triticum repens L. in some floras and scientific papers, especially European.

2. Description and Account of Variation
Perennial, spreading by seeds and rhizomes; rhizomes long (up to 1 m), slender (1.5 mm), smooth, whitish, and scaly; leaves, 9–10 mm wide, 6–20 cm long, finely pointed, flat, green, sometimes glaucous, scabrous at the margin and on the upper surface, lower surface smooth; leaf sheaths round, split, short, with overlapping hyaline margins; ligules membranous, obtuse, 0.5–1 mm long, and sometimes ciliated; stem 30–120 cm long, hollow, round, slender to somewhat stout with three to five nodes; spikes erect, straight, 5–30 cm long, with rough margins; spikes green or sometimes bluish-green, loose or compact but with the axis hard; spikelets compressed, 10–20 mm long, 3–8 flowered, sessile; spikelets one-third to half their length apart, alternate in two rows on opposite sides of the axis with the broader size appressed to it; glumes herbaceous, lanceolate to oblong, blunt or pointed, 7–12 mm long, hard and 3–7 nerved; lemma overlapping, lanceolate oblong, keeled upward, 8–12 mm long, hard and 5-nerved; palea nearly as long as the lemma with 2 rough keels; anthers 4–8 mm long; fruit a caryopsis, lance-shaped in outline, straw to dirty-gray-colored, 8.0–9.0 mm long, 1.3–1.8 mm wide; sinus U-shaped, rachilla well exposed, about one-sixth to one-fifth the length of the caryopsis. The species is hexaploid (Palmer and Sagar 1963). Chromosome counts of 2n = 42 have been obtained for Canadian material (Bowden 1965). In European plants 2n = 42 is the standard chromosome count; however, counts of 28, 34, and 35 have also been recorded (Palmer and Sagar 1963).
The combination of matted, whitish rhizomes, auricles, hairy lower sheaths, and heads resembling a slender head of wheat distinguish quack grass from most other grasses. *Agropyron repens* resembles western wheat grass, *A. smithii* Rydb. but the latter has bluish rigid leaves that tend to roll in at the edges under dry conditions, while those of quack grass are lax, rarely bluish, and always remain flat (Frankton and Mulligan 1971). *A. trachycaulum* (Link) Malte has no rhizomes and much smaller anthers. The rye grasses, *Lolium* spp., also possess slender spikes but the spikelets occur with their edges tangential to the main stem, while in quack grass the spikelets are arranged with the broader surface appressed to the stem (Frankton and Mulligan 1971).

In a study of hybridization with the genus *Agropyron*, Bowden (1965) recognized two forms of *A. repens* in Canada: f. *repens*, which is awnless or very short-awned, and f. *aristatum* (Schum.) Holmb. Skand., where the lemmas have awns that are 2-9 mm long. The floristic composition within each province consists of 66-70% f. *repens*, as determined by an examination of herbarium specimens in the Department of Agriculture Herbarium, Ottawa.

Figure 1 shows the main diagnostic features of the seed and mature plant.

3. Economic Importance

(a) Detrimental — Quack grass competes strongly with a number of cultivated crops (see Muzik 1970) in almost all agricultural areas of Canada except the drier regions of Saskatchewan, Alberta and Manitoba (compare Friesen and Shebeski 1960). Reduced yields in Canadian crops attributed to the presence of quack grass have been reported for corn and oats (up to 85% and 30-70% reduction respectively; see references in Rioux 1973), and for barley and soybeans (Rioux 1973). Further, in corn, the presence of quack grass increases ear moisture at harvest and delays tasseling and silking (Bandeen and Buchholtz 1967).

Quack grass is a luxury consumer of key nutrients. By mid-July a stand of quack grass can tie up approximately 55, 45, and 68% of the total N, P, and K, respectively, that it removes from the soil for the entire season; in a stand of the size 2,000 kg shoot dry weight per hectare, this is equivalent to 118 kg/ha of N, 17 kg/ha of P, and 67 kg/ha of K (Bandeen and Buchholtz 1967). The value of grass seed crops may be greatly reduced if contaminated with quack grass seed. Quack grass serves as an alternate food plant for several pests of grain crops, such as the cereal leaf beetle, *Oulema melanopa* (L.) (Dr. Dean Haynes, personal communication).

(b) Beneficial effects — Quack grass may be used for pasture or hay and can be found on lists of preferred plants for rangeland. Total crude protein (dry) content of quack grass is comparable with timothy at the same stage of growth. Quack grass roots and rhizomes are efficient soil binders on slopes, embankments and sandy soils. It provides cover for wildlife, including small mammals, some song birds and game.

In current experimental studies underway in Michigan, *Agropyron repens* is one of the most effective oldfield plants for reclaiming nutrients from municipal sewage effluent sprayed on vegetation in abandoned fields. If left uncut, quack grass is active mainly in the spring, but efficient uptake can be maintained throughout the growing season by a schedule of repeated mowing and harvesting. The harvested quack grass has a level of nitrogen high enough to be appropriate for cattle feed, but low enough to avoid toxicity (Drs. F. P. Reed and S. N. Stephenson, personal communication).

A methanol extract prepared from *A. repens* has been effective against mosquito larvae (*Aedes aegypti* L.) even in low concentrations; only 2 of 36 plant species tested were as effective (Supavarn et al. 1974). Under the synonym *Triticum repens*, quack grass is recorded in most herbals with many useful properties (Palmer and Sagar 1963). The rhizomes, when dried and ground, can serve as a source of flour (Fernald and Kinsey 1958).
Fig. 1. *Agropyron repens* (L.) Beauv.: diagnostic features. (a) junction between leaf and sheath showing auricles; (b) spikelet; (c) caryopsis; (bottom) growth habit.

(c) Legislation — The species is listed in the category “Primary Noxious Weed Seeds” in the Seeds Act and Regulations administered by Agriculture Canada (1967).

4. Geographical Distribution
Although originally an Old-world species only (see section 6), the current distribution of quack grass is circumpolar (Hulten 1962). Its distribution extends throughout Europe, Australia, New Zealand and the temperate zones of Asia and North and South America.

In North America, *A. repens* is found in every state in the U.S.A. but is rarely troublesome as a crop weed south of Washington, D.C. and St. Louis, Mo. (Johnson 1958). In Canada, it is found from Newfoundland to British Columbia (Boivin 1967) and occurs as far north as Natasquan in Quebec (Rousseau 1968), Goose Bay in Labrador (Hustich 1971), Fort Smith, N.W.T. (Cody 1956) and Greenland and
Alaska (Boivin 1967). It is especially common in Southeastern Canada (Bowden 1965) (see Fig. 2).

5. Habitat
(a) Climatic requirements — Specific information is unavailable. It is commonly designated as a "cool-season" grass. In Canada it is common in areas of moderate rainfall and is rare in areas of low rainfall.

(b) Substratum — Quack grass has been reported growing on a wide variety of soils, from dry sand to wet alluvium, and in pH ranges from 4.5 to 8.0 (see Doyon 1965, 1968; Rousseau 1968). In general, however, quack grass is most vigorous in neutral to alkaline soils (pH 6.5–8.0; King 1966; Dale et al. 1965). It has a high salt tolerance of 70–95 mg/100 g of soil (Tesu et al. 1972) and may be found on saline soils. In the British Isles, it is associated with arable clay soils (Palmer and Sagar 1963). In Canadian pastures, quack grass shows no drainage preference but does best on fine-structured soils (Dale et al. 1965). Rhizome growth is reduced in compacted soil (Wolcott and Carlson 1947).

(c) Communities in which the species occurs — Quack grass is a plant of open areas, mainly occurring where the native vegetation is disturbed. It is common in agricultural fields as well as in road margins, waste places, and abandoned fields and lots (Frankton and Mulligan 1971), and is especially vigorous in fallow land and in the first years after tillage ceases (Barralis 1961). Quack grass may make up > 90% of the biomass in an abandoned field for several years, and exclude colonization by herbaceous dicotyledonous species (see Werner 1975). When shrubs enter a field, quack grass is gradually reduced in biomass and finally dies out within a few years (Dr. John Cantlon, unpublished data). The species is not found under a continuous cover of shrubs and trees (Palmer and Sagar 1963). Permanent pasture tends to have very little of this grass, perhaps due to selective feeding by the grazers.
Quack grass is often found as a riparian plant on river banks (Rousseau 1968), freshwater beaches, salt beaches, and sand dunes. In maritime zones it is found on dunes and on alluvial soils, in salt and fresh water marshes, and on tidal flats.

6. History
Quack grass is a native of Europe and was introduced to New England during colonization. Josselyn (1672) who visited New England in 1639 and 1663, placed quack grass among "such plants as have sprung up since the English planted and kept cattle here." Probably it was introduced to Quebec during the same period (Rousseau 1968). Similarly, it was introduced westward during the early years of European settlement. The rapid spread of quack grass in western Manitoba and eastern Saskatchewan is likely the result of sowing infested bromegrass (Carder 1961) and/or by transportation of infested hay and straw.

7. Growth and Development
(a) Morphology — The aerial shoots and rhizomes constitute a sympodial system. Rhizome growth is renewed annually from axillary buds at the base of the aerial shoots. Axillary buds along the rhizomes are mainly dormant due to strong apical dominance exerted by the terminal bud (see section 7c). Aerial shoots are formed mainly at the end of the growing season when a rhizome tip becomes erect; they are also formed from both terminal and axillary buds any time that a rhizome becomes detached from the parent plant (see also section 10). Adventitious roots form at nodes of the rhizome; roots are short in length relative to other grasses. See Palmer and Sager (1963) for detailed description of the morphology of quack grass, Håkansson (1967–1970, 1971) for experimental studies on morphological development under various conditions of burial depth, defoliation, rhizome breakage, etc., and Rogan and Smith (1975a,b) for detailed description of the developmental anatomy and morphology of the rhizomes, shoots and leaves.

(b) Perennation — Quack grass is an herbaceous perennial, classified as a geophyte.
(c) Physiological data — Axillary buds on rhizomes of quack grass are released from inhibition when the rhizome apex is removed or when the rhizome is severed from the parent plant. Isolated rhizome segments exhibit a polarity such that buds toward the apical end develop into aerial shoots, those toward the base develop into rhizomes or remain dormant (Rogan and Smith 1976). McIntyre (1965) showed that apical dominance in rhizomes could be controlled by changing level of nitrogen. He suggested (McIntyre 1969) that apical dominance (in high-N rhizomes which were isolated from the parent plant, i.e. from the source of carbohydrate), was due primarily to intraplant competition for a limited carbohydrate supply, although the ability of the apex to compete successfully may depend on its ability to synthesize mobilizing hormones.

It has been suggested that indole-3-acetic acid (IAA) is produced in the apical region and transported into the lateral buds in sufficiently high levels to inhibit growth of the latter (Akhavein 1971). Rogan and Smith (1976) suggested that a continuous supply of gibberellin from the parent plant may be essential to maintain apical dominance. Leakey et al. (1975) found that various hormones can play a part in apical dominance in rhizome buds and that there are interactions between apical and basal factors; i.e., no single-factor explanation suffices. They suggested that auxin is the apical factor (see also Chancellor 1974) and that cytokinins (probably originating from the roots which occur both on the parent plant and at each node along the rhizome) are a major constituent of the parental factor.

Under longer photoperiods, heavier rhizomes (Williams 1971) and more numerous and thicker rhizomes are produced (Palmer 1958). The level of aboveground illumination affects the rhizomes more than it does the aerial shoots (Williams 1970a;
Palmer 1958). A reduction in level of light produces an increase in the percentage of rhizome buds developing as shoots and an increase in number of shoots produced at older (dormant) nodes along the rhizome. The formation of new rhizomes from buds is entirely suppressed at 2,690 lux (McIntyre 1970).

In a large field study (Bandeen and Buchholtz 1967), the application of nitrogen increased shoot dry weight and decreased rhizome dry weight, but the application of potassium or phosphorus had either no effect on shoots or rhizomes (K$_2$O) or increased shoot growth only (P$_2$O$_5$). Rogan and Smith (1975a) found that at low levels of nitrogen (15 ppm), there was an increase in the tendency for the buds in the axils of leaves 1 and 2 to produce rhizomes or rhizome-tillers instead of tillers. Both low temperature (10°C) and low nitrogen (15 ppm) led to the production of relatively fewer secondary rhizomes and tillers. The number of leaf primordia increased with decreasing temperature and increasing nitrogen level (up to 960 ppm) (Rogan and Smith 1975b). Rhizome buds require oxygen for development to occur (Johnson and Buckholtz 1962).

Arny (1932) found a seasonal trend of sugar accumulation in rhizomes of *A. repens*. Total soluble sugars increased, reached an early season high (8%) in late May, then decreased to 3% from June until early October, followed by an increase to about 8% in November. In contrast, in a study of the carbohydrate level in quack grass rhizomes, Schirman and Buckholtz (1966) found a fairly constant level (46%) throughout the year, although the total available carbohydrate content was slightly higher during the major accumulation period, i.e. from August to November. By the following April, the total available carbohydrate was approximately 39% of the dry weight, but the dry weight of rhizomes had dropped from 7,000 to 5,500 kg/ha.

The pattern of translocation of carbohydrates varies with seasonal time, which may be significant for control with phloem-translocated herbicides. Fiveland et al. (1972) demonstrated that more $^{14}$C-labelled carbohydrates were retained in the parent rhizomes at the 3- to 4-leaf stage than at the 2-leaf stage; shoots were photosynthetically independent at the 5-leaf stage. Rogan and Smith (1974) showed that with the growth of axillary shoots, assimilates were exported from the primary shoot to the daughter tillers and rhizomes; reciprocal translocation did not occur between tillers and the primary shoot although it did between the rhizome tillers and the primary shoot (see also Forde 1966). In mature plants the primary shoot and tillers were completely independent, but rhizome-tillers continued to receive small quantities of assimilate from the main shoot system. Shading a whole plant had no effect on tracer movement, but shading of all but one tiller caused a transfer of assimilates to the rest of the plant which was not observed in intact plants (Rogan and Smith 1974).

(d) **Phenology** — Seeds germinate in the early spring. The seedlings begin to produce tillers in the 4- to 6-leaf stage and rhizomes in the 6- to 8-leaf stage (Palmer and Sagar 1963). In Canada, the latter stage is usually reached 2-3 mo after seedling emergence. In contrast, new rhizomes start to develop at the 3- to 4-leaf stage in plants that have been developed from rhizome buds (Fiveland et al. 1972); this stage is reached around 15 May at Guelph, Ont. (Rioux 1973) and around 1 June at La Pocatière in eastern Quebec.

New rhizomes develop underground in greatest numbers during June, July and August (Evans and Ely 1935). The tip of each rhizome grows in a horizontal direction below the soil surface during the spring and summer before becoming erect in the autumn to form a primary aerial shoot (see section 7a). This shoot develops into a mature plant during the following year (in Britain; see Palmer 1958) but in a cold climate most of these newly formed shoots die in winter (Akhavein 1971). Flowering
occurs in late June to July in Canada (Frankton and Mulligan 1971). Seeds ripen in early August to early September and drop from the parent plants by late September.

In general, the plants are most active in sexual reproduction and rhizome formation in the middle of the summer, and in tillering and photosynthesis in spring and autumn. The natural seasonal cycle may be altered by cultural practices. For examples, tillering and rhizome production will follow soil disturbance at any period of the year except mid-winter, and the growth cycle may be initiated in August after a cereal crop has been removed (Palmer and Sagar 1963).

(e) Mycorrhiza — None known.

8. Reproduction

(a) Floral biology — Quack grass is wind-pollinated and virtually self-sterile. However, seeds set by enclosed spikes have been reported (see Palmer and Sagar 1963). Much genetic variation is found when quack grass reproduces by seeds (Raleigh et al. 1962, Williams 1973a).

(b) Seed production and dispersal — The amount of seed produced is highly variable. Reports range from 15 to 400 seeds per plant stem, with 25-40 most common. In arable crops, the number of seeds depends on the crop in which the quack grass was growing, the proximity of different genotypes, humidity, and the length of time between anthesis and crop harvest (Williams and Attwood 1970, 1971). Further, it has been suggested that since plants tend to be self-sterile and large stands may be a single clone as the result of vegetative reproduction, then seed formation should be much higher at the margin of a clone where inflorescences are cross-pollinated than in the center of a large stand (see Palmer and Sagar 1963).

(c) Viability of seeds and germination — Little information is available on viability levels of quack grass seeds, except indirectly via germination studies. Alternating temperatures are a requirement for germination (Chepil 1946; Andersen 1968; Palmer and Sagar 1963). Freshly harvested seed will not germinate at constant temperatures between 5 and 30 C in either light or darkness, but up to 90% germination is achieved if the temperature fluctuates diurnally between 15 and 25 C (Sagar 1961). There is no after-ripening period (Sagar 1961).

If buried, seeds may lie dormant for 2–3 yr (Carder 1961) and retain their viability for a maximum of about 4 yr (Brackney and Seely 1966). After passing through the digestive tracts of horses, cows and sheep, but not swine, seeds of quack grass retain their viability (Muenscher 1952). In the laboratory, germination is promoted by gibberellic acid and inhibited by abscissic acid but is not affected by sonication, liquid nitrogen and infrared light (Holm and Miller 1972).

The seeds possess no special morphological adaptation for dispersal, but fall passively from the parent plant. Means of long distance dispersal have not been identified to date.

(d) Vegetative reproduction — Given the relatively low number of seeds produced, and the generally higher probability of survival of vegetatively-produced plants relative to seedlings, vegetative cloning is much more important than sexual reproduction in maintaining a population on a site (see also section 10). Raleigh et al. (1962) reported that the diameter of spread of the 14 rhizomes of one parent plant was 3.04 m. The total length of rhizomes was 154 m, with 206 shoots having arisen from them.

Johnson and Buckholtz (1962) reported a seasonal activity of rhizome buds; there was a steady decrease in activity from mid-April to June, dormancy during June, and increased activity from July onward. Within broad limits, rhizome initiation and growth are not correlated with flowering of plants, e.g., flowering shoots produce the same amount of rhizome material as do vegetative shoots (at light levels above the minimum required for rhizome growth) (Palmer 1958).
Conceivably, every mature rhizome bud is capable of establishing a new plant. However, most buds along an intact rhizome are dormant and do not initiate any growth. See section 7c for a discussion of apical dominance in quack grass.

9. Hybrids
Palmer and Sagar (1963) reported hybrids between quack grass and \textit{A. junceiforme} (A. \& D. Löve) and between quack grass and \textit{A. pungens} (Pers.) Roem and Schult. Dewey (1965) formed synthetic but sterile hybrids between quack grass and \textit{A. riparium} Scribn. \& Smith. In Canada, hybrids have been reported with \textit{Elymus arenarius} L. and \textit{Elymus canadensis} L. (Lepage 1953). None of these hybrids is of known economic importance.

10. Population Dynamics
In open habitats an individual plant forms a clump during the first growing season due to extensive subtillering of primary tillers. Also, as many as 150 rhizomes or rhizome branches may be produced. In the second season the clump may develop into a patch as other clumps develop from the erected tips of the first season's rhizomes (see section 7a,d). Later, adjacent patches may coalesce to form a continuous stand or alternatively they may be contained by the presence of other species (Palmer and Sagar 1963). In a closed community an individual plant consists of a primary shoot, two or three primary tillers, and from two to four rhizomes, and clump formation does not occur (Palmer 1958 and Palmer and Sagar 1963).

Tripathi and Harper (1973) conducted a study which compared the reproductive strategies of two species of \textit{Agropyron}, \textit{A. repens} and \textit{A. caninum}, growing them for 20 wk in the greenhouse in various mixtures and from initial starts of either seeds or tillers. In both species, plants established from tillers were more vigorous and aggressive than their counterparts produced from seeds. In \textit{A. repens}, plants started from seed did not produce aboveground foliage for 10-12 days and lagged behind plants begun from tillers in biomass accumulation for the 1st 8 wk of the study. In pure stands, quack grass had 44-55\% of its total biomass in underground structures at the 20-wk harvest date (in mixed stands the percentage was somewhat less). At the same time, the percentage of total biomass accumulated in seeds was 0.1-0.9\% (slightly higher values in plants produced from tillers). The average number of seeds per plant was 30; average number of rhizome buds per plant was 215.

Williams (1973b) collected seeds from several clones of quack grass in several areas in Britain, germinated them in an unheated glasshouse, and examined the developing seedlings and clones. Comparisons of both seedlings and clones showed differences among genotypes: clones with the least weight of rhizome tended to have the most weight of spikes. Also, large variations occurred between clones established from seedlings from a given area, especially in the pattern of dry weight allocation between primary and secondary shoots and in the time the spikes emerged.

A long-term field study of quack grass is underway in an abandoned field in Kalamazoo County, Michigan. Two years previous to the initiation of the study, the field had been scraped clear of all vegetation by large earth-moving equipment during construction of a research facility. By the autumn of year 0, a uniform 2-yr old stand of quack grass was present; a portion of this area was plowed to a depth of 25 cm and then disked with a standard drag disk at two levels — 1 pass (low cultivation) and 20 passes on a single day (high cultivation). In years 1, 2, and 3, quack grass was sampled by harvest techniques (dried > 48 h at 100 °C, forced-air oven) from the two areas; in years 2 and 3, samples were also taken from the continuous surrounding quack grass stands which were then 4 and 5 yr of age, respectively. On a per meter basis, the total biomass of plants increased with time, as did all plant organs except
seeds-and-reproductive stems, which decreased after year 2. There was little difference in absolute biomass between quack grass growing in high levels compared to low levels of cultivation. Litter accumulated so that it was almost 600 g/m² by the 5th yr. The number of seeds per flower stem ranged from 12 to 30, with little pattern evident over time or treatment (Table 1). Although absolute biomass of plants steadily increased from year 1 to year 5, sexual reproduction reached highest values by several criteria in the intermediate years and then decreased dramatically (Table 1 and Werner, in preparation).

Quack grass reportedly is an allelopathic plant which inhibits the growth and germination of seeds of other plants through the release of toxic substances. However, living quack grass material has failed to produce inhibitory effects in numerous experiments (see discussion in Palmer and

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<td>-</td>
<td>54.5</td>
</tr>
<tr>
<td></td>
<td>(L)</td>
<td>5.8</td>
<td>52.4</td>
<td>40.3</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>(H)</td>
<td>5.3</td>
<td>34.7</td>
<td>33.4</td>
<td>-</td>
</tr>
</tbody>
</table>

*C = area not plowed in year 0 (see text); L = area of low cultivation in year 0 (1 disk pass); H = area of high cultivation in year 0 (20 disk passes). All values are means of 8 samples.

†Low values in years 3 and 5 may reflect difficulty of accurate root sampling and/or the fact that there was uncommonly low rainfall (year of sampling: 1976).
Sugar 1963), and it may be that only dead materials produce an inhibitory effect. In the field and greenhouse, a litter layer of dead stems and leaves of quack grass greatly inhibits the germination of teasel (Dipsacus sylvestris) seeds. The action is probably through chemical means, although it is not clear whether the inhibitor is leached from quack grass itself or is a product of microbial activity (Werner 1975).

The ability of quack grass to maintain high growth rates through very cool periods of the year, coupled with vegetative reproduction (section 8d), luxury uptake of minerals (section 3a) and possibly allelochemic toxins, make it a potentially strong competitor of crops (cf. Raleigh et al. 1962). Williams (1970a,b, 1975) demonstrated that quack grass grows faster than wheat and has a larger leaf area ratio, but has a competitive advantage only if it germinates before the wheat. The earlier that wheat was sown in pots infested with quack grass, the less it suffered from competition. So, early growth of cereal crops may have a suppressive effect on quack grass until anthesis; however, the advantage is lost when the crop begins to ripen and quack grass is freed from competition for light. In fact, the potential problem for the following year may be even greater, since quack grass plants that had early shading produced more shoots and seeds after mid-July than those that were not shaded earlier (Williams 1970a).

11. Response to Herbicides and Other Chemicals
Quack grass is thought to be encouraged by auxin herbicides, substituted phenols and modern crop husbandry techniques (Aberg 1964; Bachthaler 1969; Brimhall 1970; Hammerton 1968). Many herbicides are available but crop management methods that use herbicides to control quack grass require careful selection of herbicides and consideration of cropping sequences.

Lately, two new herbicides for the control of quack grass have been tested: pronamide and glyphosate. Pronamide is most phytotoxic to quack grass when placed in the rhizome zone (Carlson et al. 1975). Its continuous use on two soil types at La Pocatière gave an effective control of quack grass with promotion of alfalfa growth. Nevertheless, complementary control may be necessary to avoid a shift in weed problems (Table 2). Glyphosate has been shown to provide a high degree of quack grass control in fall and spring applications without residual effects on crops (Baird et al. 1971; Baird and Begeman 1972). Complete control has been achieved over an

<table>
<thead>
<tr>
<th>Species</th>
<th>Pronamide (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.0</td>
</tr>
<tr>
<td>Medicago sativa L.</td>
<td>2.5</td>
</tr>
<tr>
<td>Agropyron repens (L.) Beauv.</td>
<td>91.5</td>
</tr>
<tr>
<td>Taraxacum officinale Web.</td>
<td>0.0</td>
</tr>
<tr>
<td>Plantago major L.</td>
<td>0.0</td>
</tr>
<tr>
<td>Achillea millefolium L.</td>
<td>0.0</td>
</tr>
<tr>
<td>Chenopodium album L.</td>
<td>1.5</td>
</tr>
<tr>
<td>Capsella bursa-pastoris (L.) Medic.</td>
<td>3.0</td>
</tr>
<tr>
<td>Galeopsis tetrahit L.</td>
<td>0.0</td>
</tr>
<tr>
<td>Trifolium spp.</td>
<td>1.0</td>
</tr>
<tr>
<td>Vicia cracca L.</td>
<td>0.0</td>
</tr>
<tr>
<td>Sonchus arvensis L.</td>
<td>0.0</td>
</tr>
<tr>
<td>Equisetum arvense L.</td>
<td>0.5</td>
</tr>
</tbody>
</table>
advanced stage of development (see also Rioux et al. 1974). In quack grass, glyphosate is rapidly absorbed after surface-spraying, with a large portion transmitted to the rhizomes and untreated shoots; total photosynthesis is reduced more in quack grass than in wheat (Sprankle et al. 1975a). Mobility of the herbicide in the soil is very limited (Sprankle et al. 1975b).

12. Response to Other Human Manipulations
Careful and repeated tillage from the beginning of August until the ground becomes frozen often gives excellent control of quack grass (Godbout 1960). Moderate disking in a single soil operation may actually enhance quack grass growth by releasing dormant buds from apical suppression (Werner, unpublished data). The pattern of cultivation should be designed to break up the rhizomes and kill the resulting fragments by exhausting their food reserves (Muzik 1970; Cussans and Wilson 1970); deep burial will assist in the latter (Håkansson 1968). Programs involving rotation (or heavy cultivation) and herbicides have been particularly successful (Cussans and Wilson 1970; Evans 1968).

13. Responses to Parasites
(a) Insects and other non-domestic organisms — Insecta — Coleoptera: Brachyrhinus ligustici L. (Palm 1935); Melanotus spp. and Phyllophaga spp. (Metcalf et al. 1962). Diptera: Rhytaphage destructor (Say) (Fenton 1952). Homoptera: Macrosiphum granarium (Kirby) and Toxoptera graminum (Rondani) (Metcalf et al. 1962). Hymenoptera: Cephus cinctus Norton (CDA 1944). Orthoptera: Melanoplus spp. (Herman and Eslick 1939). Palmer and Sagar (1963) list five species of Nematoda and 24 species of Insecta found on A. repens in Great Britain. Of the flies (Diptera), two, Mayetiola destructor (Say) and Chlorops pumilionis (Bjerk.) are thought to be specific to quack grass; several other flies use quack grass as their chief food plant. These may prove of value in control of the grass.
(b) Microorganisms and viruses — Conners (1967) lists 30 microorganism species on quack grass, and the Canadian provinces where each is found. These include five species of Puccinia and three species of Ustilago. Palmer and Sagar (1963) list 22 species of fungi on A. repens in Great Britain. Hudson and Webster (1958) give the succession of fungi on decaying shoots of quack grass. (Caution should be practiced in assuming that a species of fungus found on both quack grass and cereal crops are the same strain; Novakova and Zacha (1975) studied in detail Tilletia controversa Kuhn on quack grass and wheat in Czechoslovakia and were unable to transmit the pathogen from quack grass to any wheat variety and finally concluded that the wild grass was not a source of infection for wheat in their area.)

Agropyron mosaic virus (also known as couch grass streak mosaic virus) is found on quack grass. This yellow-green streak mosaic, mainly seen on younger leaves, has little effect on the vigor of the plant. There is not much information on the virus from Canadian sources. The first report of its occurrence in Great Britain (Catherall and Chamberlain 1975) describes a virus that is serologically related to a Canadian isolate. It was experimentally transmitted by the mite Abacarus hystrix to wheat and by sap inoculation to 17 other species of festacoid grasses.
(c) Higher plant parasites — None recorded.

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DOYON, D. 1965. Les paturages semi-naturels à Festuca rubra sur certains sols dérivés de


NOVAKOVA, J. and ZACHA, V. 1975. Contribution to the knowledge of Tilletia contraversa Kuhn on Agropyron repens (L.) P.B.] Ceska Mykol. 29: 83–89. [In Czech.]


WILLIAMS, E. D. 1973b. Variation in growth...


