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SMUT DISEASES OF CULTIVATED PLANTS IN CANADA

By

W. J. CHEREWICK
Laboratory of Plant Pathology, Winnipeg

DEPARTMENT OF AGRICULTURE
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CONTENTS

PREFACE

The last general account of the smut diseases of cultivated plants in Canada was prepared by Güssow and Conners in 1929 (Smut diseases of cultivated plants, their cause and control). Since then knowledge of the smut fungi, particularly the species affecting cereal crops, has advanced considerably, making possible a better understanding of many problems encountered in the control of smut diseases. Investigations on physiologic specialization have led to a new concept of varietal resistance that has placed the breeding of resistant varieties on a sounder basis. Investigations on sexuality, genetics, and hybridization have thrown new light on the origin of physiologic races of smuts, the inheritance of morphological and physiological characters, frequency of mutation, and species relationships. Improvements in fungicides and treating machines have provided farmers with more effective and easier methods of seed treatment for smut control. Much of this new knowledge has appeared in technical papers that are not readily accessible to farmers, teachers, and students in Canada. The present publication is intended to provide them, as well as the general reader, with a brief account of present-day knowledge of some of the common smut fungi, the diseases caused by them, and measures for their control. In a work of such limited scope, it has not been possible to do justice to many interesting and important topics. The subject matter has been considered mainly from the viewpoint of agriculture, but sufficient information about the biology of the smuts has been included to enable the general reader to understand the processes of development, reproduction, and infection, and the principles underlying control. To students of biology, it will be apparent that, notwithstanding the advances that have been made in our knowledge of the smuts, many questions about them still remain unanswered. It is hoped that this publication may prove of sufficient interest to students to encourage some of them to undertake further research on this interesting and important group of fungi.

The author is indebted to Mr. W. Popp for permission to use some of his unpublished data; to Mr. W. Clark for taking photographs and preparing plates; and to colleagues at the Laboratory of Plant Pathology, Winnipeg, especially Dr. W. F. Hanna, for helpful suggestions in the preparation of the manuscript.

W. J. CHEREWICK,
Laboratory of Plant Pathology,
Winnipeg, Manitoba.

INTRODUCTION

Smut diseases are caused by minute organisms, known as fungi (singular, fungus). The fungi are among the simplest forms of plant life. The smuts, together with the plant rusts and mushrooms, are members of a large group of fungi known as the Basidiomycetes.

Since fungi lack chlorophyll, they cannot manufacture their own food and must depend upon other forms of plant life to provide it for them. A great number of fungi live on dead tissues of plants and animals and are known as saprophytes. Many others have developed a parasitic mode of life, requiring living tissues for their perpetuation. The smut fungi belong to the latter group. These organisms have developed to such a high state of parasitism that many species cause little, if any, outwardly perceptible disturbance in the host tissues until formation of their reproductive bodies, known as spores, takes place.

As a group, smut fungi are parasites, mainly of flowering plants. They develop in the stems, leaves, or floral organs and, in some perennial plants, they invade underground organs, such as bulbs, rhizomes, or even roots.

When in a state of active growth, the smut fungi consist of delicate vegetative threads, known as hyphae. The hyphae, collectively called mycelium (Fig. 2, A and F), penetrate the tissues of the host plant and absorb nourishment from them. After a period of development in the host tissues, the mycelium produces an abundance of spores, technically known as chlamydospores (Fig. 1). In most of the cereal smuts, spore production takes place just before the plants come into head, the spores replacing most of the normal tissues of the head. In stalk smut of rye and onion smut (Fig. 6 and 13), the spores are produced in long streaks on the leaves, whereas, in corn smut (Fig. 12), they are formed in masses of varying sizes, called smut galls, on any of the above-ground parts of the plant. The spores appear in practically all cases as a sooty mass. They are comparable to seeds of the higher plants inasmuch as they reproduce their kind. They are not, however, seeds in the true botanical sense. They are minute, roundish cells, each containing a fused or so-called diploid nucleus. Smut spores develop from the ordinary cells of mycelium without any special spore-bearing organs and, therefore, are called chlamydospores. The smuts are most easily recognized in the fruiting stage, when spores are produced in various kinds of pustules or sori. The sorus may be naked or covered (either by tissues of host origin or a membrane of fungal origin) and it may consist of spores only or contain also strands of sterile mycelium or vascular threads of host tissue.

Smut chlamydospores are one-celled and usually occur singly, but in some species they are united in groups, known as smut balls (Fig. 1, C), each composed of two to several cells. Smut balls usually contain both fertile and sterile cells, the latter being colourless or lighter coloured than the fertile cells. The spores are formed from a closely septate mycelium, which, generally, is used up completely, leaving the spores without stalks or even scars. They usually have a dark-coloured wall either smooth or variously ornamented.

In some species, the spores can germinate as soon as they become ripe, and even when they are still in the sorus. In other species, they remain dormant for varying periods of time. Mature spores in some species of cereal smuts may remain viable for several years.

Most smuts can be grown on culture media, and some species form chlamydospores in culture. Studies on sexuality, variability, mutation, and other aspects of the biology of the smut fungi are often made on culture media, where the entire process of development can be kept under observation.

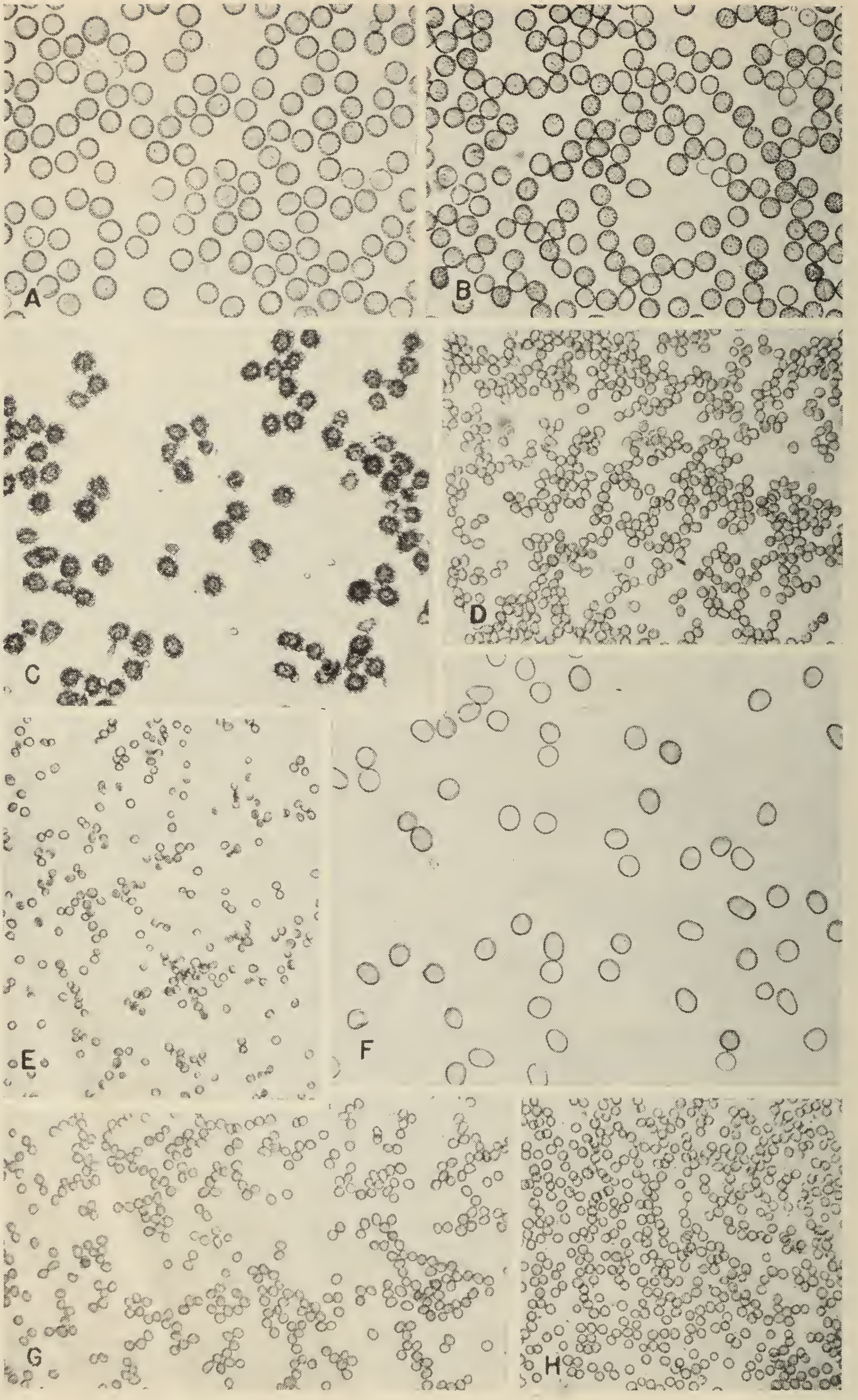

Figure 1.—Photomicrographs of smut chlamydospores. Magnifications, 484 app. A Dwarf bunt of wheat (*Tilletia caries*). B. Ordinary bunt of wheat (*T. caries*). C. Onion smut (*Urocystis cepulae*). D. Head smut of millet (*Sphacelotheca destruens*). E. Covered smut of barley (*Ustilago hordei*). F. Bunt of wheat (*Tilletia foetida*). G. Head smut of grasses (*Ustilago bullata*). H. Corn smut (*U. maydis*).

About 50 species of smut fungi are known to occur in Canada. Many of these attack plants of little or no economic importance and are of interest only to students of the fungi. At least 17 or 20 species (depending on the classification used) attack cereals, forage crops, and other cultivated plants and may cause considerable loss if proper control measures are neglected. Wheat, barley,

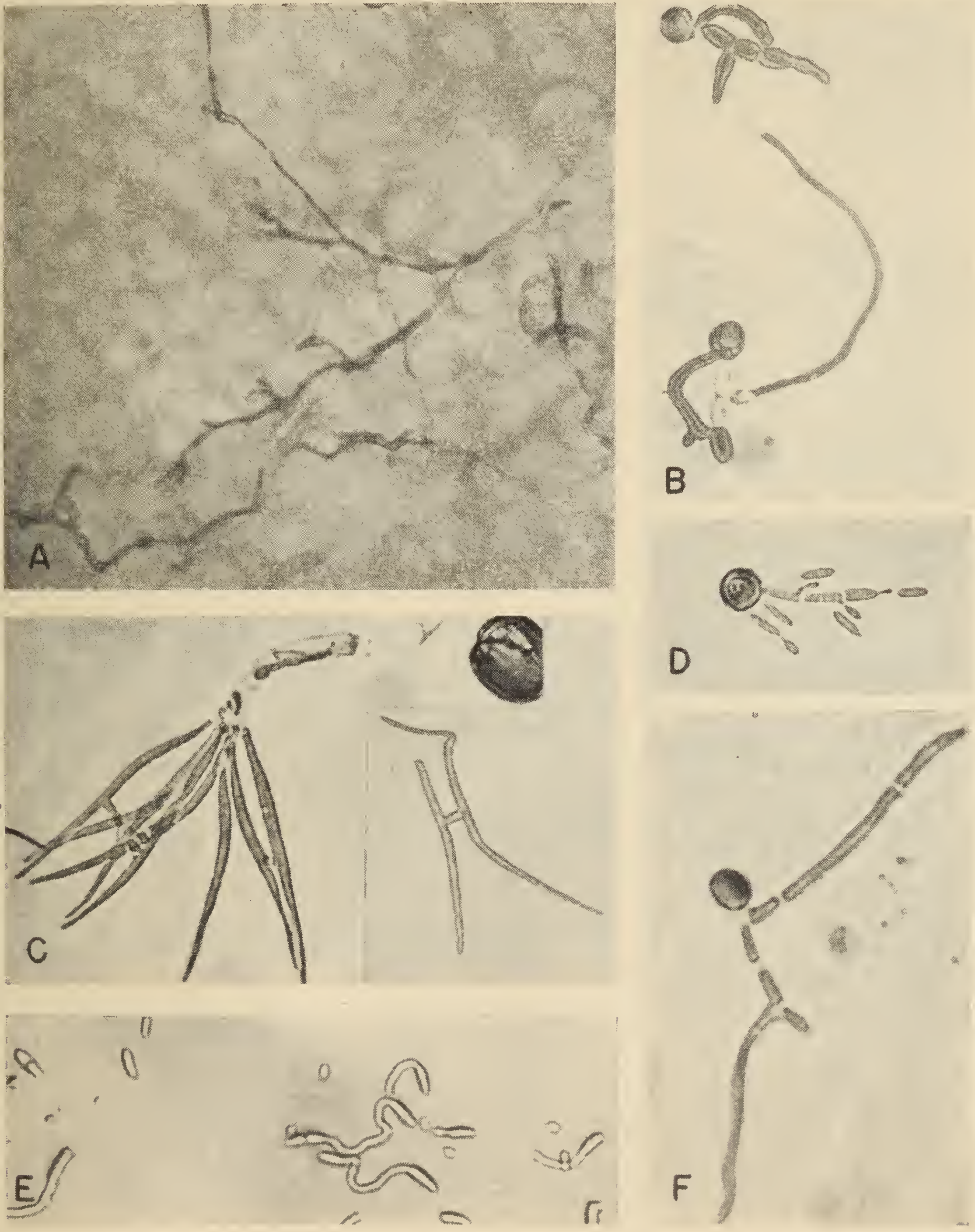

Figure 2.—A. Portion of wheat embryo permeated by loose smut mycelium. B. Germinating spores of covered smut of oats (*Ustilago kolleri*), showing fusions between promycelial cells. Fusions of this type occur commonly in this and other species of *Ustilago*. An infection hypha has grown out from the promycelium of the lower spore. C. Germinating bunt spore (*Tilletia foetida*), showing promycelium and terminal sporidia. Inset, a pair of sporidia joined together by a conjugation tube. D. Germinating spore of covered smut of oats (*Ustilago kolleri*), showing promycelium and sporidia—a type of germination common to many species of *Ustilago*. E. Fusions between compatible sporidia of oat smut (*U. kolleri*). F. Germinating spore of loose smut of barley (*U. nuda*), showing branching of the promycelium. Magnifications, A, 450; B, D, and F, 800; C, 1,300; E, 1,000. (Photomicrographs A, B, D, E, and F by Mr. W. Popp, and C, by Dr. W. F. Hanna)

oats, rye, corn, sorghum, and millet are each susceptible to one or more species of smuts which have become distributed throughout the world wherever these crops are grown. In the absence of proper control measures, they are responsible for diseases of great economic importance.

As is true with most other micro-organisms, the classification of the smut fungi has been, and still is, in a state of flux. None of the classifications so far proposed is entirely satisfactory to all those concerned with smut diseases. The most recent trend has been to define species of smut fungi according to morphological characters alone rather than on the basis of parasitism. The author has followed the groupings of Fischer and Hirschorn (34) and Ainsworth and Sampson (1), although specific names as previously used in Canada have been retained.

ECONOMIC IMPORTANCE

Smut diseases are almost coextensive with the culture of their host plants and they constitute one of the most serious hazards in the production of many crops. The smuts of wheat, barley, oats, corn, sorghums, onions, and various forage grasses are well known to Canadian farmers, since they occur in all parts of Canada where these crops are grown. Estimates of losses caused by different smut diseases have been given by many investigators (13, 20, 45, 49, 51, 56, 66). Accurate data on the extent of such losses in any country are difficult to obtain because more than one factor is involved. Besides reducing the yield of the affected crop, smut may impair its quality either for seed or for food, and at least some smuts may be more or less toxic to animals and man. Figures on smut losses are usually based on reduction in yield and do not take into account other types of injury, some of which are of considerable importance.

Although smut diseases are still prevalent and destructive, the losses caused by them at present are insignificant in comparison with the losses experienced before highly effective seed disinfectants were developed. During the early period of agricultural development in Western Canada, fields of wheat with 40 per cent or more of bunt were not uncommon (45). Similar losses occurred in other cereal crops (51). In the United States, fields of wheat with from 40 per cent to as high as 87 per cent of bunt were often found (66). In Russia (101), losses from bunt up to 55 per cent in some fields of wheat were reported in 1927. In fact, in some of the world's best wheat areas, bunt was the main limiting factor in production.

With the development of successful seed treatment methods, bunt has practically disappeared from the better-farmed districts in Canada, remaining only as an indication of careless farming practices. Smut losses in barley and oats in Canada are still heavy. However, with a better understanding among farmers of the necessity for proper seed treatment of all cereal seed, losses in these crops could be reduced to a negligible figure.

In cereal crops, particularly wheat, two distinct factors are involved in the losses caused by smut. In the first place, there is an actual reduction in yield as a result of the development of smutted instead of normal heads, and in the second, there is a reduction through the weakening of plants that are infected, even though they do not produce smutted heads (55, 101). The loss may range from a trace to the greater part of the crop, depending on the percentage of smutted heads and infected plants. An additional loss is sustained in marketing smutted grain. Dockage, or discount charged on smutted grain, at elevators amounts to a considerable item if smut is present in appreciable quantities. The lower price paid for "smutty" wheat is made necessary by the fact that such wheat must be thoroughly washed before milling, otherwise the flour will be tinted grey by the bunt spores and is likely to have the musty odour characteristic of bunted wheat.

The approximate loss from smut in fields of oats and barley is not difficult to estimate. The percentage of smut may be determined by counting the number of smutted and healthy plants in a given area in several different places chosen at random. From the average percentage of smut thus obtained, the loss in bushels or dollars may be roughly estimated by calculating what the yield of the crop would have been if smut had not been present. For example, an examination of several fields chosen at random in each district of the province of Manitoba in 1948 (13) revealed that there was an average of 5·8 per cent smut in barley and 1·1 per cent smut in oats. The total production of these two cereal grains in Manitoba was approximately 45 and 60 million bushels respectively. The loss resulting from smut would be, therefore, approximately 667,340 bushels of oats and 2,770,700 bushels of barley or, at the average prices prevailing during the winter of 1948-49, a total loss of over $3,500,000. The above figures do not represent, however, the entire loss caused by smut diseases in these two cereals. It has been shown that smut-infected plants are more susceptible to seedling blights and other diseases (55, 128, 135, 157). Also, infected plants are adversely affected even when they produce no smutted heads (101). In experiments at Winnipeg and Lethbridge on physiologic specialization in the cereal smuts, it has been frequently observed that in some varieties of grain certain races of smuts cause an appreciable reduction in the number of seedlings and mature plants. Plants of such varieties may be killed at various stages of their development. Therefore, the actual reduction in yield would be greater than is shown by the percentage of smutted heads or plants, particularly in fields where smut is more abundant.

Because surveys of wheat smuts in Canada in recent years have not been extensive, the present losses from smut in the wheat crop are not well known. Bunt of wheat is probably less prevalent in Manitoba since the introduction of bunt-resistant varieties of common wheat, such as Regent and Redman. In other provinces, where more susceptible varieties of wheat predominate, no appreciable change in the prevalence of bunt is evident. On the other hand, loose smut of wheat has probably increased slightly in Manitoba because Regent and Redman are less resistant than Thatcher, and because the durum wheat varieties Carleton and Stewart are susceptible to this disease. The licensing and rapid increase in Canada of Lee wheat, which is highly susceptible to loose smut, may be expected to bring about a further increase in the prevalence of this disease. If the prevalence of surface-borne smut spores on seed samples (Table 1) and the number of carloads of wheat from Western Canada grading smutty (Table 2) are reliable indications of the general prevalence of smut in wheat, then the estimate of the average annual loss in yield because of smut, as given by Craigie (20) for Manitoba, would probably be applicable to the whole of Canada. His estimate for the years 1916 to 1937 was $\frac{3}{4}$ per cent (loose smut $\frac{1}{2}$ per cent and bunt $\frac{1}{4}$ per cent). Based on a total production of wheat in Manitoba for 1948, of 57 million bushels, a loss of $\frac{3}{4}$ per cent would amount to over 430,000 bushels, or in the neighbourhood of $646,000. As the corresponding loss for oats and barley in Manitoba in 1948 has already been estimated at $3,500,000, it will be seen that the combined loss for wheat, oats, and barley in the province that year resulting from reduction in yield by smut was in excess of four million dollars.

The estimated loss in yield caused by smuts of the three cereal grains in Manitoba is applicable, in the main, to other provinces of Canada. A survey made in 1949 in the three Prairie Provinces revealed that the prevalence of coarse grain smuts was approximately the same in the parkland areas of Manitoba and Saskatchewan and decreased only slightly in Alberta. Bunt of wheat, on the other hand, was much more prevalent in southwestern Alberta than in the other two provinces, so the total percentage loss from smut in cereal grains may be considered to be approximately the same in each of the three provinces. In British Columbia and the eastern provinces of Canada, smut is known to cause similar, if not greater, losses in cereals.

TABLE 1.—OCCURRENCE OF SURFACE-BORNE SMUT SPORES IN SAMPLES OF WHEAT, OATS AND BARLEY SEED FROM MANITOBA, SASKATCHEWAN, AND ALBERTA[1]

Year seed produced	Wheat		Oats		Barley	
	Samples examined	% bearing smut spores	Samples examined	% bearing smut spores	Samples examined	% bearing smut spores
1945	6,069	51·2	1,600	90·3	1,602	95·1
1946	8,267	71·3	2,978	89·3	1,043	96·4
1947	9,173	66·8	2,800	88·3	687	94·2
1948	7,442	60·6	2,405	85·9	1,369	92·4
1949	9,570	44·6	2,936	81·1	1,679	88·9
1950	11,993	45·6	5,331	73·5	3,149	89·2
1951	2,730	47·9	1,106	84·4	1,124	95·1

[1] Results of tests on farmers' seed samples made by the Line Elevators Farm Service, Winnipeg, Man. Data supplied by Dr. F. J. Greaney, Director.

TABLE 2.—TOTAL SHIPMENTS OF WHEAT, AND SHIPMENTS OF SMUTTY WHEAT, FROM POINTS IN WESTERN CANADA IN THE PERIOD 1938–1951[1]

Crop year	Hard Red Spring		Durum		Alberta Winter		Other Classes		Mean % smutty
	Total cars	Smutty cars	Total cars	Smutty cars	Total cars	Smutty cars	Total cars	Smutty cars	
1938	154,563	317	11,127	46	412	86	14,394	16	0·26
1939	214,007	387	5,980	62	271	28	8,710	15	0·22
1940	166,040	443	4,407	35	278	16	3,958	5	0·29
1941	176,391	176	1,447	5	386	8	814	4	0·11
1942	97,000	206	2,409	12	487	35	129	3	0·26
1943	227,988	526	3,059	62	336	4	429	5	0·26
1944	238,427	713	4,638	98	270	2	2,886	6	0·33
1945	164,405	418	2,589	77	1,106	19	2,249	3	0·30
1946	178,890	541	4,807	198	1,831	96	3,434	8	0·45
1947	131,838	418	5,862	90	981	28	2,899	1	0·38
1948	152,428	194	9,002	18	1,769	83	3,509	4	0·18
1949	167,959	286	6,513	54	1,113	50	3,970	3	0·22
1950	172,161	277	9,418	16	710	34	2,656	2	0·18
1951	239,964	101	6,993	10	373	9	1,782	0	0·05
1930	Highest number of cars grading smutty since 1915 (3,779 cars)								1·81
Mean	1915–1951 inclusive								0·46

[1] Information obtained from the Inspection Branch, Board of Grain Commissioners, Winnipeg, Man.

From 1915 to 1951 inclusive, a period for which records are available, a total of 32,386 carloads of wheat from Western Canada graded smutty. This represents an average of 875·3 carloads, or approximately 1,313,000 bushels of wheat, grading smutty each year. The discount on "smutty" wheat varied from year to year and for different grades of wheat, but an average would probably be somewhere between 8 and 10 cents per bushel. In addition, therefore, to the loss in yield already mentioned, a further loss is incurred through the discount on smutty wheat, which, during the past 35 years, would amount to approximately $120,000 annually for Western Canada.

Losses attributable to impairment of the health and vigour of animals that have consumed grain or fodder contaminated with smut spores are more difficult to appraise. Many controversial statements are to be found in the literature on toxicity or nontoxicity to animals of smut-contaminated feeds. Experiments made in Kansas (96) proved that corn and sorghum smuts were in no way dangerous or poisonous to horses, cows, and calves. The only disturbance noted was coughing and sneezing at times because of the dusty nature of the spores. Other investigators (70) similarly found that food contaminated with smut spores was not toxic to any of the ordinary farm animals, although such food could not be declared harmless under all circumstances. On the other hand, in Montana, according to Güssow and Conners (45), "a lot of cows were fed on smutty hay, and within 12 hours after the first feed, one-half of them died with symptoms of gastritis and cerebral excitement. No more of the hay was fed, and no more deaths resulted." Experiments in France (23) demonstrated that spores of loose smut of wheat were toxic to young mice. Feeding mice on groats mixed with 4 or 8 per cent spores, or injecting them subcutaneously with an aqueous spore extract caused hyperaemia accompanied in most cases by posterior paralysis and, in some, by intense pruritus. Adult mice were not adversely affected by ingestion of smutted groats.

Mayerhofer and Dragisic (91) investigated corn smut poisoning in children at the Zagreb University Children's Hospital and concluded that such poisoning (ustilaginism) is closely allied to true infantile acrodynia, from which it differs mainly in its etiology. Head smut of sorghum, *Sphacelotheca reiliana* (Kuhn) Clint., may also be implicated to some extent in smut poisoning in children. On the other hand, according to Zillig (165), *Ustilago esculenta* P. Henn. developing in the inflorescence of *Zizania latifolia* Turcz., changes it to cauliflowerlike galls, which are relished as a vegetable in China and Japan. In other words, at least one smut is used as human food.

There is no doubt, however, that some smuts may contain alkaloids more or less toxic to animals, and that most kinds of smut spores, when present in abundance, make food unwholesome, particularly to very young animals and to pregnant females.

THE FUNGI CAUSING SMUT DISEASES

The smut fungi are not confined to cereals and other members of the grass family. They attack a large number of plant species belonging to widely different families. In Canada, smuts attack onions, arrow-head, wild tomato, aster, gum weed, and numerous other broad-leaved plants, as well as the cereals and many sedges and grasses. Some smuts attacking perennial plants give rise to systemic infections and hibernate in the vegetative state in the overwintering parts of the plant. The mycelium spreads each year into the growing shoots to produce spores in the appropriate part of the host. A majority of the smuts, however, are annual and, when their spores ripen, the vegetative life of the fungus comes to an end. Reproduction then depends upon the spores eventually reaching an environment favourable for their development into a new generation. In this connection, account must be taken of the production of the smut spores and the time of their dispersal, as well as the manner in which they infect their host. For convenience, the smuts under consideration will be grouped into three main classes: seedling-infecting, flower-infecting, and local-infecting.

Seedling-infecting smuts.—Bunt of wheat, the oat smuts, covered and false loose smut of barley, and a number of other smuts belong to this group. These smuts infect their host plants by means of spores that are present on the surface of the seed, or in the soil in close contact with the seed. Spores of loose smut of oats sometimes become lodged under the hull of the seed and, if conditions are favourable, they germinate there, producing hyphae that later infect the young seedling. In all instances, the seedling-infecting smuts gain entrance to the host plant by penetrating the coleoptile of the very young seedling.

When a spore of this group of smuts germinates, it usually produces a club-shaped germ tube, known as a promycelium, on which secondary spores, called sporidia, develop (Fig. 2, B and D). The sporidia are usually of two opposite sexual groups. When two sporidia of opposite sex come in close proximity with one another, they become united by a fusion hypha and from it an infection hypha develops. It is the infection hypha that penetrates the seedling coleoptile, thereby enabling the smut mycelium to become established in the underlying tissues of the host plant. Thus, regardless of how the inoculum is carried, whether on the seed or in the soil, actual infection, under natural conditions, takes place in the early seedling stage. Once infection is initiated, the fungus advances internally through the tissues of the seedling until, in a susceptible variety, it reaches the growing point. From then on it keeps pace with the development of the host plant. When the plant develops to a certain stage of growth, spore formation of the smut fungus is initiated either in the leaves and stems, as in the stalk smut of rye, or in the head, as in the grain smuts of wheat, barley, and oats. The spore masses in most cases are then blown away by wind or scattered by rain droplets and other agencies and thus contaminate the soil and the seed of healthy plants. The greatest dispersion of spores, however, takes place during harvesting operations. Smut spores on the seed may remain viable until the seed is sown and begins to sprout, when the same series of events is repeated. Smut spores present in the soil may be an important source of infection of fall-sown grain, particularly wheat. In northern regions, however, the spores do not usually survive the low temperatures of winter and so are of little consequence in the infection of spring-sown grain.

The seedling-infecting smuts may be controlled by ordinary seed treatments with fungicides that disinfect the surface of the seed and to some extent protect the germinating seed in the soil after planting. The use of resistant varieties, when available, in conjunction with proper seed treatment greatly facilitates the control of this group of smuts.

Flower-infecting smuts.—The loose smut of wheat and of barley are the only smuts of cultivated plants that will be considered in this group. The smutted heads emerge a little earlier than the healthy heads, and spores from them are disseminated during the blooming period of the healthy plants. When a spore alights on a stigma of the host floret in the proper stage of development, it promptly germinates, forcing its infection hypha through the style into the ovary. On reaching the ovary, the fungus produces a small mat of mycelium in the young embryo (Fig. 2, A) with so little interference to the tissues of the ovary that it develops into an outwardly normal-appearing kernel. When the infection process is complete, the fungus becomes dormant and remains so until the seed begins to germinate. Then the mycelium of the fungus becomes active again and in its growth keeps pace with the growing point of the plant until the head is formed. The mycelium usually destroys all the tissues of the inflorescence and, just before the emergence of the head, replaces them by masses of spores enclosed in a delicate greyish membrane. The membrane ruptures soon after emergence of the head, releasing powdery masses of spores. In a few days the spores are blown or washed away, leaving a bare rachis instead of a normal wheat or barley head.

Since loose smut is carried within the embryo of the seed, it cannot be controlled by ordinary seed disinfectants. Apart from the growing of resistant varieties, the only practical method of control has been to treat the seed with hot water. This method has not been widely used, as most farmers do not possess the equipment needed to control accurately the temperature of the hot water bath. Recently (152) it has been found that loose smut of barley may be controlled by soaking the seed in a chloranil (Spergon) solution. If this treatment proves to be generally satisfactory, it should facilitate the control of this smut.

Local-infecting smuts.—Corn smut (Fig. 12) is the only representative of this group of smuts that is known to occur on cultivated plants in Canada. The chlamydospores overwinter in the soil. During early summer they germinate producing secondary spores, the sporidia, which are picked up by air currents and may eventually be blown to young corn plants, causing local infections. The infections may be on any above-ground part of the plant, for instance, the ear, tassel, node, or leaf. After the fungus permeates the plant tissues surrounding the point of infection, a smut gall develops which, at maturity, consists mostly of masses of smut spores.

The only satisfactory way of controlling corn smut is to grow resistant varieties. Crop rotation, destruction of smut galls before they mature, and general cleanliness will help to reduce losses from this smut.

Dissemination of Smut Spores

In general, the smut fungi are disseminated as chlamydospores which, owing to their minute size and buoyancy, are readily carried about by air currents. Heald and George (59) found that a spore-trap, located a mile and a half from the nearest threshing machine in the state of Washington, collected over 10,000 spores per square inch during one week. Examinations of spore-traps exposed at places in Manitoba[1] indicated the presence of smut spores in the air before any of the local crops were in head. The latter observations prove the long-distance dissemination of smut spores by wind.

Although wind is an important agent in the dissemination of smut spores, it is not the only one. Threshing machines, granaries, seed bags, and seed-handling equipment are all important agencies in carrying smut spores from contaminated to clean seed. Rain is a contributing factor in the dissemination of the smuts, inasmuch as it washes down air-borne spores, which may eventually become lodged on the seed of the host plant. It also splashes the spores from smutted to healthy heads in the field. However, as is true of many other plant diseases, man himself is the worst offender in disseminating the smut fungi. He transports smutted seed from district to district, from country to country, and from continent to continent, thus enabling the pathogens of smut diseases to become established wherever their host plants are cultivated.

Longevity of Smut Spores

A few decades ago, before currently known control methods were developed, the longevity of smut spores was a subject of great practical interest to students of smut diseases. The storing of seed grain for a number of years was considered as a possible means of controlling smut until it was demonstrated (160) that chlamydospores, particularly those of the seedling-infecting smuts, might retain their viability for as long as twelve years. It then became apparent that the germinative power of the seed would be greatly impaired before the infective power of the spores was lost. Smut spores present in the soil or in plant debris left in the field, and even manure from animals fed on smutted grain, were considered as probable agents in the dissemination of smut diseases.

Experiments made at Winnipeg (52) proved that bunt spores, particularly those in intact bunt balls in wheat heads left on the surface of the soil, may overwinter in Western Canada. Nevertheless, general experience seems to indicate that in Western Canada smut spores overwintering in the field are of little or no consequence in initiating infection in spring-sown grain crops. Many of the sopres that remain in the field after fall threshing is completed may germinate before the ground freezes. Those that fail to germinate in the fall

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[1] Unpublished data by B. Peturson, Laboratory of Plant Pathology, Winnipeg.

are subjected, during the winter and early spring, to drying, wetting, freezing and thawing, and their viability is greatly reduced. The effectiveness of seed treatment in controlling smut in cereal grains lends support to the view that soil-borne smut inoculum is not an important source of infection in Canada except in winter wheat areas, such as southern Alberta, where the soil remains relatively dry between threshing time and the seeding of another winter wheat crop, and certain parts of British Columbia where dwarf bunt of wheat has been found[1]. The relatively high percentage of carloads of Alberta Red Winter wheat grading smutty (Table 2) seems to indicate that soil borne inoculum is possibly an important factor in southern Alberta.

The viability of smut spores passing through the digestive system of an animal has been shown (70) to be very low. Only spores passing through pigs apparently retained their viability to some degree, while those passing through other farm animals were almost entirely killed. Similarly, spores of corn smut lost their viability after having been left in silage for a few weeks (107). It is doubtful, therefore, if smut can be effectively disseminated through barnyard manure spread in the field.

From a scientific point of view, it is of great interest that smut spores may retain their viability for a rather long period of time. Out of 77 species of smut fungi from herbarium specimens tested by Fischer (32), 24, ranging in age from a few years to as many as 25, contained viable spores. In general, smut species of the family *Tilletiaceae*, to which bunt of wheat belongs, showed the greatest longevity. One species of bunt contained viable spores after storage in a herbarium for 25 years. Covered smut of barley (*Ustilago hordei*) contained viable spores after 23 years of storage.

The spores of the flower-infecting smuts (*Ustilago tritici* and *U. nuda*) do not retain their viability nearly so long as those of other smuts. In nature, they are carried by air currents to the florets of their host plants and there germinate and cause infection. Since infection can take place only during the brief period of a week or two while the host plants are in flower, prolonged viability is of no particular advantage to the spores of flower-infecting smuts. However, it has been found that spores of these smuts, when stored in a cool, dry place, may retain their viability for several years (144). The mycelium within the embryo of the seed may remain viable for a much longer period (144), probably as long as the seed itself.

Factors Influencing Smut Infection

Smut fungi, like all other plants, are influenced profoundly in their development by environmental conditions. Especially is this noticeable in the smuts carried over from season to season in the chlamydospore stage. It has been well established that, at least among the cereal smuts, environmental influences may be operative, not only at the time of infection, but also throughout the entire growing season, and the period of harvesting and storage of the seed grain. In other words, smut disease is a result of the interaction of host and pathogen under the conditioning influence of environment. Factors, such as temperature, moisture, aeration, soil type and compactness, and soil fertility and reaction, play an important part in the development of smut diseases. The influence of some of these factors is discussed briefly in the following paragraphs.

Temperature.—The effect of date of seeding on the development of smut was observed several decades ago (19, 150). Elucidation of the factors involved, however, took a relatively long time (14, 28, 30, 31, 61, 72, 85, 93, 101, 115, 116, 139). In general, smut fungi are adapted to the cultural conditions best suited

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[1] Specimens of dwarf bunt were collected by W. R. Foster, Provincial Plant Pathologist, Victoria, B.C.

to their particular hosts. Wheat, for example, is usually sown in Canada rather early in the spring, when soil temperatures are still relatively low. Seeding of oats and barley takes place later, when the soil is warmer. The optimum temperature for infection by the bunt organism is 10°—15° C., as compared with 20°—25° C. for the seedling-infecting smuts of oats and of barley. Temperatures conducive to a very rapid growth of infected seedlings after emergence may result in the plants outgrowing the parasite and producing normal seed (101), whereas temperatures or other factors adverse to a rapid development of seedlings during the pre-emergence period usually increase the incidence of smut (101, 139).

With respect to the flower-infecting smuts (*Ustilago tritici* and *U. nuda*), the greatest influence exerted by temperature is during the blooming period of the host, when infection is taking place. Cool weather prolongs the flowering period and, therefore, favours the entrance of spores into the flowers, whereas, in a moist warm atmosphere and dry soil, flowering proceeds rapidly while the head is still in the boot, thus minimizing the chances of flower inoculation (148).

Moisture.—The fact that the loose smuts usually are relatively uncommon in regions where the air humidity is low during the flowering period of their host plants has long been recognized. Wheat and barley varieties grown under the dry atmospheric conditions of California rarely develop loose smut, but, when grown under more humid conditions, the same varieties may prove to be extremely susceptible (136). Rain followed by sunshine usually causes the heads of wheat and barley to emerge before the florets open and later, when the heads come into flower, the glumes spread widely, thus favouring the chances of flower inoculation. Under humid conditions, smut spores on the stigmas of the host germinate and develop infection hyphae much faster than under arid conditions.

Soil moisture does not seem to have a very pronounced direct effect on the seedling-infecting smuts, but, as air is required for the germination of smut spores (83, 160), soils that are poorly aerated, due to an excess of moisture, provide an unfavourable environment for high infection. The soil moisture content required for optimum infection varies with the temperature and other factors but, generally, a moisture content equivalent to 20—40 per cent of the moisture-holding capacity of the soil is conducive to good infection (14, 28, 30, 31, 61, 71, 85, 93, 115, 116). Apparently smut spores can germinate with less moisture than is required for quick germination of cereal seed (27). Relatively dry soil, therefore, like any other factor that may retard the pre-emergence development of host seedlings, is favourable for smut infection. Similarly, in the case of the local-infecting smut of corn, it has been observed that this disease is most prevalent during relatively dry seasons (72). This may be partly because the inoculum of corn smut is disseminated more readily in dry weather.

It has long been known that seed of oats and barley artificially smutted with the seedling-infecting smuts does not yield consistently as high percentages of smutted plants as naturally inoculated seed. The reason for this became obvious when it was discovered (37, 141, 163) that naturally inoculated seed contains smut spores and mycelium underneath the seed-hulls. The amount of inoculum is thus substantially increased at, or very close to, the vital point of attack. As a result of this discovery, the importance of weather conditions following pollination and during the maturation period of the crop became obvious. Moisture and temperature conditions prevailing during this period are especially important in relation to the germination of spores underneath the seed-hulls, and thereby influence indirectly the amount of smut in the succeeding crop.

Soil reaction.—Factors such as soil type, compactness, and fertility, probably influence smut infection indirectly, by either favouring or hindering a rapid development of the host seedlings and by affecting aeration and other soil-environmental factors. Soil reaction, however, may have a direct effect upon smut development. Gassner (39) showed that the highest percentage of wheat bunt occurred in sandy soils, while in acid moorland and clay soils little or no smut developed. On the other hand, Leukel (83) obtained more smut in clay than in sandy soils. Application of lime to acid sandy soil increased smut infection, indicating that acid soil is unfavourable for infection. Other experiments (85, 99) indicate that, at least for certain smuts, neutral or slightly acid soil is the most favourable for good infection.

The above remarks on the effects of environmental factors on the development of smut diseases are sufficient to indicate the close adaptation of the smut fungi to the conditions under which their specific hosts thrive. For a more complete discussion of the effects of various environmental factors on the development of the cereal smuts, an excellent summary by Tapke (143) is suggested.

Reproduction of Smut Fungi

It has already been indicated in the foregoing paragraphs that the smut fungi are well adapted to their particular hosts in their response to environmental factors, the dissemination and longevity of their spores, and the timing of their fructifications. The production of large numbers of chlamydospores by all species of smut fungi ensures, not only their survival, but also their rapid and widespread dissemination. Chlamydospore formation is of further importance in the life cycle of the smuts in that it is at that time that sexual reproduction takes place, and this provides an opportunity for hybridization and the recombination of various characters, including pathogenicity. The smut fungi do not possess sexual organs of any kind, so the sexual process involves merely the association and eventual fusion of pairs of nuclei. The chlamydospores, or sexual form of reproduction, is distinct from asexual or vegetative reproduction, which is characterized by the sporidia. These can be grown on culture media in the laboratory very much like the yeasts.

Sexual reproduction.—In the species of smut fungi that have been investigated, the very young chlamydospore has been found to contain two nuclei. With the maturation of the spore these nuclei fuse, and it is generally accepted that the mature spore contains a single diploid nucleus. A meiotic, or reduction, division occurs in the germinating spore or in the promycelium and each sporidium or hyphal branch arising from the promycelium receives a single haploid nucleus. When compatible sporidia or hyphal branches fuse, the haploid nuclei present in them become associated in pairs and from the fused cells binucleate (technically known as dikaryotic) infection hyphae arise.

Immediately after infection takes place the smut mycelium grows both inter- and intra-cellularly but, as its development progresses, more and more mycelium becomes intercellular, deriving its nourishment from the host cells by short hyphal branches (1). Just before fructification the mycelium branches profusely, producing variously curved, curled, or branched hyphae which force the host cells apart and form a smut sorus. The individual cells of the mycelial mat in the sorus eventually separate, develop thicker walls, and turn into spores. In some species, practically all the hyphal cells in the sorus develop into chlamydospores, whereas, in others, some cells lose their dikaryophase and become either sterile accessory cells, as in the spore-balls of *Urocystis* spp., or form a membrane around the sorus, as in *Sphacelotheca* spp.

Unlike the cereal rusts, which can continue indefinitely their vegetative reproduction (in the uredial stage), the smut fungi reproduce sexually in every chlamydospore generation. A physiologic race of rust remains unchanged through successive generations of the uredial stage, unless a mutation occurs, even though it is not in a homozygous or true-breeding condition. On the other hand, a physiologic race of smut, unless it is homozygous, may be expected to undergo segregation during the sexual process that accompanies the formation of chlamydospores in each generation, and so give rise to new races. From the viewpoint, of pathogenicity, therefore, an important distinction must be made between races of these two groups of fungi, the rusts and the smuts. Nevertheless, by continuous selection and purification a physiologic race of smut can be reduced to a pure-breeding condition with respect to pathogenicity.

Vegetative reproduction.—On artificial media, the smut fungi may be cultured as monosporidial, or haploid, lines that will continue to reproduce without genetic change except through mutation. Monosporidial cultures are regularly employed in studies on the genetics and hybridization of the smut fungi and sometimes in the isolation of physiologic races. Since monosporidial lines reproduce readily on artificial media it is possible that they reproduce also in nature. Sporidia of corn smut, for instance, have been observed to germinate and multiply in soil and in moisture that collects in leaf axils (75, 110).

The best known example, however, of the vegetative reproduction of smut fungi in nature is provided by onion smut, *Urocystis cepulae*. Anderson (3) found that spores of this organism may germinate in the soil and develop a considerable amount of mycelium that can, under favourable conditions, maintain its viability for many years. This mycelium may break into small pieces that persist in a dormant state for some time, and then start to grow again when favourable conditions return. Vegetative reproduction may continue in this manner for a number of years in the absence of the host.

Physiologic Specialization

According to Reed (112), physiologic specialization in plant pathogenic fungi was considered as early as 1879, but it was not until 1894, when Eriksson, a distinguished rust investigator, published the results of his experiments, that the existence of this phenomenon was established beyond doubt. His discovery marked one of the most important advances in the study of plant disease fungi. Kniep (76), in 1919, was the first to suggest the occurrence of physiologic races in the smut fungi. He noticed differences in the appearance of sporidial cultures of the anther smut of violet (*Ustilago violacea* Pers.). Not long afterwards, it was demonstrated (164) that physiologic races of this smut could be differentiated on the basis of their ability to infect certain members of the Caryophyllaceae and not others. In other words, collections of the same smut fungus, although appearing alike morphologically, differed in their parasitic behavior.

In his studies on the effects of environmental factors on the infection of barley varieties by covered smut (*Ustilago hordei*), Faris (28) subjected, in the greenhouse and in the field, a group of varieties to three different collections of the smut and found distinct differences in their pathogenicity. Furthermore, when Hannchen barley was inoculated with spores from smutted heads of that variety, 72 per cent infection was obtained, but, when Hannchen was inoculated with spores from hooded barley, collected in the same district, infection was only one per cent. Faris concluded that differences in the pathogenicity of different collections of smut could be explained only on the basis of "specialized races" of the fungus. In his pioneer work on physiologic specialization in the cereal smuts, he isolated five races of *U. hordei*.

Reed (113) studied two collections each of the loose and covered smuts of oats (*Ustilago avenae* and *U. kolleri*) and found two distinct races in each of them. The classical investigations of Faris (28, 29) and Reed (113) were soon followed by similar studies on other smuts of agricultural crops (17, 22, 67, 98, 106, 121, 145, 162) and physiologic races were found in all the species studied. The number of known races in each of the most important smut fungi is increasing rapidly. For example, in the United States, there have been described 31 races of the smooth and the rough-spored bunt fungi (*Tilletia foetida* and *T. caries*) (120), 22 races of the loose and covered smuts of oats (*Ustilago avenae* and *U. kolleri*) (69), 11 races of loose smut of wheat (*U. tritici*) in the eastern soft wheat region (8) and 11 races in the hard red spring wheat region (100), 13 races of covered smut of barley (*U. hordei*) (142), and 13 races of false loose smut of barley (*U. nigra*) (145).

In Canada, studies on physiologic specialization in the cereal smuts at the Laboratories of Plant Pathology, Winnipeg and Lethbridge (12), indicate the presence of at least 13 races of covered smut of barley (*Ustilago hordei*), 12 races of false loose smut of barley (*U. nigra*), 10 races each of the loose smuts of wheat and barley (*U. tritici* and *U. nuda*), 5 races of covered smut of oats (*U. kolleri*), 14 races of loose smut of oats (*U. avenae*), and 15 races of smooth and rough-spored bunt of wheat (*T. foetida* and *T. caries*).

Other investigations on physiologic specialization in the smut fungi have been reported in different countries and the total number of races identified is, no doubt, much higher than that found for the United States and Canada. However, since different investigators have not used the same varieties of host crops to differentiate races, a comparison of their results is not yet possible.

Hybridization and Genetics

In attempting to produce smut-resistant varieties of agricultural crops, the plant breeder is at once confronted with the question of the stability of the parasite. The fact that the smut fungi are composed of numerous physiologic races in itself greatly complicates the breeding problem. The stability of these races, their origin, and the possibility of new ones arising that may be able to attack varieties resistant to existing races, are all matters of great interest and importance.

The increasing amount of smut in previously resistant varieties (62), emphasizes the necessity of obtaining fundamental information concerning, not only the prevalence and distribution of physiologic races, but also the possibility of new races arising by hybridization both within and between species of smut fungi.

Although fusion of sporidia in certain smuts had been observed by earlier investigators, Kniep (76), in 1919, was the first to show that fusion occurs only between certain pairs of sporidia. This discovery led him to conclude that the smut with which he was experimenting (*Ustilago violacea*) must consist of two sexual strains or, in other words, that it was heterothallic. Zillig (164) confirmed the work of Kniep and also showed that conjugation occurred between sexually opposite strains of different physiologic races. In his further work, Kniep (77) observed conjugation between sporidia of a number of smooth-spored species of *Ustilago*, between some echinulate-spored species, and also between some of the reticulate-spored species. He obtained conjugation between certain smooth-spored and echinulate-spored species, but no conjugations were observed between sporidia of reticulate-spored species and those of either smooth- or echinulate-spored species. Dickinson (24) observed hyphal fusion on the host tissue between monosporidial cultures of *U. hordei* and *U. nuda*, but he did not grow his plants to maturity to determine the outcome of such fusions. These investigations proved beyond doubt that interspecific fusions are common in the smut fungi, but none of them showed that interspecific crosses were able to cause infection of the host plant.

Hanna and Popp (50) found that *Ustilago avenae* and *U. kolleri* are heterothallic and that the sporidia of each species consist of two sex groups. Monosporidial cultures mated readily with those of opposite sex of the same or the other species, and plants inoculated with interspecific hybrids produced smutted panicles intermediate in appearance between the loose and covered types. The hybrid chlamydospores were echinulate. In later investigations (109), proof of dominance of the factor for echinulate spore over that for smooth spore was obtained by back-crossing the F_1 hybrid with both of the parent cultures.

In his studies on hybridization between *Tilletia* species, Flor (35) obtained infection of wheat plants by hybrids of *T. caries* and *T. foetida*. Similar studies have been made of *Sphacelotheca sorghi* and *S. reiliana* (151), and of *Ustilago hordei* and *U. nigra* (2), and in each case the host plants became infected with the smut hybrids. Crosses between *U. hordei* or *U. nigra* and *U. avenae, U. kolleri,* and *U. tritici* led to hyphal fusions and the initiation of infection hyphae but plant infections failed (2).

The investigations summarized in the foregoing paragraphs show clearly that new races of the smut fungi may originate through hybridization, both between existing races of a single species and between closely related species. Field observations indicate that new races appear frequently in nature, and it is probable that many of them are of hybrid origin. It is well known, for instance, that when varieties of wheat having resistance to the prevailing races of bunt are grown, new races virulent to them tend to appear (64). Similarly, the occurrence in the field of smutted oat panicles, intermediate in appearance between the typical loose and covered smuts (109) may be attributed to inter-specific hybridization. On the other hand, there is evidence (2, 158) that, under natural conditions, certain of the sporidia-forming smut fungi initiate the binucleate or parasitic phase through fusion of adjacent promycelial cells (Fig. 2, B). Such a process would tend to reduce the opportunities for new races to arise through hybridization.

A further complication with respect to hybridization and physiologic specialization in the smut fungi arose when it was discovered that there may be more than two mating groups in some species. Hanna (46), studying the corn and sorghum smuts *Ustilago maydis* and *Sphacelotheca reiliana,* found that in each of these species some chlamydospores produced sporidia belonging to four mating groups. Flor (35) concluded that there are four or more such groups in *Tillitia* spp., but later Holton (65), studying a large number of monosporidial cultures of *Tilletia* spp., was able to find only two mating groups. The total number of factors governing the mating of haploid cultures has not as yet been determined with certainty for any smut species. As a wider range of material is studied, additional factors are likely to be found. For the present, however, it may be concluded that by far the most common condition in any one species is two mating groups.

For a more complete summary of literature on the cytology and genetics of smut fungi "The British Smut Fungi" by Ainsworth and Sampson (1) is recommended.

Control Methods

Smut diseases may be controlled by seed treatment, the growing of resistant varieties and, in some instances, by crop rotation. In general, good farm practices contribute to smut control. Seed grain should be of high quality and well cleaned, as cleaning removes smut balls, debris, and considerable numbers of smut spores. With the aid of seed treatment, it is relatively easy to control smut in partially resistant varieties, but susceptible varieties require careful and regular treatment to keep down smut losses.

Seed treatments.—Seed treatment for the control of smut, particularly bunt, has been practised for the last three centuries. Before the true nature of smut diseases was known many farmers conceived various methods of treatment on the theory that certain stimulants were needed to enable the seed and subsequent plants to resist disease; hence the use of lime, decoctions of various ashes, and fermenting animal liquid manures (146, 159). With the discovery of the infective nature of smut, the use of various seed disinfectants for its control became evident. Schulthess (126) suggested the use of copper sulphate, and Kühn (82), after investigating its effect on smut spores as well as upon seed, recommended a definite formula consisting of immersing the seed for 12 to 14 hours in a 0·5 per cent solution of copper sulphate. Geuther (40) suggested the use of formaldehyde for the control of smuts in general, and Bolley (9) was the first to introduce formaldehyde seed treatment in the United States. In his experiments, Bolley used copper sulphate, mercuric chloride, formaldehyde, and hot water. He considered mercuric chloride superior to all other fungicides, with the possible exception of formaldehyde, which at that time had received only preliminary tests. As a consequence of these early investigations on the control of the cereal smuts (9, 40, 81, 82, 126), copper sulphate and formaldehyde became standard seed disinfectants. The difficulties inherent in the application of wet seed treatments and the rather extensive seed injury caused by them stimulated further research for better fungicidal materials.

In 1902 Tubeuf (149) reported the successful control of bunt by dusting the seed with copper carbonate, thus introducing for the first time a dry method of seed treatment. For some reason, the merits of the copper carbonate treatment were not recognized until 1917, when Darnell-Smith (21) published his results of three years' experiments on the control of smut by copper carbonate dust. This seed disinfectant soon became popular, particularly in the United States, because of its superiority over copper sulphate and formaldehyde in that it did not injure the seed and did not require elaborate and time-consuming methods of dipping or soaking. Being a dry treatment, it could be applied some time in advance of seeding without danger of injury to the seed during storage, thus saving valuable time during seeding operations. Serious disadvantages of the copper carbonate treatment, however, were its ineffectiveness in the control of coarse grain smuts, and the clogging of the seed-drill when treated seed was left in the drill during rainy or moist weather.

Riehm (118) was apparently the first to use an organic mercury compound for seed disinfection. It was a chlorophenol mercury compound, called Uspulun, and was applied in a water solution by a dipping method. Shortly after Riehm's report on the effectiveness of organic mercury as a seed disinfectant, several other mercuric compounds were developed, such as Germisan, Chlorophal, and Semesan, but none of them became widely used in Canada or the United States. Between 1928 and 1930, 2 per cent ethyl mercury chloride, the original Ceresan applied in dust form, was tested (43, 56) and found to be effective in the control of bunt as well as other cereal smuts. In 1936, Ceresan was replaced by New Improved Ceresan, with 5 per cent ethyl mercury phosphate as the active ingredient. About the same time, other mercuric compounds appeared on the market. The only one of these that became widely used in Canada was Leytosan, containing 7 per cent phenyl mercury urea. In 1950, New Improved Ceresan was replaced by Ceresan M, containing 7·7 per cent ethyl mercury p-toluene sulfonanilide as the active ingredient. It was adapted for use either as a dust or a slurry. Another mercuric compound, methyl mercury-dicyandiamide, in oily solution, was introduced in Canada under the trade name of Panogen.

Besides organic mercury disinfectants, formulations, such as hexachlorobenzene (Anticarie, Bunt-no-more) for the control of bunt only, chloranil (Spergon), dithiocarbamates (Fermate, Zerlate), thiuram sulphides (Arasan, Tersan), and many others have appeared on the market. In fact, so many different agricultural chemicals, including seed disinfectants, are being produced that it is difficult to keep adequately informed about all of them. Most of the fungicides that are registered and put on the market are adapted for certain specific uses, but none so far has excelled some of the organic mercury compounds as all-round cereal seed disinfectants (84, 88).

An ideal seed disinfectant would be one that is cheap, non-poisonous, non-corrosive to machinery, easy to apply to the seed and non-toxic to it even in excessive doses, and yet effective in controlling seed-borne diseases and protecting young seedlings from plant pathogens present in the soil. The organic mercury seed disinfectants do not possess all these merits. They are toxic to man and

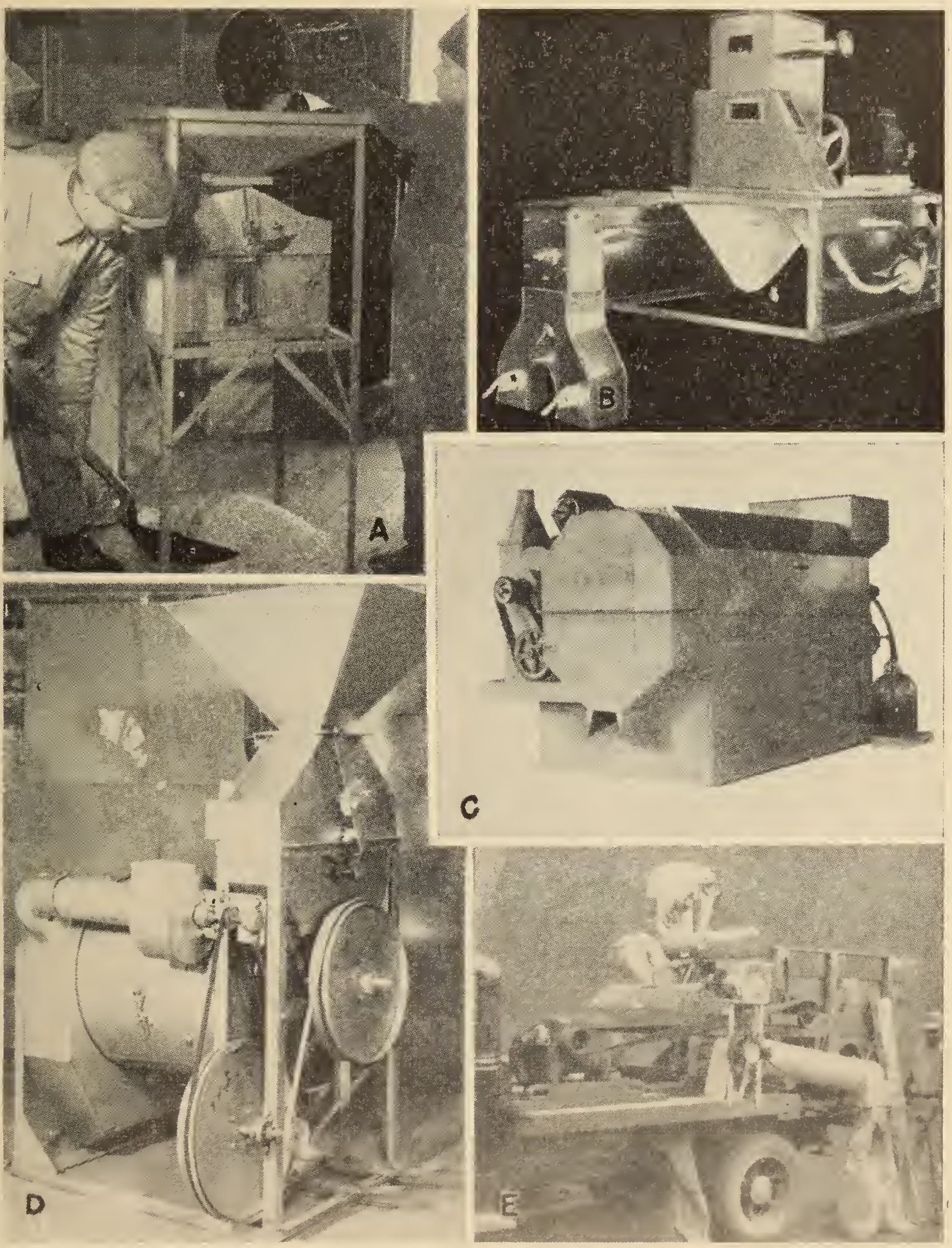

FIGURE 3.—Illustrations of seed-treating machines. A. Kemp treater for dust disinfectants. B. Gustafson treater for slurry disinfectants. C. Roecker's spray treater for slurry or liquid disinfectants. D. Panogen treater for applying Panogen in liquid form. E. A mobile outfit for custom cleaning and treating of seed in one operation.

animals, and proper precautions must be exercised by persons handling them if discomfort or sickness is to be avoided. A properly fitted respirator (gas mask) should be worn when treating seed with any of the mercuric compounds and, if at all possible, treatment should be done out-of-doors or in a well ventilated building so that air currents will carry the toxic fumes or dust away from the operator.

Notwithstanding their toxicity to man and animals, some of the organic mercury seed disinfectants possess very desirable properties. They have a fair margin of safety, being harmless to the seed unless applied in considerable excess, give good control of the surface-borne smuts and some other seed-borne diseases, and provide a certain amount of protection to the germinating seed. Some of them may be applied in the form of a concentrated solution or a thick suspension (the slurry method), thus eliminating the disagreeable dust hazard during seed-treating operations.

To obtain proper control of smut and other seed-borne diseases with the common organic mercury disinfectants presently in use, seed should be treated at least a day before seeding in the case of wheat and sorghums, and a week or more before in the case of coarse grains and grasses, so that the disinfectant can permeate the pile of seed and kill spores and other kinds of inoculum. The present trend appears to be towards the development of non-volatile organic mercury disinfectants that will dispense with the need for storing treated seed before seeding. Seed treated with formaldehyde, copper sulphate, or materials composed of a mixture of seed disinfectant and insecticide (82, 88, 96) should be sown within 24 hours after treatment to avoid seed injury. In all seed treating operations, it is very important that the seed and disinfectant be well mixed to ensure thorough coverage and an even distribution of the disinfectant. The present trend towards concentrated liquid or slurry treatments is vrey commendable from the standpoint of reducing the hazard of poisoning to operators of seed treaters, but liquids and slurrys applied in small quantities are more difficult than dusts to spread evenly over the seed (87). It is unwise to attempt to treat seed, as is sometimes done, with a loading auger or an inefficient machine, especially if the disinfectant being used is in the form of a slurry or concentrated liquid.

A number of different types of treating machines are now being offered for sale. In general, the cost of a machine is a rough index of its capacity and efficiency. This results from the fact that machines of good capacity that dispense the disinfectant accurately and distribute it evenly over the seed are more expensive to manufacture than those of simple design. Of the machines that have recently come into general use in Western Canada, two may be mentioned here—the Slurry and the Panogen (Fig. 3, B and D). In the Slurry machine, mixing of seed and disinfectant is done by a special paddle auger operating in a trough; in the Panogen machine, mixing takes place in a revolving cylinder. Although these machines show distinct advances over the older types in uniformity of coverage, further improvement in this respect would result in better smut control with the disinfectants now in use (78). Another treater, possessing a number of interesting features, was designed recently by Mr. H. G. Roecker, of Forever Industries, Winnipeg (Fig. 3, C). This machine sprays a concentrated liquid disinfectant over the seed in the form of a mist, ensuring uniform distribution of the disinfectant. A collecting device protects the operator from escaping fumes.

The advantages of the so-called dry treatment methods, including dusts, slurrys, and concentrated solutions, may be summarized as follows:

1. Dry treatments are easily applied and the seed does not become wet or swollen.

2. Grain may be treated some time in advance of seeding rather than during the busy period of seeding operations.
3. The germination of treated seed is not impaired if recommendations are carefully followed.
4. The cost of seed treatment is reasonable.
5. Smut is controlled as effectively as by the wet methods.
6. A certain amount of protection is provided for the seed and young seedlings.
7. Better stands are generally obtained from treated seed than from untreated seed.

Seed and seedling examination for the presence of loose smut.—Seed treatments that control the seedling-infecting smuts do not control the floral-infecting smuts, such as loose smut of barley and of wheat, *Ustilago nuda* and *U. tritici.* The hot water treatment, which has long been used for the treatment of loose smut of wheat and barley, and the Spergon treatment for loose smut of barley, which has not as yet been tested under farm conditions, are the only treatments for loose smut. Since it is difficult to treat large quantities of grain with hot water unless special treating and drying equipment is available, it is important to have a method that will determine the degree of loose smut infection and, therefore, the need for treatment. Such a method, developed by Russell (123) and Popp (108), consists of separating the embryos from the caryopses of the seed by boiling the seeds for a few minutes in a potassium hydroxide solution, then staining them in methyl blue and examining each one with the microscope after it has been flattened on a glass slide under a cover slip. The deeply stained mycelium is quite evident in the lightly stained tissues of the embryo (Fig. 2, A).

Russell (123) examined embryos of a number of common varieties of barley and found a close correlation in all varieties between the percentage of infected embryos in a particular lot of seed and the percentage of smutted plants produced from it. In other words, the presence of loose smut infection in barley embryos is a good index of the amount of smut that will develop in the crop grown from a particular lot of seed. Embryo examination can, therefore, be utilized to determine whether or not the hot water treatment is necessary.

During his examination of seed embryos for loose smut infections, Popp (108) found that, in some varieties of wheat inoculated with certain races of loose smut, infected embryos did not always develop into smutted plants. Loose smut infection in such varieties may proceed as far as the penetration of the embryo and the development there of a certain amount of mycelium, but after germination of the infected seed further development of the mycelium is inhibited and a healthy plant is produced. Inhibition of mycelial growth apparently occurs mainly in the first internode of the plant so that examination of the growing point in the seedling stage provides a better index of adult plant infection in wheat than does embryo examination. As growing points of seedlings can be examined about as quickly as embryos, both methods are of practical use in determining loose smut infection in wheat and barley.

Resistant varieties.—The easiest and most effective method of smut control in any crop is to grow resistant varieties. Although it is possible to keep losses from the seedling-infecting smuts at a minimum with good seed treatment practices, control of the flower-infecting smuts, *Ustilago nuda* and *U. tritici,* presents a much more difficult problem. The local-infecting corn smut, *U. maydis,* can be effectively controlled only by growing resistant varieties.

Resistance to smut diseases is inherent in certain varieties of cereals and other crops but, unfortunately, these varieties seldom meet marketing standards or are lacking in one or more important agronomic characteristics, and so are not profitable to grow. In order to combine desirable agronomic qualities with resistance to smut and other important diseases, breeding of new varieties by hybridization must be resorted to. A few decades ago it might have seemed a relatively simple task to combine smut resistance and quality in a new variety, but with the discovery of physiologic races of the smut fungi (17, 29, 106, 113, 121) breeding for smut resistance became a difficult and complex undertaking. Even before a breeding program can be undertaken, it is necessary to devise methods of distinguishing different races of the smut fungi. Then a large number of smut collections from different parts of the country must be tested to find out the number, prevalance, and distribution of races. In cereals, it is sometimes necessary to make use of the resistance to smut and other diseases present in several different varieties. The production of a new variety that is sufficiently pure to be released for commercial production may, therefore, require ten years or more. Despite the difficulties in breeding for smut resistance, considerable progress has already been made in this direction. A few well known examples of smut resistant varieties are: Thatcher wheat, highly resistant to loose smut; Regent and Redman wheat, resistant to bunt; and Fortune and Garry oats, resistant to loose and covered smut. Some of the newer corn hybrids are resistant to corn smut.

CLASSIFICATION

Changes in the classification and nomenclature of the smut fungi have been made at various times. The most recent of these (1, 34), if adopted, would necessitate the introduction of a number of new names and the discontinuance of certain well known ones. As these new names have not yet come into general use in Canada, it has been decided to employ in the present publication the older ones with which most agriculturists are familiar. The names given here to the smuts of cereals are taken from the revised list published by Stevenson and Johnson (133) in 1944.

All the common smut fungi on cultivated plants in Canada belong to two families, which can readily be distinguished as follows:—1. Promycelium septate, sporidia or hyphal branches lateral—Ustilaginaceae 2. Promycelium non-septate, sporidia or hyphal branches terminal—Tilletiaceae

USTILAGINACEAE SCHROETER

Ustilago (Persoon) Roussel, Flor. Calv. p. 47, 1806.

Sori in any part of the host, exposed at maturity, powdery or, less frequently, agglutinated. Spores single, dark coloured, small to medium in size.

1. Spores smooth, 4-12 μ in diam. Sori in individual spikelets.	
(*a*) Spores lighter coloured on one side	
Hosts: *Hordeum* spp.	*U. hordei*
Hosts: *Avena* spp.	*U. kolleri*
(*b*) Spores uniformly coloured	*U. crameri*
2. Spores verrucose or echinulate	
(*a*) Spores small, 4-9 μ in diam., germinating with lateral hyphal branches	
Hosts: *Hordeum* spp.	*U. nuda*
Hosts: *Triticum* spp.	*U. tritici*

(*b*) Spores small, 4-9 μ diam., germinating with lateral sporidia

Hosts: *Avena* spp.	*U. avenae*
Hosts: *Hordeum* spp.	*U. nigra*

(*c*) Spores medium, 5-14 μ in diam.,

Sori in spikelets	*U. bullata*
Sori in galls on any part of a plant	*U. maydis*
Sori in streaks in leaves and leaf sheaths	*U. striiformis*

Sphacelotheca De Bary, Vergl. Morph. Biol. Pilze, p. 187, 1884.

Sori in inflorescence, frequently confined to the ovaries, each limited by a definite false membrane of colourless, sterile, fungus cells. Spore mass powdery, dark coloured, surrounding a central columella (chiefly of host tissue).

1. Spores olive or reddish brown, smooth 5-8 μ in diam., sori in individual ovaries

(*a*) False membrane over sori firm, breaking up into threadlike groups of sterile cells	*S. sorghi*
(*b*) False membrane over the sori fragile, breaking up into small groups or individual sterile cells	*S. cruenta*

2. Spores light brown, 7-11 μ in diam., finely punctate, sori destroying the entire inflorescence	*S. destruens*

TILLETIACEAE SCHROETER

Tilletia Tulasne, Ann. Sci. Nat., Bot., III, 7: 112, 1847.

Sori in the inflorescence, usually displacing the ovary and the cariopsis with a dark, powdery spore mass. Spores single, 15-30 μ in diam., germinating by a non-septate promycelium with terminal sporidia.

Spores smooth	*T. foetida*
Spores reticulate	*T. caries*

Urocystis Rabenhorst, Herb. Viv. Myc. 2: 393, 1856.

Sori usually in the leaves and stems. Spores usually dark, powdery, borne in groups of one to several permanently united fertile cells more or less completely surrounded by a cortex of colourless or tinted sterile cells. Spores germinate with a short promycelium and terminal sporidia or hyphal branches.

Host: *Secale* sp.	*U. oculta*
Hosts: *Triticum* spp.	*U. tritici*
Hosts: *Allium* spp.	*U. cepulae*

DESCRIPTION OF SMUT DISEASES AND CONTROL METHODS

Bunt of Wheat and Rye, *Tilletia caries* (DC.) Tul. and *Tilletia foetida* (Wallr.) Liro

This disease has long been known as "stinking smut of wheat" because of the unpleasant odour that is sometimes given off by grain contaminated by bunt spores. The odour, which resembles that of decaying fish, is due to a volatile substance, trimethylamine (47, 53), present in the spores. Grading regulations provide that wheat which has an unmistakable odour of smut, or which contains smut spores, smut balls, or portions of smut balls shall be classed as "smutty". Such wheat sells at a discount, as it must be thoroughly washed before being milled. With discovery (47, 53) that some races of bunt fungi are odourless, "stinking smut" ceased to be an appropriate name for the bunt disease. Furthermore, bunt can no longer be regarded as a disease affecting wheat alone, since it is now known that certain races of the bunt fungi may infect rye and other hosts (34, 38, 102).

Figure 4.—Bunt of wheat. A. A plant affected by dwarf bunt (right) and one affected by ordinary bunt. B. Healthy head of wheat (left) and three bunted heads. C. Normal wheat kernels (left) and bunt balls (right)

The symptoms of bunt are usually not conspicuous until infected plants have headed. Some varieties of wheat infected with certain races of bunt fungi show noticeable dwarfing of the plants combined with small light-coloured spots on the leaves, or a grey cast along with the spotting of the leaves during the period of internodal elongation (11, 18, 119). One race of *Tilletia caries* causes an extreme dwarfing of infected plants (7, 63, 161). This race or variety[1] of wheat bunt (Fig. 4, A), usually referred to as "dwarf bunt of wheat", has been known for a number of years to occur in the United States (120), but its presence in Canada was not observed until 1948, when dwarf bunt was collected in British Columbia. It was found in one locality in Ontario in 1952.

Smutted heads of wheat are usually bluish green in appearance and remain green longer than normal heads. Quite commonly smutted heads of the Club wheat varieties become more slender and lax than normal heads, whereas heads of the more lax types may appear denser. Awns may fail to develop, or fall off as the smutted heads ripen. The bunt balls frequently are conspicuous after they reach full size, as they spread the lemma and palea apart (Fig. 4, B). They are larger and more numerous in the spikelets than normal kernels of grain. The bunt balls are at first greyish green to bluish green in colour, later changing to various shades of brown as they reach maturity.

A plant may be wholly or partially smutted. Sometimes all the heads of a plant are affected, and at other times only one or two. The heads themselves may be partially smutted, both normal grains and bunt balls occurring in the same head. These variations are apparently due to the effects of environmental factors on the development of the host and the disease. In varieties of wheat having considerable resistance to bunt, usually only partially smutted grains are found. Such grains develop to normal size and shape, with only portions of the caryopses being displaced by smut spores. Moreover, infection of plants may occur without final development of smut spores in the head. In susceptible varieties, this may be the result of environmental factors conducive to a rapid development of the infected plant in which the growing point escapes from the pathogen, whereas in resistant varieties the physiological reaction of the host may be unfavourable for the completion of the life cycle of the pathogen. Whatever the reason for the abortive infection, the infected plants may be weakened and their yield reduced (125), or they may be predisposed to infection by other pathogens (55).

Bunt balls (Fig. 4, C) do not normally break open in the field until threshing time. When smutted wheat is threshed, a large proportion of the bunt balls are broken and the spores thus set free contaminate sound grain. It is not generally realized that there may be from six to nine million spores in each bunt ball (58). When badly infected wheat is being threshed, the spores are present in such enormous numbers that a black cloud may sometimes be seen issuing from the threshing machine. Spores may be carried by air currents for several miles, some of them settling on the way on wheat fields that would otherwise be free from smut.

Bunt of wheat is caused by two closely related species of smut fungi, *Tilletia caries* and *T. foetida*. Pathologically and physiologically the two species are alike. The only distinguishing characteristic is spore morphology. The chlamydospores of *T. caries* are finely reticulate (in the race causing dwarf bunt of wheat the reticulations are more prominent), and those of *T. foetida* are smooth. The spores are light to dark brown, globose to subglobose, 15 to 30 microns in diameter, produced in sori within the ovaries of the host, with the outer tissues of the caryopsis forming a more or less persistent membrane. On germination, the chlamydospore usually produces a non-septate and rather stout tube, called the promycelium, bearing a crown of sporidia at its apex (Fig. 2, C). The sporidia are hyaline, slender, somewhat tapering at the ends and non-septate. When in close proximity with one another, the sporidia usually conjugate in pairs by means of a slender fusion tube (Fig. 2, C). Some-

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[1] Recently described as a new species. (Fisher, G. W. *Tilletia brevifaciens* sp. nov., causing dwarf smut of wheat and certain grasses. Research Studies State Coll. Washington 20: 11-14, 1952.)

times three or more sporidia may be joined together in this way. Sickle-shaped secondary sporidia may develop from single primary sporidia or from two or more that have undergone conjugation.

The cardinal temperatures for the germination of chlamydospores are approximately 5°, 10°-18°, and 25° C. (61, 101), while the optimum temperature for infection varies from 5° to 10° C., depending on the variety of wheat and the species and race of the pathogen (30, 101, 129). Spores of dwarf bunt of wheat germinate best at 5° C. (86).

Although both species of bunt fungi are present throughout Canada, the rough-spored species (*Tilletia caries*) is more common on durum wheat and, in the northern part of Western Canada, on hard red spring wheat. In the southern part of Western Canada, the smooth-spored species (*T. foetida*) predominates on hard red spring wheat (49).

Life cycle of the causal organisms.—The cycle of development of the two species is very similar, with the exception of the race of *Tilletia caries* causing dwarf bunt. Seedling infection occurs commonly from seed-borne spores. In the drier sections of winter wheat areas, infection may result as well from spores present in the soil. Infection is initiated by one or more binucleate hyphae. These may arise from primary sporidia that have conjugated or from secondary sporidia (basidiospores) produced from them. When an infection hypha comes in contact with the seedling coleoptile, it penetrates the young and tender tissues and, if successful in reaching the growing point, develops there systemically during the growing season. Just before heading of the infected wheat plant takes place, smut sori begin to develop within the ovaries, replacing both the germ and the endosperm with chlamydospores. The smut balls are ruptured during threshing, liberating large numbers of spores, some of which adhere to healthy seeds where they remain dormant until the seed is sown, when the whole sequence of events is repeated.

The race causing dwarf bunt of wheat infects mainly by soilborne inoculum (63, 86). Seed-borne spores of this race produce very little infection in comparison with soil-borne spores (6, 161). This may be the result of the rather low temperature and the relatively long period of time required for germination of the spores (86). Spores present in the soil and germinating there prior to the seeding of wheat would have time to produce infection hyphae before the seedlings had grown beyond the susceptible stage.

Physiologic specialization in the two species of wheat bunt fungi has been studied by a number of investigators (62, 102, 120, 121) and, although several morphological and physiological differences between certain races have been observed, pathogenicity is the most important criterion for differentiating races and is the one that is considered in breeding for bunt resistance. Holton and Rodenhiser (68, 120), using a group of eleven varieties of winter and spring wheats as differentials, were able to identify 16 races of *Tilletia caries* and 15 of *T. foetida* in collections of bunt from the United States, Canada, and Mexico. They (120) concluded that the distribution of particular wheat varieties is the most important factor governing the prevalence of specific races of the bunt fungi within a given area. The reactions of the 11 differential varieties to the 31 races of bunt fungi are given in Table 3.

In Canada, the survey for physiologic races of bunt has not been completed, but eight races of *Tilletia caries* and seven of *T. foetida* have already been identified (12, and unpublished data).

Control measures.—The various methods and chemical compounds that have been used in controlling bunt of wheat are closely associated with the history of the disease itself. Bunt of wheat was the first plant disease shown experimentally to be of infectious nature. In 1755, Tillet (146) proved the infective character of the bunt "dust" by sowing seed artificially blackened with bunt spores alongside rows sown with clean seed. He obtained high percentages of bunt in the former and only sound wheat in the latter. He failed to recognize, however, that the causal agent was a fungus or even a parasite. Prevost (111) was the first to observe germination of spores of *Tilletia* and the production by them of primary and secondary sporidia, thus demonstrating that bunt was caused by a fungus. The actual penetration of wheat seedlings by infection hyphae of the bunt fungus was demonstrated by Kühn (81), who, for the first time, established the basic principle of seedling infection in cereal smuts.

TABLE 3.—REACTIONS[1] OF WHEAT VARIETIES TO PHYSIOLOGIC RACES OF *TILLETIA CARIES* AND *T. FOETIDA*

Species and race	Hybrid 128 C.I. 4512	Ridit C.I. 6703	Oro C.I. 8220	Hohenheimer C.I. 11458	Hussar C.I. 4843	Albit C.I. 8275	Martin C.I. 4463	White Odessa C.I. 4655	Ulka C.I. 11478	Marquis C.I. 3641	Canus C.I. 11637
T. caries											
1	S	R	R	R	R	R	R	R	S	I	R
2	S	R	R	R	R	R	R	R	S	R	R
3	S	R	R	R	R	R	R	R	S	S	S
4	S	R	R	R	R	I	S	S	S	S	R
5	S	R	R	R	R	I	S	S	S	S	S
6	S	R	R	R	R	S	S	S	S	S	R
7	S	R	R	R	I	S	S	S	S	S	I
8	S	R	R	R	S	S	S	S	S	S	S
9	S	R	R	I	R	R	R	R	S	I	R
10	S	R	R	S	R	R	R	R	R	I	R
11	S	S	R	R	R	R	R	R	I	S	S
12	S	R	R	S	R	S	I	S	S	R	R
13	S	S	R	R	S	S	R	S	I	S	I
14	S	R	R	R	R	S	R	S	S	R	R
15	S	R	R	S	S	S	S	S	S	S	S
16	S	R	S	S	R	R	R	R	S	I	I
T. foetida											
1	S	R	R	R	R	R	R	R	S	I	R
2	S	R	R	R	R	R	R	R	S	S	R
3	S	R	R	R	R	R	R	R	S	S	S
4	S	R	R	R	R	S	S	S	S	I	R
5	S	R	R	R	R	S	S	S	S	S	R
6	S	R	R	R	I	S	S	S	S	S	S
7	S	R	R	R	S	S	S	S	S	I	S
8	S	S	S	R	R	R	R	R	S	S	S
9	S	I	R	R	I	S	R	S	S	I	S
10	S	R	R	R	R	R	R	R	S	I	S
11	S	R	R	R	R	R	R	R	S	I	S
12	S	R	R	R	R	S	R	R	S	I	I
13	S	R	R	S	R	R	R	R	S	S	R
14	S	R	R	R	R	S	I	S	S	S	R
15	S	R	R	R	S	S	S	S	S	S	I

[1] R=resistant, 0—10% infection; I=intermediate, 11—40% infection; S=susceptible, 41—100% infection.

The discovery that bunt is caused by a living organism and that infection of wheat plants occurs in the early seedling stage led to the development of seed disinfectants. Copper sulphate, the first seed disinfectant widely used in Canada, was followed by formaldehyde. Both of these disinfectants were applied as wet treatments, either by the dip or sprinkle method, leaving the seed grain wet and difficult to handle. Both caused considerable injury to the seed under certain conditions. Organic mercury dusts, introduced in Canada soon after 1930, obviated the necessity for wetting the seed. They are not injurious to the seed and provide not only excellent control of bunt and some other seed-borne diseases but also a certain amount of protection to the germinating seed in the soil. Organic mercury compounds can now be applied in powder form, in concentrated solution, or in suspension (slurry) and, provided they are distributed evenly over the seed in proper dosages, they are very effective in controlling smut (88). The chief reason why organic mercury seed disinfectants are not used more generally by farmers is that they are toxic to animals and man. When proper precautions are observed in handling them, the danger of toxic effects is slight.

Seed disinfectants having hexachlorobenzene as their active ingredient give good control of bunt, but they do not control certain other seed-borne diseases or provide protection to the seed in the soil. Such disinfectants are, therefore, useful only for the specific purpose of controlling bunt.

Seed treatments for the control of bunt and certain other seed-borne diseases are not likely to give satisfactory results if the seed contains bunt balls and other debris. To obtain the best results, the seed used should be of good quality and thoroughly cleaned before it is treated. If an organic mercury disinfectant is used, it is important to treat the seed one or more days before seeding (88).

Resistant varieties.—Although proper seed treatment gives good control of bunt, except in districts where the inoculum is carried over in the soil, it is nevertheless desirable to have varieties of wheat resistant to this disease. This is not so much to enable seed treatment to be dispensed with as to provide additional protection against infection. Very few, if any, varieties of wheat are immune from bunt, and even resistant varieties may suffer some damage if conditions for infection are very favourable. But if the natural resistance of a variety is supplemented by seed treatment, the likelihood of infection is reduced to a minimum. Moreover, seed treatment with organic mercury disinfectants has beneficial effects other than smut control. For these reasons seed treatment should be practised with resistant as well as with susceptible varieties.

The development of disease-resistant varieties of wheat and other cereals is being undertaken by plant breeders in a number of countries. In Canada, three bunt-resistant varieties of wheat have already been developed. These are Renown, resistant to all known races of bunt fungi in North America (120), and Regent and Redman, resistant to all races prevalent in the Prairie Provinces. All three varieties were produced at the Laboratory of Cereal Breeding, Winnipeg, Man. Plant breeders in several of the provinces are engaged in the development of disease-resistant varieties of wheat, the ultimate goal being to produce varieties that are suitable for the particular regions where they are to be grown and immune from or highly resistant to all races of the smut fungi and other important plant disease organisms.

Loose Smut of Wheat and of Barley, *Ustilago tritici* (Pers.) Rostr. and *Ustilago nuda* (Jens.) Rostr.

According to the principles of taxonomy, there is no valid reason for separating the fungi causing loose smut of wheat and of barley into two distinct species. The morphology and life histories of the two species are identical, as are the symptoms of disease on the two hosts (Fig. 5). The only difference between them is in pathogenicity: loose smut of wheat does not attack barley, and loose smut of barley does not attack wheat. However, the two specific names have become so well known by long usage that it seems advisable to continue their use here. For convenience, the two smuts will be considered together as they are indistinguishable, except for the hosts they attack.

The loose smut of wheat and of barley were probably known as early as bunt of wheat. Tillet (146) mentions loose smut of wheat, but he thought it was only a stage of development of bunt. Other early writers referred to this smut, but it was not until 1896, when Maddox (89) determined its mode of infection, that loose smut of wheat was definitely differentiated from bunt. Brefeld (10) in 1903 and Hecke (60) in 1904, working independently and apparently without any knowledge of Maddox's work, again demonstrated flower infection by the loose smut of wheat and of barley. They also observed mycelium of the fungus in the embryos of the host, thus making the evidence of flower infection complete.

FIGURE 5. Loose smut of wheat and barley; normal heads on the outside and smutted heads between. A. Durum wheat (left) and common wheat (right). B. Awned barley (left) and hooded barley (right).

Plants infected with loose smut head out somewhat earlier than healthy plants. As a result of a rapid elongation of the top internode, the smutted heads are usually raised above the healthy heads, thus making the smut very evident at the time of heading of the crop. In general, when a plant is infected all its heads are smutted, but occasionally plants are found with some smutted and some sound heads. Also, partially smutted heads may occur in which some of the upper spikelets have escaped infection. Partially smutted heads are common in varieties having some resistance to the disease.

In a smutted head, as a rule, each affected spikelet is entirely transformed into a mass of smut spores. The smutted head at first is covered by a delicate greyish membrane that soon disappears, setting free a dark brown powdery mass of spores. The spores are blown off by the wind and washed off by rain, leaving a bare rachis. The maximum dispersion of spores occurs when the host plants are in full flower, thus providing the best opportunity for host reinfection and hence the perpetuation of the smut fungus.

The spores are approximately spherical, minutely echinulate, about 4 to 9 microns in diameter, and, when viewed through a microscope, appear lighter coloured on one side. On germination, they produce 1- to 4-celled germs tubes or promycelia, but no sporidia. Fusions occur between the cells of the promycelium, followed by the growth of long, slender, branching hyphae.

Spores of the loose smuts germinate well at temperatures of 20°—25° C. In other words, temperatures prevailing during the blooming period of the hosts are usually favourable for the germination of the spores and the infection of the young developing seed. High humidity is apparently necessary for good infection (136). Moisture, therefore, might be a limiting factor in the development of the loose smuts.

The effect of environmental factors on the development of loose smut in plants arising from infected seed has not been sufficiently investigated (143) to permit definite conclusions to be made. It is known, however, that conditions conducive to a very rapid growth of the infected seedlings may enable the plants to outgrow the mycelium of the smut fungus and to produce normal heads.

Life cycle of the causal organisms.—As has already been mentioned, the mature spores are dispersed at the time healthy plants are flowering. According to Oort (104), strong winds disseminate spores rather evenly over a distance of approximately 100 meters, while light winds cause an erratic spread, probably the result of vertical air currents. The spores that are deposited between the glumes and come in contact with the stigma or young ovary germinate, producing infection hyphae. The infection hypha penetrates the ovary wall and, if this takes place during the flowering period or shortly after, the mycelium finds its way into the growing point of the embryo (36). The mycelium develops in the embryo without any external evidence of its presence and remains dormant until the kernel germinates (10, 60, 89).

When infected seed is sown and starts to germinate, the mycelium becomes active again and continues to develop within the seedling, keeping pace with the growing point until the head is formed. In the head, all the tissues of a spikelet are destroyed, and replaced by smut spores. Under conditions favourable for rank and succulent growth of the host plant, spores may also be produced in long sori in the upper leaves.

Physiologic specialization occurs in both species of the loose smut fungi. Bever (8) and Moore (100), in the United States, each reported 11 races of loose smut of wheat. Oort (105) studied the same smut in the Netherlands and identified six races. Since each of these investigators used a different group of differential hosts, a comparison of the races they identified is not possible

In Canada, physiologic specialization in the loose smut of wheat and of barley has been studied at the Winnipeg Laboratory of Plant Pathology (12, 48) and, at the time of writing, ten races of each have been isolated. Differentiation of races of loose smut of wheat was based on the group of varieties selected by Oort (105), except that his two winter wheat varieties, Bersee and Von Rümkers Dickhopf, were replaced by Kota and Red Bobs and two additional varieties, Reward and Pentad, were added to the group. In the barley smut, the selection of differential varieties was made by the author.

The reactions of differential varieties of wheat and barley to races of the respective smuts are presented in Tables 4 and 5.

Control measures.—The hot-water treatment developed by Jensen (73) in 1888 still remains the only practical method of control for loose smut. As mentioned earlier, promising results have recently been obtained with a Spergon treatment (152), but it is still in the experimental stage. A modification of Jensen's hot-water treatment, as reported by Murphy[1], consists in pre-soaking the seed in cold water for from four to five hours, dipping it in water at 49° C. (120° F.) for approximately two minutes, and then placing it for ten minutes in

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[1] Communications from the War Service Committee, Upper Mississippi Valley Plant Pathologist, Rept. 2: 16-18. 1942. (Mimeographed)

water at a temperature of 52·8° C. (127° F.) in the case of barley, and 53·9° C. (129° F.) in the case of wheat. Immediately after treatment, the seed is cooled and dried.

Dickson (25) found that pre-soaking the seed in cold water for six hours and then treating it for 13 minutes at 53° C. (127·4° F.) did not give complete control of loose smut in all varieties of barley. But pre-soaking for 12 to 18 hours in cold water followed by treatment for 13 minutes at 53° to 54° C. (127·4° to 129·2° F.) gave complete control of the smut without greatly reducing germination of the seed. Russell (122) reported that schedules for hot-water seed treatment, as recommended by Dickson and others, destroyed up to 92 per cent of seed of barley varieties grown in Saskatchewan. He proposed a schedule of pre-soaking seed grain for five hours in water at approximately 22·2° C. (72° F.), then placing it in a hot-water bath at a temperature of 51·7° to 52·2° C (125° to 126° F.) for 11 minutes, and finally dipping it in cold water and then drying it.

TABLE 4.—REACTIONS[1] OF WHEAT VARIETIES TO RACES OF LOOSE SMUT (*USTILAGO TRITICI*)

Host	R.L. No.	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10
Mindum	568	R	R	S	S	R	R	S	R	R	R
Renfrew	135	R	S	R	R	R	R	R	R	R	R
Flor. × Aurore	2,846	S	S	R	R	R	R	R	S	R	S
Kota	571	S	R	R	R	R	R	R	R	R	R
Little Club	223	S	R	R	R	S	R	S	R	S	R
Van Hoek	2,847	S	R	R	R	R	S	R	S	S	S
Reward	79	S	S	R	R	S	S	S	S	S	S
Carma	2,848	R	S	R	R	R	S	R	R	R	S
Vilmorin 29	2,849	R	R	R	R	R	R	R	R	R	R
Red Bobs	1,827	S	S	R	R	R	R	S	R	R	S
Pentad	203	R	R	R	S	R	R	R	R	R	R

[1] R=Resistant—0-10% smut; S=Susceptible—over 10%

TABLE 5.—REACTIONS[1] OF BARLEY VARIETIES TO RACES OF LOOSE SMUT (*USTILAGO NUDA*)

Host	C.A. No.	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10
Regal	742	S	S	S	S	S	S	S	S	S	S
O.A.C. 21	1,086	S	S	R	R	S	S	S	S	R	S
Wh. Hul	785	S	R	S	R	R	S	S	S	R	S
Bay	112	S	S	R	S	S	S	S	R	R	R
Warrior	1,144	R	S	S	R	R	R	S	R	R	R
Compana	1,154	R	S	R	R	R	R	R	R	R	R
Trebi	753	R	S	S	R	R	R	R	R	R	R
Montcalm	1,135	R	S	R	R	R	S	R	R	R	S
Titan	1,118	R	S	R	R	R	R	R	R	R	R
Valki	139	R	R	R	R	R	R	R	R	R	R

[1] R=Resistant—0-10% smut; S=Susceptible—over 10%

The slight differences in the effectiveness of the hot-water treatment, as reported by different investigators, seem to indicate variations in the response to the treatment, of infected seed of different varieties and of seed lots of the same variety grown and stored under different conditions. If such differences exist, it may be advisable to follow a method recommended by the local authorities. In any case, a schedule for hot-water seed treatment must be such as to give complete control of the smut.

Because of the difficulty of treating and drying large quantities of grain on the ordinary farm, the hot-water treatment has not come into general use.

But, for seed growers who deal with relatively small lots of high quality seed, it offers a practicable method of controlling loose smut. An easier and more effective control for loose smut may result from the development of resistant varieties. Of the commercial varieties of wheat and barley that are at present widely grown in Western Canada, only Thatcher wheat is highly resistant. Certain varieties of barley have been found to be resistant to loose smut, but they are inferior in one or more agronomic characters and would not be profitable to grow. However, plant breeders are hopeful that resistant varieties possessing other desirable characteristics will soon be developed.

Flag Smut of Wheat and Stalk Smut of Rye, *Urocystis tritici* Koern. and *Urocystis occulta* (Wallr.) Rab.

Flag smut of wheat has never been reported in Canada, but, since it is present in the United States (7) and its symptoms on the host and its life history are essentially the same as those of the stalk smut of rye (1), which occurs in Canada, it is included in this description.

FIGURE 6.—Stalk smut of rye. Note curling and splitting of the culms and leaves.

Stalk, or stem, smut of rye has been known since the early years of the 19th century, being first reported in England by Berkeley in 1836 (124). At present, it is known to occur throughout the world wherever rye is commonly grown. Flag smut of wheat was first reported in Australia in 1868, according to McAlpine (92), and was first found in the United States in 1919 (71). This smut is now known to occur also in Japan, China, India, Egypt, South Africa, and southern Europe (103).

The chlamydospores of these smuts are spherical or oval, 10 to 16 microns in diameter, and borne in groups, or spore balls, of from one to five spores. The spore balls are completely or partially surrounded by sterile, colourless to pale yellow cells. The spores germinate in water in about 24 hours, producing a promycelium, which may be either unicellular or 2- to 3-celled. At the apex of the promycellium, there develop two to six sporidia, which at first are upright and crowded together, then gradually diverge somewhat to form finger-like processes. According to Stakman *et al* (131), the sporidia of stalk smut of rye usually fuse in pairs before binucleate infection hyphae develop, although sometimes they produce slender, uninucleate hyphae that may fuse later to form binucleate infection hyphae.

The optimum temperature range for germination of the spores of flag smut of wheat and stalk smut of rye is 20°—25° C., and the optimum for infection is 14°—21° C. (85, 103). A relatively dry soil with a pH of about 7 is conducive to host infection and subsequent development of the disease (85). According to Noble (103), flag smut of wheat is one of the most destructive diseases in Australia and in some countries in Asia where, in susceptible varieties, losses up to 70 per cent of the crop have been reported. Stalk smut of rye has not been reported as causing very extensive damage except in localized areas (132). In Canada, where rye is only a minor crop, this smut is of little economic importance.

The symptoms of these two smuts are evident from the late seedling stage until maturity of the crop. Greyish black linear sori first appear in the leaves, extending into the leaf sheaths and later the culms. Sometimes even the glumes may be affected. In wheat, the affected upper leaves are usually twisted and curled more than in rye, and heavily infected plants seldom head out. The epidermis over the smut sori breaks open, exposing dark brown spore masses, thus making the symptoms more conspicuous. The affected plants are more or less dwarfed as a result of the reduced elongation of the culms, especially in the more susceptible varieties.

Life cycle of the causal organisms.—Chlamydospore production in these smuts continues from the late seedling stage until the crop matures. The greatest dispersion of spores takes place during threshing of the infected crop, when sound seed grain becomes contaminated. Thus spores may be carried over on the seed or in the soil to infect young seedlings. The mode of infection and early development in these smut diseases are similar to those of wheat bunt. Once the infection hypha reaches the growing point of the host seedling, the fungus develops rapidly, penetrating different tissues of the seedling, until the fourth or fifth leaf stage, when the production of chlamydospores in the parenchymatous tissues is initiated. The narrow linear sori develop between the veins of the leaves and leaf sheaths and at first are covered by the epidermis, which later ruptures, releasing the powdery spore mass.

Physiologic specialization has been reported for the fungus causing flag smut of wheat. Holton and Johnson (67) have distinguished two races in the United States; race 1 from Kansas and race 2 from Washington. Oro wheat is resistant to race 1 and susceptible to race 2. Yu *et al* (162) differentiated 12 races on five varieties of wheat in China.

Control measures.—Seed treatments with organic mercury compounds give good control of seed-borne inoculum (85) and reduce the infection from soil-borne spores. Control of these smuts in some of the areas where they have been very destructive has been achieved largely by the growing of resistant varieties. This method of control has met with considerable success in the central United States, where the enforced use of resistant wheat varieties has helped to check the spread of the flag smut.

Loose Smut of Oats and False Loose Smut of Barley, *Ustilago avenae* (Pers.) Rostr. and *Ustilago nigra* Tapke

These two species are similar in morphology, life cycle, and the symptoms they produce on their respective hosts. They differ only physiologically in that one (*Ustilago avenae*) attacks oats and related species of grasses and the other (*U. nigra*) attacks barley and some species of grasses (1, 34).

Figure 7.—False loose smut of barley (A), and loose smut of oats (B). A healthy head is shown at the left in each photograph.

Loose smut of oats has been known for many years (73, 81) and occurs throughout the world where oats are grown (92). False loose smut of barley, although only recently described (137), is also widespread but, as it can be differentiated from loose smut of barley (*Ustilago nuda*) only by its method of spore germination, data on its distribution are not extensive. Both smuts cause heavy losses when seed treatments are not regularly applied.

Infected plants head out at the same time as healthy plants and the spores are shed over a longer period than in the case of the loose smut of wheat and of barley. Usually the entire spike is affected, although partially smutted heads with upper florets producing sound grain are not uncommon. The sori are at first covered by delicate membranes as the smutted heads emerge, but these soon rupture, releasing the dark brown, powdery spores.

The spores are globose to subglobose, 4 to 9 microns in diameter, and dark brown, with echinulations varying from slight to pronounced. When a spore germinates it forms a promycelium, usually with three septa. Each of the four cells of the promycelium produces an ovate sporidium which may multiply by yeast-like budding or conjugate with another sporidium to form a binucleate cell from which an infection hypha develops (Fig. 2, B and D). The four sporidia on a promycelium are equally divided between two sexual strains, and conjugation occurs between compatible pairs (2, 24, 109).

In 1908, Falck (27) reported what now appears to have been a very important discovery, but its significance was not appreciated at that time. He examined oat florets after blossom inoculation and found that some spores on the stigmas had germinated. Later in the season, he found mycelium underneath the glumes, and also penetrating the outer layers of the caryopsis in the inoculated florets. In 1922, Zade (163) rediscovered spore germination in oat flowers, and this was confirmed by Gage (37), and later by Tapke (141). These investigators showed that spores germinate on the developing caryopsis, producing mycelium that penetrates the tissues of the inner surface of the glumes and the outer surface of the caryopsis, thus establishing the inoculum at or close to the vital point of attack. This explained the usual ineffectiveness of non-volatile seed disinfectants in the control of oat smut and also the difficulties in obtaining high percentages of infection by dusting the seed with dry spores just before planting. The sub-hull inoculum has an advantage in space relationship with the germinating seed as well as in the protection it receives from adverse environmental conditions before infection takes place.

Although it has not been established experimentally that the spores of false loose smut initiate flower infection in barley similar to that of loose smut in oats, it is probable that this occurs. At the time of spore dispersal, the spores of false loose smut must settle in considerable numbers in barley florets and, under favourable conditions, germinate there, producing mycelium that invades the glumes and the outer surfaces of the caryopses.

The discovery that, in oat smut, seed inoculation occurs during the maturation and harvesting of the crop and even during storage of the seed (37, 140, 163) brought to light the importance of environmental conditions throughout the entire cycle of development of the smut. Relatively warm humid weather during the period from flowering to the harvesting of the crop would favour germination of smut spores that become lodged in the host florets and the establishment of an effective inoculum.

Life cycle of the causal organisms.—Loose smut of oats and false loose smut of barley differ from the loose smut of wheat and of barley (*Ustilago tritici* and *U. nuda*) in that, although the spores of the former, and probably also those of the latter, germinate and produce a certain amount of mycelium under the seed hull, actual infection occurs not in the developing embryo but in

TABLE 6.—REACTIONS[1] OF VARIETIES OF OATS TO RACES OF *USTILAGO AVENAE*

Race	Anthony C.I. 2143	Black Diamond C.I. 1878	Victory C.I. 560	Gothland C.I. 1898	Monarch C.I. 1876	Fulghum C.I. 708	Black Mesdag C.I. 1877	Camas C.I. 2965	Nicol C.I. 2925	Lelina C.I. 3404
A- 1	S	S	S	R	R	R	R	R	R	R
A- 2	S	S	S	R	R	R	R	S	R	R
A- 3	S	S	S	R	S	R	R	R	R	R
A- 4	S	S	S	R	S	R	S	R	R	R
A- 5	S	S	S	S	R	R	R	R	R	R
A- 6	S	S	S	S	S	R	R	R	R	R
A- 7	S	S	S	S	S	R	R	S	R	R
A- 8	S	S	R	R	R	R	R	R	R	R
A- 9	S	S	R	R	R	S	R	R	R	R
A-10	S	R	S	S	R	R	R	R	R	R
A-11	S	R	S	S	R	R	R	R	S	R
A-12	R	S	R	R	R	S	R	R	R	R
A-13	R	R	R	R	S	R	R	R	R	R
A-14	S	S	S	R	R	S	R	R	R	S
A-15	R	S	R	S	S	S	R	R	R	S

[1] S=Susceptible—over 10% smut; R=Resistant—0-10% smut

the young seedling. When seed is planted and begins to germinate, the sub-hull inoculum or surface borne spores produce infection hyphae that penetrate the young coleoptile. If the hyphae reach the growing point of the seedling, a systemic infection results.

Physiologic specialization in loose smut of oats was first reported by Reed (113) and in false loose smut of barley by Tapke (138). Reed continued his studies of physiologic specialization in the oat smut fungus and (114) identified 29 races of *Ustilago avenae.* Holton and Rodenhiser (69), using ten varieties of oats, retested some of Reed's races together with a number of other collections and differentiated only 15 races. Their results are summarized in Table 6.

In Canada, races 1, 5, and 10 of loose smut of oats have been isolated. In addition, there appear to be at least 11 other races or biotypes that, as yet, have not been positively identified.

In false loose smut of barley, Tapke (138, 145) differentiated two races in 1936 and 11 additional races in 1951. Seven of the latter were found in the United States and four were identified from 16 collections of the smut obtained from Israel. The reactions of the differential hosts to the 13 races of false loose smut, as reported by Tapke (145), are shown in Table 7.

Races 2, 4, 5, 6, 8, 9, and 10 of false loose smut, together with at least five other races or biotypes, have already been isolated in Canada. There are indications, however, that many more races may be found by the time a country-wide survey is completed.

TABLE 7.—REACTIONS[1] OF VARIETIES OF BARLEY TO RACES OF *USTILAGO NIGRA*

Race	Excelsior C.I. 1248	Hannchen C.I. 531	Himalaya C.I. 1312	Lion C.I. 923	Nepal C.I. 595	Odessa C.I. 934	Pannier C.I. 1330	Trebi C.I. 936
U.S. R1	R	R	R	R	R	S	R	R
" 2	R	S	R	R	R	S	R	S
" 3	R	R	R	S	R	S	R	S
" 4	R	S	R	S	R	S	R	S
" 5	R	S	S	S	S	S	R	S
" 6	S	S	S	S	S	S	R	S
" 7	R	S	S	R	S	S	R	S
" 8	S	R	R	S	S	S	R	S
" 9	R	R	R	R	S	S	R	R
Israel R10	R	S	R	S	R	S	R	R
" 11	R	S	R	S	R	S	S	S
" 12	S	S	R	S	S	S	S	S
" 13	S	S	S	S	S	S	S	S

[1] S = Susceptible—over 10% smut; R = Resistant—0-10% smut

Control measures.—Application to the seed of a volatile organic mercury seed disinfectant one week or more before seeding gives good control of loose smut of oats and false loose smut of barley. Growing resistant varieties would aid in the control of these and other smut diseases, and concerted efforts are being made by plant breeders to develop such varieties. The most important commercial varieties of oats and barley now grown in Canada are susceptible and it is therefore advisable to treat all seed of these crops in order to reduce smut losses.

Covered Smut of Oats and of Barley, *Ustilago kolleri* Wille and *Ustilago hordei* (Pers.) Lagerh.

The fungi causing the covered smut of oats and of barley also attack certain species of grasses (34). They are similar in life history, morphology, and the symptoms they produce. The two smuts are coextensive with their hosts and cause considerable losses where proper seed treatment is not practised.

The smut sori, developing in the spikelets, are rather compact and more or less concealed by the glumes in oats and some grass species. In barley, the glumes are largely consumed, leaving the smutted head enveloped in a rather persistent membrane. The smutted heads emerge at the same time as the healthy heads.

Figure 8.—Covered smuts of oats and barley. A. A normal head and two smutted heads of oats. B. Normal heads of barley on the outside and smutted heads between. Awned (left) and hooded barley (right).

The spores are smooth, globose to sub-globose, olive brown, lighter coloured on one side, and range from 4 to 12 microns in diameter. On germination, each spore forms a characteristically 4-celled promycelium and four ovate sporidia. Under favourable conditions, the sporidia may form an abundance of secondary sporidia by budding. Fusion of compatible sporidia or of cells of the promycelium is necessary for the development of a binucleate infection hypha.

Life cycle of the causal organisms.—The covered smut of oats and of barley are carried over from season to season as seed-borne spores, although development of sub-hull mycelium during maturation of the crop and storage of the seed is common under favourable conditions (37, 141). Infection occurs in the very young seedling from hyphae originating from seed-borne spores or sub-hull mycelium. The hyphae penetrate the young coleoptile and push into the embryonic growing point. Further development of the parasite proceeds in association with the differentiating tissues of the stems and floral structures. Seedling infection is influenced by soil conditions (28, 116, 139), especially soil temperature and moisture.

Physiologic specialization in these smuts was discovered by Faris (29) and Reed (113). In 1940, Reed (114) reported 14 races of *Ustilago kolleri.* Holton and Rodenhiser (69), on the basis of the reactions of the same set of differentials they used for *U. avenae,* isolated seven races. The reactions of the differential hosts to seven races of *U. kolleri,* as given by Holton and Rodenhiser, are summarized in Table 8.

From 120 collections of *Ustilago kolleri* from different parts of Canada only races 1 and 3 of Holton and Rodenhiser have been identified. There are, however, at least three additional races or biotypes that have been isolated from the collections but not yet identified.

TABLE 8.—REACTIONS[1] OF VARIETIES OF OATS TO RACES OF *USTILAGO KOLLERI*

Race	Anthony C.I. 2143	Black Diamond C.I. 1878	Victory C.I. 560	Gothland C.I. 1898	Monarch C.I. 1876	Fulghum C.I. 708	Black Mesdag C.I. 1877	Camas C.I. 2965	Nicol C.I. 2925	Lelina C.I. 3404
1	S	S	S	R	R	R	R	R	R	R
2	S	S	S	R	S	R	R	R	R	R
3	S	S	S	S	R	R	R	R	R	R
4	S	S	R	R	S	S	S	R	R	R
5	S	S	S	R	S	R	S	R	R	R
6	S	S	R	R	R	R	R	R	R	R
7	S	S	S	S	R	R	R	R	R	S

[1] S=Susceptible—over 10% smut; R=Resistant—0-10% smut

Tapke (142) followed Faris in the study of specialization in *Ustilago hordei* and in 1945 reported 13 races. His results are summarized in Table 9.

In Canada, more than 135 collections of *Ustilago hordei* have been studied and races 1, 2, 5, 6, 7, 10, and 11 have been identified. Six additional races or biotypes have been isolated but not yet identified.

TABLE 9.—REACTIONS[1] OF VARIETIES OF BARLEY TO RACES OF *USTILAGO HORDEI*

Race	Excelsior C.I. 1248	Himalaya C.I. 1312	Hannchen C.I. 531	Lion C.I. 923	Nepal C.I. 595	Odessa C.I. 934	Pannier C.I. 1330	Trebi C.I. 936
1	R	R	S	R	R	S	R	R
2	R	R	R	S	S	S	R	R
3	S	R	R	S	S	S	R	R
4	R	S	R	R	S	S	S	S
5	R	R	R	S	R	S	R	S
6	R	R	S	S	R	S	R	S
7	R	R	R	R	S	S	R	R
8	R	R	R	R	R	S	R	R
9	S	R	R	R	S	S	R	R
10	R	S	S	S	S	S	S	S
11	R	S	S	S	S	S	R	S
12	R	S	R	R	S	S	R	R
13	S	R	S	S	S	S	R	S

[1] S=Susceptible—over 10% smut; R=Resistant—0-10% smut

Control measures.—Control measures for the covered smut of oats and of barley are the same as for the loose smut of oats and the false loose smut of barley.

The Loose and the Covered Kernel Smut of Sorghum, *Sphacelotheca cruenta* (Kühn) Potter and *Sphacelotheca sorghi* (Lk.) Clint.

Sorghums are generally warm climate crops and are very important in India, Egypt, China and the southern United States (117). They are grown to some extent in Canada mainly as forage crops. The sorghums are subject to two closely related kernel smuts; a loose smut, caused by *Sphacelotheca cruenta*, and a covered smut, caused by *S. sorghi*. The latter is the most prevalent in the United States and Canada (45, 117).

Figure 9.—Covered kernel smut of Black Amber sorghum, with a normal plant (right). Note the dwarfing of the smutted heads.

Losses from the kernel smuts are not limited to the destruction of grain alone. The quality of the fodder is also affected and, in the case of broom corn, the stems may be rendered unfit for manufacturing purposes, particularly when affected by the loose kernel smut.

Infected plants may be readily recognized when the heads emerge from the sheaths and, in the case of the loose kernel smut, by their dwarfed appearance. The kernels are replaced by elongated protruding smut balls covered with a thin membrane produced by the fungus. The membrane of the loose kernel smut ruptures early, releasing a black powdery spore mass. In the covered kernel smut, the membrane is tougher and usually persists as the grain ripens. The spores of both species are borne around an elongated central columella, or axis, of host tissue, the presence of which differentiates *Sphacelotheca* from *Tilletia* or *Ustilago*.

The chlamydospores are round to elliptical, 5 to 8 microns in diameter, olive to reddish brown in colour, with indistinct echinulations or reticulations on the wall surface. On germination, they produce 4-celled promycelia with laterally borne sporidia. Secondary sporidia are produced on culture media.

Life cycle of the causal organisms.—Infection by the loose and the covered smut of sorghum occurs in the early stages of seedling development. Both fungi become established in the primordial tissues of the growing point and thereafter develop systemically within the host. Spores are produced in the kernels and, in the case of loose kernel smut, in the adjacent floral tissues as well. The spores are disseminated during the ripening and threshing of the crop and are carried over from season to season on the seed and, in drier regions, in the soil.

Infection may occur over a wide range of such soil conditions as temperature, moisture, and reaction, but the optimum condition seems to be 20°—25° C. in a relatively dry and neutral or slightly acid soil (115).

Physiologic specialization was first suggested by Tisdale *et al* (147) in 1927. They observed three different strains in the covered smut and two in the loose smut. Later Melchers (94) differentiated two races of loose smut. Pierce Kaferita is susceptible to race 1 and resistant to race 2; White Yolo is resistant to race 1 and susceptible to race 2.

Melchers *et al* (97, 98) studied specialization in the covered kernel smut and in 1932 reported five races, which were differentiated on five varieties of sorghum (Table 10). In these tests, one selection from Spur feterita and three from the cross Red Amber × fererita remained immune from all five races of the smut.

TABLE 10.—REACTIONS[1] OF VARIETIES OF SORGHUM TO RACES OF *SPHACELOTHECA SORGHI*

Variety		Smut races				
		1	2	3	4	5
Dwarf Yellow milo	C.I. 332	R	S	R	R	R
White Yolo	K.B. 2525	R	S	R	S	R
Pierce kaferita	K.B. 2547	R	R	S	R	R
Feterita	S.P.I. 51989	R	R	R	R	R
Kafir × feterita	H.C. 2423	R	R	S	R	S

S = Susceptible—over 10% smut; R = Resistant—0-10% smut

Control measures.—These two sorghum smuts can be controlled by seed treatment with such disinfectants as Arasan, Spergon, Copper Carbonate, and Ceresan. According to Leukel (84) and others (54), Ceresan gave the best control.

Head Smut of Panicum Millet, *Sphacelotheca destruens* (Schlecht.) Stevenson and A. G. Johnson

The head smut of panicum, or broom-corn, millet is distinct from the sorghum smuts described in the preceding section in that it modifies the entire inflorescence into one smut gall (Fig. 10). The gall is enclosed in a greyish-white membrane of fungus origin. As the infected plant matures the membrane ruptures irregularly, exposing a dusty, dark brown spore mass and numerous long fibres of the vascular tissues of the host panicle. The spores are subspherical or irregular in shape. When examined under high magnifications, they are seen to be finely punctate, and range from 7 to 11 microns in diameter.

Spores germinating on culture media usually produce promycelia, with lateral, ovoid to elliptical sporidia. According to Martin (90), certain promycelial cells commonly produce hyphal branches instead of sporidia.

The method of spore dissemination and infection, and the measures recommended for the control of this smut are the same as for the kernel smuts of sorghum.

FIGURE 10.—Head smut of *Panicum* millet, with a normal plant (left).

Millet Smut, *Ustilago crameri* Kcke.

Millet smut, although of little economic importance in Canada, is one of the most important diseases of fox-tail millet in China and other Asiatic countries, where the crop is grown on a large scale for human food. The ovaries of infected plants are replaced by smut spores enclosed by the floral envelopes. As the plants mature the brittle floral bracts may break, releasing a loose, reddish-brown spore mass, or they may persist, forming smut balls similar to but much smaller than those of bunt of wheat. Smutted plants somewhat resemble oat plants affected with covered smut and are conspicuous from the black appearance of the panicles.

The spores are oval to sub-spherical, very minutely echinulate, and 7 to 12 microns in diameter. They germinate in the same manner as spores of the seedling-infecting smut of oats and of barley, with 4-celled promycelia and lateral sporidia.

Physiologic specialization has been studied by Wang (156), who identified six races on a group of 12 varieties of millet. The differences in the reactions of differential varieties of millet to the six races of the smut, as reported by Wang, do not seem sufficient, however, to distinguish more than three races.

The dissemination of spores, method of infection, and the control measures recommended are the same as for the kernel smuts of sorghum.

Head Smut of Grasses, *Ustilago bullata* Berk.

Head smut of grasses is common in Western Canada and may affect a number of cultivated and native grass species, but is probably most common on western rye grass. The sori formed in the spikelets may involve all or part of the floral bracts They are enclosed in the epidermal membranes of the floral structures, which persist in varying degrees in different grass species. In

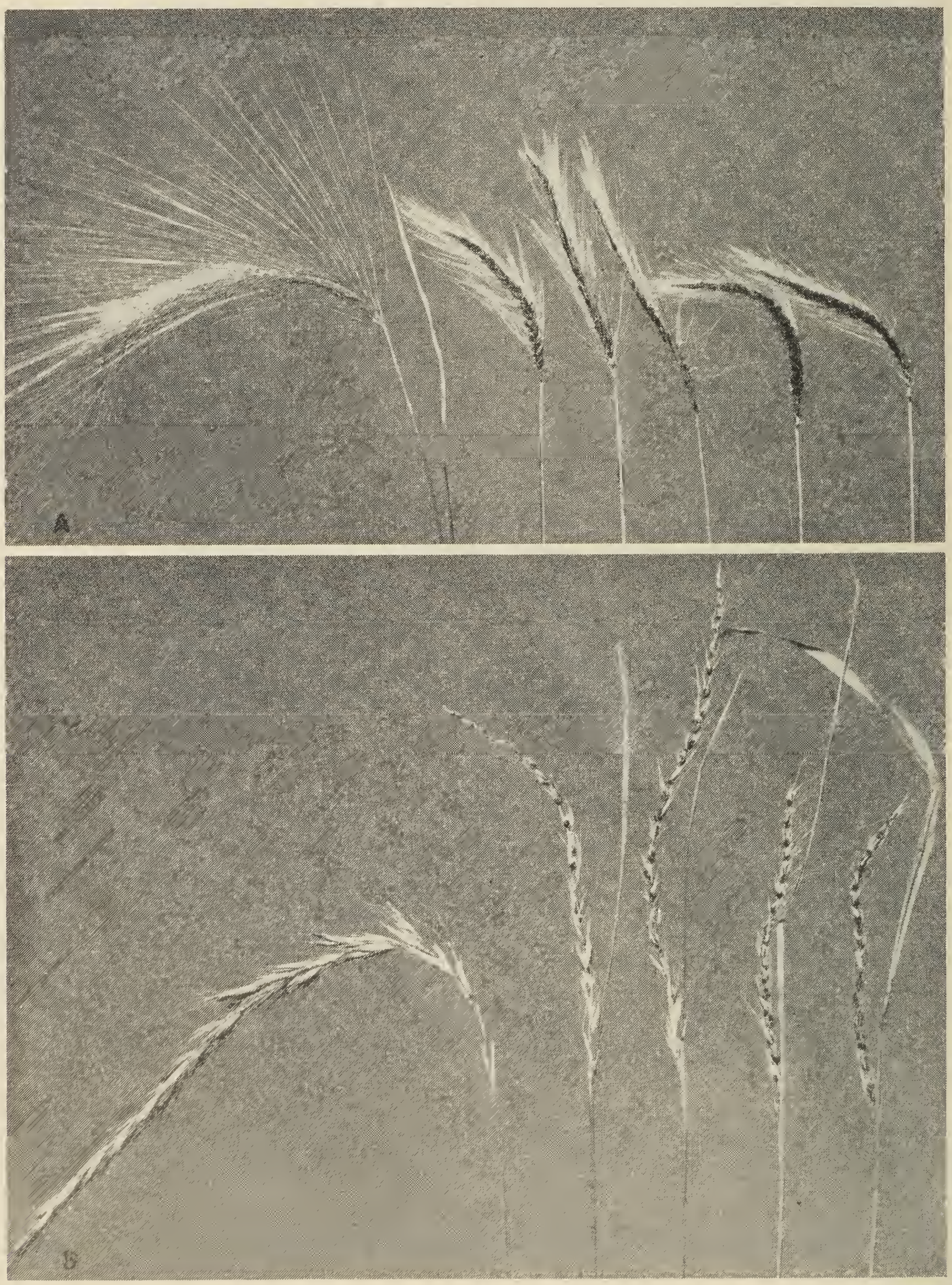

FIGURE 11.—Head smut of grasses. A. Wild barley (*Hordeum jubatum*). B. Slender wheat grass (*Agropyron trachycaulum*). A healthy head is shown at the left in each photograph.

western rye grass, for example, this smut resemble in appearance covered smut of oats. The enclosing membrane ruptures sooner or later, exposing the powdery dark brown to purple black spore mass.

The spores are mostly globose to sub-globose, but sometimes irregular to polyhedral, usually dark brown, minutely echinulate to verrucose, 5 to 14 microns in diameter but mostly 7 to 9 microns. They germinate with from one to three promycelial branches, each of which is 1- to 3-celled and bears oval or oblong sporidia.

Infection occurs in the seedling stage and usually all the stems produced by an infected plant bear smutted heads. In perennial grasses, the smut mycelium becomes established in the overwintering parts of the plant and persists there year after year, invading the new stems as they develop. Plants bearing this systemic type of invection produce little if any seed and serve as a continuing source of inoculum for the contamination of seed harvested from healthy plants in the same field. Resistant lines in some grasses have been reported by Fischer (33), who differentiated eight races of the smut fungus.

Seed treatments with common seed disinfectants control the disease in the case of seed-borne inoculum.

Stripe Smut of Grasses, *Ustilago striiformis* (West.) Niessel

Stripe smut affects a large number of cultivated and wild grasses but is most common on timothy, red top, orchard grass, and Kentucky blue grass. Although it has been reported to cause serious losses in the United States, this smut is not of economic importance in Canada.

The sori develop mainly as long, narrow, almost black stripes in the leaves and leaf sheaths. The affected plants are more or less dwarfed and the development of the inflorescence is restricted. The leaves usually break along the old sori, and this shredding effect on the leaves and leaf sheaths may be quite conspicuous.

The spores are globose to ellipsoid, dark olive brown, rather prominently echinulate, and usually 9 to 12 microns in diameter. Spore germination occurs directly or after a resting period, depending on the race of the fungus and the species of the host (34). The spores of some collections germinate with the production of branched promycelia bearing sporidia; those of others do not form sporidia. According to Davis (22) and Kreitlow (80), infections originate mainly from seedborne spores and, therefore, seed treatment with surface disinfectants will control this smut.

Corn Smut, *Ustilago maydis* (DC.) Cda.

Corn smut is probably the most widely distributed disease of corn. In warm and moderately dry districts, it causes serious damage to susceptible varieties (72, 79). Although corn smut is not ordinarily carried over on the seed, like most cereal smuts, this may occur. Corn smut was reported in Germany for the first time in 1833 (127) and in Australia in 1938 (5). Seed-borne spores were probably responsible for introducing the disease into these and other countries where corn is now grown. Once established, the pathogen perpetuates itself by the production of extremely large numbers of hardy spores (79, 107).

The loss in yield resulting from corn smut varies with the time the plants become infected and with the size, number, and location of the galls. Galls above the ears on the main stalk are twice as injurious as those below the ears, the extent of yield reduction varying directly with the size and number of the galls on each plant (74). Plants grown from seed taken from the base and tip of the cob or from damaged seed are more susceptible to smut than those grown from well developed sound seed (79).

FIGURE 12.—Corn smut, showing smut galls on stems and cobs. **Inset.** Corn cob with husks partially removed to show smut galls on individual kernels.

Corn smut differs from the smuts considered earlier in this publication in that it causes local rather than systemic infections (110). Infections may occur on the tassels, ears, stalks, leaves, and even on brace roots; in other words, on any above-ground part of a plant that is in a stage of active growth. The smut mycelium stimulates an excessive development of the permeated host tissues and thus an overgrowth, or gall, begins to form. At first, the gall consists of plant tissues permeated by a mass of mycelium. Later, the host cells are killed, except for the connecting tissues, and the mycelium is transformed into spores. The galls are covered by silvery grey membranes that eventually rupture to release the powdery, dark olive brown spores.

The spores are globose to sub-globose, rather prominently echinulate, and mostly 9 to 12 microns in diameter. On germination, a spore produces a 4-celled promycelium, from each cell of which a sporidium develops. Usually two of the four sporidia on each promycelium are of one sexual group and the other two of the opposite group. Under certain conditions, sporidia of opposite sex conjugate (46).

The cardinal temperatures for the germination of chlamydospores and the production of sporidia are 8°, 26-34° and 38° C. (75). According to Kornfeld (79), severe infection may be expected to follow a mean June temperature exceeding 20° C.

Life cycle of the causal organism.—The method by which the corn smut fungus gains entrance to its host in nature has not been fully elucidated. Hyphae from sporidia of either sexual group are able to penetrate the epidermal cells of the corn plant and develop fine mycelial threads in the underlying tissues (46). Infections of this type, initiated by haploid hyphae, cause no apparent injury to plants and never bring about the formation of smut galls and chlamydospores. It is only when plants become infected with diploid mycelium originating from sporidia of the two sexual groups that smut galls and chlamydospores are formed. Whether the most common mode of infection in the field is by diploid hyphae from sporidia of opposite sex that have undergone conjugation, or by haploid hyphae that after penetration fuse with other haploid hyphae of opposite sex, has not been determined.

An interesting exception to the characteristic requirement of sexual fusion in this smut was discovered by Christensen (15) and others (16). They found that some cultures, each derived from a single sporidium, when injected into plants, were able to cause infection and produce galls containing chlamydospores. Some of these so called solopathogenic lines went through successive generations without a reduction division for sex or pathogenicity, but more frequently chlamydospores produced by the solopathogenic lines germinated with the formation of normal, unisexual sporidia. In nature, according to Walter (155), chlamydospores germinating on susceptible tissues of a corn plant sometimes produce promycelia that penetrate the tissues directly without the production of sporidia. Ordinarily, however, the production of sporidia and their subsequent fusion commonly intervenes in the natural propagation of this extremely variable fungus (16).

The spores of corn smut are very resistant to freezing and drying, and may remain viable in soil or crop residues for several years (57, 79, 107). They are disseminated by wind and rain from the time the smut galls begin to ripen until the crop is harvested. Delayed germination in a certain proportion of the spores, not only lengthens the period of abundant inoculum, but ensures the carry-over of the inoculum from season to season. Furthermore, the abundant production of sporidia by yeast-like budding and their adaptation to wind dissemination with particles of soil, still further increase the chances of infection under favourable conditions.

Infection of young tissues of a corn plant may occur at any time during the vegetative development of the plant. Primary infections in the early part of the season are caused by wind-borne sporidia produced by the overwintered chlamydospores. Subsequent infections may be caused either by sporidia from spores present in soil or crop residues, or directly by chlamydospores from mature galls.

Control measures.—In areas where only small plots of corn are grown, destruction of smut galls before the spores mature, crop rotation, and general sanitation aid in controlling the disease. These methods of control, however, are not effective in areas where the crop is grown in short rotations on contiguous acreages. Under such conditions, resistant varieties offer the only satisfactory means of smut control.

Although it has been demonstrated (57, 72) that resistance and susceptibility to corn smut are conditioned by genetic factors, the production of resistant varieties has proved to be a difficult undertaking because of the extreme variability of the smut organism. Physiologic specialization in the corn smut fungus has been studied by Christensen and Stakman (17) and their associates (16) and a number of distinct races have been isolated. The variability in this smut is so great, however, as a result of hybridization and mutation, that a very large number of types may be produced. According to Stakman (130), more than 5,000 distinct cultural types have been produced in breeding experiments started with two smut races. Nevertheless, many of the more recent hybrid corn varieties are moderately resistant to the prevalent variants of the smut.

Onion Smut, *Urocystis cepulae* Frost

The smut attacking onion is closely related to flag smut of wheat and stalk smut of rye. It appears that onion smut originally developed on wild host species in America and thence passed over to the cultivated onion (3). It was

FIGURE 13. Onion smut, showing smut sori in scales and leaves. (After J. C. Walker, 1944.)

first reported on cultivated onions in the eastern United States in 1857, and from there it apparently was introduced into Europe. Eventually it spread into the northern States and Canada (3, 134). The most recent introduction of onion smut was into New Zealand, where it was observed for the first time in 1938 (41, 42).

Onion smut does not thrive in areas with high temperatures (95, 154), but in the temperate zone, where the soil is relatively cool during the period of onion seed germination, it is the most destructive disease of onions and other closely related crops, such as leeks (3, 153). Once the disease becomes established, the causal organism can perpetuate itself in the soil for many years (3). Szembel (134) observed heavy infection of onion smut on a plot on which the disease had occurred ten years before but which in the intervening period had not grown onions or other susceptible crops. This would indicate either that the spores in the soil remained viable during the ten years or that the fungus perpetuated itself as a saprophyte.

Infection of the host occurs only in the early seedling stage. Onion sets or seedlings with true leaves already developed when transplanted into contaminated soil are not attacked by the smut. The optimum temperature range for spore germination and infection is 13°—22° C. (154). Above 25° C. spore germination declines rapidly, and at 29° C. or above no germination or infection occurs. The disease symptoms appear soon after the onion seedlings emerge above ground. Brown to black elongated blisters form within the tissues of both scales and leaves. the latter usually being slightly thickened and often abnormally curved. The infected leaves are usually killed and, when they become dry, the smut blisters split open, exposing a black mass of spores— which fall to the ground.

Most of the infected seedlings die within from three to five weeks after germination and, in the small percentage of those that survive until midseason or harvest, new leaves and scales become infected as they develop. Such plants usually produce small and imperfect bulbs, which are subject to rot and other diseases. Occasionally, plants are so lightly infected that more or less normal bulbs may develop. These may eventually find their way to the market and in that manner the smut may be introduced to new locations.

The spore balls of onion smut contain one, or occasionally more, ovoid, brown, fertile spores 12 to 16 microns in diameter, with small oval, brown-tinted, sterile cells that almost completely cover the spores. The spores germinate, producing short, hemispherical promycelia that give rise to several branching hyphae (3). Apparently no sporidia are produced by this fungus, and nuclear association prior to infection has not been observed (3).

Life cycle of the causal organism.—When the spores are liberated, either by rupturing of the smut sori or by decay of the infected parts of onion that have fallen to the ground, they may germinate at once or remain dormant for from a few weeks to several years. Spores that germinate may develop a considerable amount of mycelium in the absence of a susceptible host. With the onset of unfavourable conditions, the mycelium breaks into small pieces, which may remain for several months in a dormant state. When favourable growing conditions return, the pieces of mycelium may resume growth (3). In this manner, the smut is able to perpetuate itself in the soil for several years in the absence of its host (1, 3, 134).

When seeds of a susceptible host (onions or leeks) germinate in soil infested with the onion smut fungus, the organism penetrates the young tissues of the seedling plants and spreads rapidly through the developing scales and leaves, where smut sori develop as long streaks. Infected plants are usually killed within a few weeks (3, 153).

Control measures.—According to Anderson (4) the 54 varieties of cultivated onions that he tested all proved to be susceptible to smut. Of the various methods of control that he tried, the formaldehyde drip treatment proved to be the most effective. This method consists of running a stream of formaldehyde solution into the furrow with the seed. A solution containing one pint of 40 per cent formaldehyde in eight gallons of water, applied at the rate of 100 gallons per acre, gives good control of the smut, but better results are obtained by using twice as much solution at one half the strength (42, 44, 153). The solution may be applied to the row from a specially made tank attached to the seeder (45).

Although the formaldehyde drip treatment gives satisfactory smut control, it has certain disadvantages. A large quantity of water must be used and consequently the amount of labour required at planting time is greatly increased. Besides, there is a danger of seed injury, which varies with the kind of soil and its moisture content. More recently (26), experiments with fungicides in dust form, mixed with a fertilizer, have resulted in a much simpler method of control. Fermate or Arasan mixed with 5-8-7 fertilizer and applied before seeding at the rate of 58 pounds of the fungicide per acre has given satisfactory control of onion smut.

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