4-21-1950

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IN RELATION TO WINTER WHEAT BREEDING

DELMAR C. TINGEY

FACULTY RESEARCH LECTURE
NO. 9
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In Relation to Winter Wheat Breeding

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This lecture by Professor Delmar C. Tingey is the ninth in a
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dent faculty at the Utah State Agricultural College. The occasion
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Professor Tingey was elected by the committee to the ninth
lectureship thus sponsored. On behalf of the members of the
Association we are happy to present Professor Tingey's paper:
THE BUNT PROBLEM IN RELATION TO WINTER WHEAT
BREEDING.

COMMITTEE ON FACULTY RESEARCH.
FOREWORD

This publication is a review of some of the more important problems encountered in breeding winter wheat varieties for resistance to races of bunt. The studies essentially cover a period from 1925 to 1942. War work for three years and other responsibilities since have delayed the publication of this material. Therefore, much of the information presented appears in print for the first time. A review is given of the first experiments on dwarf bunt. This early work on dwarf bunt was largely done before this disease became recognized as a problem in other areas.

In order to present the experimental data on which this review was based 20 tables were prepared, which were condensed from many others, with the expectation of including them with the discussion. However, in order to conserve space all the tables but one were deleted. To those who prefer to read from tables it is hoped they will not be overly disappointed. Plans are under way to present the research data in a more complete publication.

ACKNOWLEDGEMENTS

The writer thanks the Faculty Association for the opportunity of presenting the lecture and for the publication of this review. Appreciation is also extended to the committee for the helpful suggestions in the preparation of the manuscript and to Dr. E. L. Waldee and Dr. D. W. Thorne who critically reviewed it and made valuable suggestions, and to Dr. R. H. Walker, director of the Experiment Station, for permission to use the data from annual Experiment Station reports.

Delmar C. TingeY.
The Bunt Problem
In Relation to Winter Wheat Breeding

by DELMAR C. TINGEY

Department of Agronomy
Utah State Agricultural College

Man is forever in search of new and better crops. He has for centuries been a persistent and fairly successful plant breeder. Ancient Chinese are credited with breeding superior varieties of rice and hybrid flowers. Indians in America produced remarkable varieties of corn, and it was not until modern corn breeders developed “hybrid corn” that they produced superior yielding varieties.

The discovery of Mendel’s work on hybridization 50 years ago pointed the way to almost limitless possibilities in plant improvement through breeding. Mendel discovered that if two related individuals were hybridized, it was possible in later generations to obtain progeny with any combination of characters in which the two parents differed. Genetic studies since have shown that by the recombination of genetic factors it is also possible to obtain progeny with characteristics not possessed by either parent. Organisms are thus found to be far more plastic in their hereditary basis than was formally believed. Further proof of these concepts had been demonstrated in breeding new, improved, disease-resistant varieties in many crops. From these concepts and accomplishments, it was assumed that new and better wheat varieties possessing resistance to bunt could be developed in the hope of alleviating a serious bunt problem. As a result of the serious disease situation that existed in dry land wheat, a project on wheat breeding for bunt resistance was initiated at the Utah Agricultural Experiment Station in 1925. This paper is a review of the problems encountered and some accomplishments in breeding bunt-resistant varieties.

THE BUNT PROBLEM

Bunt Is a Common Disease of Wheat

Bunt is a common fungus disease of wheat. Other names for this disease are covered and stinking smut. The latter name is descriptive of a pronounced odor similar to decaying fish which is characteristic of the smut balls and spores. Bunt is one of the
oldest known plant diseases (12). It was known as far back as 500 B.C., and although a great amount of knowledge regarding this disease has been accumulated from then to the present time, it is still a serious agricultural problem.

Reference will be made in this paper to two types of bunt: one in which the infected culms are about the same height as non-infected, and one in which they are about a third or half the height of normal culms; this latter type of bunt will be referred to as “dwarf bunt” to distinguish it from the ordinary type of bunt which will be referred to as bunt.

When the spores of bunt in sufficient amounts become smeared on the wheat kernel, which happens in harvesting grain infected with bunt, it is graded “smutty.” Before smutty wheat can be used for milling purposes, it must be washed; otherwise, the quality is not seriously impaired. Farmers usually refer to bunt disease as smut. Smut, however, is a term used to include many diseases.

There are only two species of bunt fungi in the United States, and both are common in all wheat areas of the west. These have until recently been designated at Tilletia tritici (Bjerk.) Wint. and Tilletia levis Kuehn. In keeping with International Rules of Botanical Nomenclature, T. tritici and T. levis are now designated as T. caries (DC) Tul and T. foetida (Wallr.) Liro, respectively (1). Because the older nomenclature appears in all the records and tables dealing with these two species reviewed here, it will be followed throughout this discussion in the interest of consistency.

The two species differ primarily in the characteristics of the spores in the smut balls. Spores of T. tritici are distinctly reticulated and those of T. levis are smooth. Species are readily identified by examining spores under the microscope.

HOW THE BUNT ORGANISM INFECTS WHEAT

The life cycle of the two species of bunt fungi appears to be the same. The minute plant parasite normally grows in the meristematic tissue of the wheat plant. In threshing and handling bunt-infected wheat, the smut balls are broken and the powdery spores become attached in the crevices and brush end of the wheat kernels or become mixed in the soil.

Under favorable conditions the spores germinate simultaneously with the wheat seed, producing secondary spores known as sporidia, which are of two types. The infection hyphae, or fung-
THE BUNT PROBLEM

us threads, produced by these primary and secondary sporidia penetrate and develop along with the wheat plant until it begins to head. At this time the hyphae break up to form spores, resulting in the production of smut balls in place of wheat kernels (1).

Farmers are interested in knowing those factors that result in the minimum bunt infection, but a plant breeder, in testing varieties or strains of wheat for resistance to bunt, is interested in creating as high a percentage infection as possible. Production of a high infection of dwarf bunt at will has been difficult because of lack of adequate knowledge of the factors influencing severity of dwarf bunt infection. However, part of this difficulty has been overcome by artificial soil inoculation and seeding in moist soil when temperatures were favorable for dwarf bunt infection.

Many factors, no doubt, act together to influence bunt infection, and these are about as numerous and variable as those influencing the wheat plant. Two important ones, in addition to sufficient moisture for germination of the bunt spore, are temperature and spore load.

Since the organism must enter the seedling plant and develop with it to heading, there are two sources of variation, the conditions during and those after the infective period. Conditions favorable for the bunt organism may not be favorable for the host, either before or after infection and vice versa. The right combination of all favorable factors results in maximum infection. Under field conditions it would not be possible to control all these factors, if known; consequently, one can expect seasonal variation in the amount of bunt infection.

SEED TREATMENT FOR BUNT CONTROL

Seed treatment, the principle method for controlling bunt, dates back to 1637 (12). Copper sulfate or better known locally as the "vitrol treatment" was first recommended for smut control in 1761 (12). This method is still used by some farmers. Later, about 1897, the formalin treatment came into use followed by copper carbonate dust (1915), dusts containing ethyl mercury chloride (1929), and dusts containing ethyl mercury phosphate a few years later (1). Improved methods of seed treatment and several new inorganic fungicides have been developed since the war.

Under conditions where soil infection does not occur, seed treatment has been reasonably effective in controlling bunt unless the seed at the time of treating was carrying an excessive load
of spores. However, in the arid regions of the West and particularly in the Intermountain area where fall wheat is grown on dry lands, seed treatment has been ineffective as a method of bunt control. Under these conditions the development of bunt resistant varieties is essential in the production of dry land wheat.

THE ECONOMIC IMPORTANCE OF BUNT

Bunt is a world problem. It occurs wherever wheat is grown, and this crop is grown in all the important agricultural areas of the world.

There are no accurate estimates of the annual losses from this disease in wheat, but they must be enormous. As early as 1914 the losses in yield in eastern Washington amounted to 5 to 10 million bushels annually. In addition, bunt lowered the quality of much of the wheat that was harvested. In this same period, there was estimated to be a half million dollar loss in machinery and grain as a direct result of fires from bunt explosions (1). In 1918 it was further reported that bunt had been present in recent years in nearly all the wheat fields of Idaho, Washington, and Oregon in amounts varying from a trace to as high as 87 percent of the heads infected.

A bunt situation similar to that of the Pacific Northwest occurred in northern Utah and southern Idaho, except that the peak of infection was delayed 5 years. While the percentage of cars of wheat grading smutty is not an accurate index of the actual percentage of smut in the field it does give some indication of the prevalence of smut in an area. Grading reports do not indicate the amount of smut in the grain, so that light and heavy smut are both graded smutty.

Grading records show that as early as 1923-24 nearly one-fourth of the cars of winter wheat coming from northern Utah and southern Idaho graded smutty (fig. 1). By 1929-30, this had increased to nearly 75 percent. From this high percentage there was a sharp decline to 1931-32, this remained steady for two years, and was followed by a sharp increase until 1935-36. Since then the disease has been declining gradually.

Surveys of winter wheat fields in 1929 revealed smut in most of the fields visited, the amount varying from a trace to as high as 80 percent of the heads infected.

Bunt does its greatest damage by reducing the yield of wheat. Experiments with Utah Kanred wheat infected with 25 percent dwarf bunt at Paradise, Utah, showed 35 percent yield reduction. At North Logan 12 percent dwarf bunt reduced the
acres yield 26 percent. In another experiment at Paradise, Utah, 33 percent bunt infection reduced the yield an average of 35 percent. Under these conditions, dwarf bunt reduced yield rela-

tively more than bunt. Resistant varieties, which had a light infection of from 1 to 5 percent bunt, showed a relatively greater reduction in yield than was the case with susceptible ones.

The total damage to the wheat crop in northern Utah and southern Idaho in one year, when bunt is serious, is estimated at $2,000,000 and for Utah about a fifth of this amount. The loss in Utah alone for one serious bunt year is 3 to 4 times the total amount spent on winter wheat breeding for bunt resistance since it began 25 years ago.

DWARF BUNT AND ITS ROLE IN THE SMUT PROBLEM

Two kinds of bunt, known locally as "low" and "tall" smut, were well recognized by farmers in northern Utah in the early '20's or possibly before. Low bunt-infected culms as previously indicated were usually distinctly dwarfed, being from a third to half the height of non-infected culms, varying with the variety and with soil conditions (fig. 2). A small percentage of culms on
low bunt-infected plants would be nearly normal height. Low bunt was considered in this area to be *Tilletia tritici*. Because of the characteristic dwarfing of infected culms by low bunt, it was often referred to as dwarf bunt. This name is more descriptive of infected plants since they resemble the dwarf wheat plants that occur in some wheat crosses. Dwarf bunt is more generally used in the literature, though many farmers still refer to it as low smut. This disease will be referred to in this paper as dwarf bunt. Dwarf bunt, except in some seasons, was far more prevalent than the common bunt.

Dwarfing of infected culms with increased tillering is the most visible characteristic of dwarf bunt as compared with common bunt. It also produces small, round, hard smut balls that are dry and powdery when broken. In most varieties infected with dwarf bunt there is a pronounced spreading effect of the kernels in the spikelets giving a fan-shaped appearance to the spike. Reticulations on the spores are pronounced, but it is not possible to identify dwarf smut by this characteristic alone.

**Origin and History of Dwarf Bunt**

The origin of dwarf bunt is not known. It could have originated as a mutation or by hybridization from other common bunt fungi. Crossing certain varieties of wheat will give rise to progeny in the F2 and later generations that are distinctly different from the parents (8). Such results with wheat suggest that through genetic factor interactions, a natural hybrid of two bunt fungi could have resulted that gave rise to the organism that causes dwarf bunt.

In the early '20's dwarf bunt was already well established in Cache and Box Elder Counties, but was more prevalent in the former county. Farmers in different dry land areas have reported that they could not recall any difficulty with dwarf bunt before the early '20's and some not before the late '20's. However, because of its wide distribution in northern Utah and southern Idaho, it must have been present in the area for many years prior to that time. A Utah bulletin on the grain smuts by Louis A. Merrill and B. F. Eliason suggests that dwarf bunt may have been present in this area even before 1903 (3). They state, “To the close observer it is easily seen that the smutted plants, or parts of plants, are permanently dwarfed. In many instances the infected plants do not head out at all. If these plants are examined it will be found that the enclosed head is very badly smutty ... and 20 to 30 percent of the crop may be smutty.”
In another Utah bulletin by Stewart and Stephens on “The effect of formalin on the vitality of seed grain” published in 1910 (7), the writers indicate that complaints were quite general in the state that the formalin treatment was not effective. This ineffectiveness could easily be explained if the infection had been by the dwarf bunt organism since it causes infection largely through the soil.

If dwarf bunt appeared in Utah prior to 1903, why did it take 15 or 20 years for it to become established throughout the area? Some of its characteristics could account for that. However though dwarf bunt was common in the early '20's, it was not until 1929-30 that it reached its peak (fig. 1). Thus a period of 8 or 9 years elapsed from a spotted distribution to where a high percentage of fields was infected.
Dwarf Bunt Through Soil Infection

The major cause of the serious smut condition

The increasing seriousness of wheat bunt in the late '20's presented a puzzling problem because it was generally considered that seed treatment was an effective method of control. This belief was reported by Richards and Bracken in 1926 (6) in a Utah publication on "Control of stinking smut of wheat with copper carbonate" when they stated that "Effective methods for the prevention of these losses by smut are now available to every grain grower." Experiments that had been conducted on the use of copper carbonate and other methods for bunt control furnished data to support such a belief in seed treatment.

In 1926 the writer (10) reported some preliminary results on the use of copper carbonate as a seed treatment for bunt control and showed it to be highly satisfactory. Repeated experiments the following two years supported these conclusions, except that it was shown that copper carbonate did not give satisfactory control where wheat seed carried considerable smut.

Copper carbonate had been used rather generally in Utah for several years prior to 1926. But the increase in its use coincided with the increasing prevalence of smut. Some agriculturists felt that since copper carbonate was a dust treatment, farmers in general were not equipped to treat the grain thoroughly. However, to correct this condition farmers were encouraged to take their grain to a central cleaning and treating plant. In 1924 one of these plants began operation at Nephi, and a year or two later several others were in operation in Cache Valley where bunt seemed to have increased more rapidly than elsewhere in northern Utah or southern Idaho.

To settle the question on the effectiveness and thoroughness of farmers' treating methods, seed was obtained from grain drills from 15 wheat growers in Cache Valley in 1929 and again in 1930. The farmers' untreated seed was treated in the agronomy laboratory at the College at Logan prior to planting. The farmers' treated seed and that treated in the agronomy laboratory were planted at North Logan under soil conditions known to be free from smut but when temperature and moisture conditions were favorable for smut infection. Data from these surveys demonstrated conclusively that farmers had actually done a good job of treating their seed and that copper carbonate with either 18 or 54 percent copper gave equally good control. On a number
of the farms where the treated seed was being sown at the time the collections were made, however, there was a relatively high percentage of bunt in the wheat.

Soil infection by dwarf bunt was definitely established experimentally in 1929. Observations several years prior to that time had led one to suspect dwarf bunt was soil borne. The reason that soil infection had not been demonstrated earlier was the fact that all experimental plantings had been made on the same farm at Newton where the dry land yield nurseries were located for several years prior to the time the breeding for smut resistance began. This field had not shown soil infection and did not show severe soil infection until some years later, yet it was only a short distance from a field where dwarf bunt had been prevalent for several years.

It would not have been possible even in 1929 to demonstrate experimentally that soil infection was a problem if the experiments had not been repeated at five other locations. Three of the five fields on which plantings were made showed moderate soil infection, all with dwarf bunt.

In 1930 experiments were conducted at seven locations. Again all plantings that showed soil infection were with dwarf bunt. Severe soil infections were found at North Logan and Paradise; on old land, moderate, and on new land, light soil infection at Wellsville. Soil infection was light at Clarkston and in the early seeding at Newton. Plantings in Box Elder and Juab Counties showed little or no soil infection. Various seed treatments did not show any consistent advantage of one over another on either infected or uninfected soil.

From these experiments there remained little doubt that soil infection was a major problem, and that dwarf bunt was, no doubt, largely the specific cause of the serious smut situation that had developed.

Some Additional Characteristics of Dwarf Bunt

Dwarf bunt, besides causing infection through the soil and distinct dwarfing of the infected culms, has a number of other interesting characteristics. In breeding varieties for resistance to disease, it is highly advantageous to be able to transmit the disease at will. This is comparatively easy to do with common bunt. Inoculation is done by thoroughly dusting the seed with powdered smut balls and sowing in moist soil when temperature conditions are favorable for the organism during the germinating and emerging period of the wheat.
SEED INOCULATION NOT SATISFACTORY WITH DWARF BUNT

When the same techniques used in inoculating wheat with bunt were used with dwarf bunt, the infection was not satisfactory. This was first demonstrated in 1929 when 12 collections of dwarf bunt were used to inoculate a set of differential wheat varieties. The inoculated seed was sown when moisture and temperature conditions were considered favorable for infection with this disease; the results were disappointing, the bunt varied from none to a light infection.

The first inoculation made in 1925 with a collection from a dwarf-bunt-infected field resulted in a relatively high percentage of the plants infected with dwarf bunt on susceptible varieties (10'). In 1931 there was a moderate infection with dwarf bunt, the highest was 46 percent, and in 1932 the infection was again light. Under favorable conditions it is possible to get a moderate infection of dwarf bunt from seed inoculations. A moderate infection, in breeding for resistance, is not satisfactory; furthermore, seed inoculation with dwarf bunt is too variable to be relied on.

Unsatisfactory infection from seed inoculation with dwarf bunt spores necessitated the planting of strains to be tested under field conditions where the soil was known to be naturally infected with this organism. In genetic studies, this gave no control of other races present under such conditions.

To solve this difficulty, studies were made to determine the advisability of artificial soil inoculation. Since dwarf bunt normally caused infection through the soil it seemed reasonable to expect this method to be successful. These soil inoculations were made on irrigated land where soil infection has never been a problem. Furthermore, irrigation gave better control of soil moisture. The soil inoculation method has proved reasonably successful and definitely more reliable than seed inoculation.

DWARF BUNT ORGANISMS SEEM TO REMAIN IN SOIL FOR PERIOD OF YEARS

In the Pacific Northwest, two types of soil infection have been recognized (11): One where the smut balls are broken in threshing the grain and the spores blow to the fallow land; the other results from plowing under infected heads that pass through the thresher unbroken. Studies have shown (11) that spores in

Later studies established that it was rather certain that the inoculum used in these early studies was a mixture of dwarf and common bunt, races 2-1 and 3-t.
unbroken balls retained their viability for a year after they were plowed under. Thus they would be available to infect the new wheat seedlings. Soil infection through spore showers, as they are called, during harvest would only cause infection in moist soil for about a month. It was the belief of Woolman and Humphrey (11) that the spore showers during harvest were the principal factors of soil infection in the Northwest. When these studies were made only tall races existed in that area. Smut showers have no doubt played an important role in spreading dwarf bunt in Utah and southern Idaho, but the evidence is against them as the only source of contamination once a field becomes infected.

**Dwarf Bunt Organism Causes Little or No Infection When Wheat is Sown Late and Emerges During Winter**

Dwarf bunt causes little infection if the grain is sown late so that the wheat emerges during the winter. This is probably because of low temperatures. Late sowing is not practical in commercial wheat production since it is difficult to know when winter will start and, if preceded by a rainy period, sowing is prohibited. Furthermore, late planting increases the hazards of poor stands, so that the end result may be lower yields than with the bunt infection.

The first data showing that dwarf-bunt-inoculated grain sown late results in low infection was obtained from experimental plantings in 1930 at Paradise and North Logan. Further evidence came from additional plantings made on these same farms the following two years. In years with insufficient fall rains when wheat emerges during winter, dwarf bunt incidence is light or absent. Data from artificial soil inoculation with both dwarf and ordinary bunt have shown a definite differential behavior from late plantings.

**Relation of Temperature to Infection by Dwarf Bunt**

Woolman and Humphrey (11) report that wheat sown in soil at a temperature above 66°F is practically free from bunt infection. They state, however, that this is not necessarily true if the soil is infected. In reviewing Volkart's work they (12) report that the optimum temperature for spore germination is between 60.8°F and 64.4°F; at 77°F, there was no germination, but the spores remained uninjured. Holton and Heald (1) reviewing Faris' data with constant temperature on bunt infection, stated
that \( T. \textit{levis} \) gave highest infection at 41°F and decreased rapidly at 59°F. Infection with \( T. \textit{tritici} \) was obtained only between 41°F and 59°F.

Experiments over a three-year period 1931-33 at North Logan and Paradise on dates of planting wheat in soil infected with dwarf bunt, show that infections were as high with temperatures in the 60°F range as with temperatures in the 40 and 50°F ranges.

Soil inoculation with dwarf bunt 5 days ahead of planting compared with seed inoculation with bunt race 4-1, each sown at short intervals from August 29 to December 13, shows that dwarf bunt infects wheat at higher temperatures than bunt, race 4-1. Furthermore, dwarf bunt gave some infection even from the first date of sowing, whereas the race 4-1 did not show infection until about a month later. Dwarf bunt infection also dropped off more rapidly on the later dates than bunt, race 4-1. Seeding on the last date when the soil froze soon after sowing resulted in no dwarf bunt but 12 percent infection of bunt, race 4-1. These data further showed the erroneousness of associating an average temperature with amount of disease infection. Three dates with the same average temperature, 46.2°C, gave 47, 38, and 4 percent infection with dwarf bunt and 18, 20, and 53 percent with bunt, race 4-1.

The infection was not high for either bunt. Compared with data for other years, it is evident that there are other factors that are as important or more important than temperature, or it may be that temperature is the important factor, but under field conditions, it cannot be accurately determined. That is, a favorable temperature for a short period may be the determining factor. Dwarf bunt in the soil makes infection possible throughout the fall planting season.

\textbf{DWARF BUNT DOES NOT CAUSE SMUT IN SPRING-SOWN VARIETIES}

Dwarf bunt does not cause smut in spring-sown varieties. This behavior is different from that of ordinary bunt. However, on dry land, spring sowing is not desirable because of low yields. The first data showing the dwarf bunt organism did not cause smut in spring-sown varieties came from experimental plantings made in the spring of 1931, ’32, and ’33. No dwarf bunt appeared in any of these spring-sown varieties. These spring plantings were made to determine if dwarf bunt lived over winter. It appeared that either dwarf bunt did not live over winter or that it did not infect spring-sown grains. The answer to this problem came in
1931 when the F³ progeny from a number of crosses involving one susceptible parent were inoculated with dwarf bunt and planted in the early spring. From this planting not a single head of dwarf bunt appeared in the wheat of either parent or progeny. There was again a small percentage of bunt, caused probably by the light mixture of this in the inoculum. Other studies have further shown that dwarf bunt does not cause smut in spring-sown grain.

**Only One Race of Dwarf Bunt**

From extensive testing and rechecking it has never been possible to isolate different races of dwarf bunt. A planting made in 1936 on artificially inoculated soil produced the highest infection ever obtained with dwarf bunt under experimental conditions. Susceptible varieties smutted as high as 95 percent. A number of collections of dwarf bunt were used to inoculate the soil on different plots on which the differential varieties of wheat were sown. Similar plantings were made from seed inoculation. These latter treatments were sown in clean soil.

Two of the dwarf bunt collections gave evidence of differential behavior in 1936; however, studies made the following year failed to establish differences between the two collections.

**Dwarf and Common Bunt Infection Variable**

Seven years' experiments with artificial soil inoculation with dwarf and ordinary bunt have shown both to vary from low to high infections. In five of the seven years there was a dwarf bunt infection of 45 percent or more in susceptible varieties. The two years of low or moderate infection resulted from late sowings when the grain emerged during winter. There is an interaction between season and incidence of dwarf versus ordinary bunt. In the artificial soil inoculations there have been years when infection of both bunts was moderate, in others the infection with dwarf bunt (1926) was high and with bunt only moderate while in 1937 the reverse was true. This behavior occurred even though different dates of sowing were made. These conditions make it difficult to test resistance in strains of wheat. In years when the infection is light or moderate, moderately resistant strains of wheat appear to be resistant.

5One head was found in spring grain that had the characteristics of dwarf bunt.
PHYSIOLOGIC RACES OF BUNT

In addition to the two species of bunt fungi, *Tilletia levis* and *Tilletia tritici*, there are within each species races which are comparable to strains of varieties in wheat. These races are identified by the degree of infection that takes place in each of a number of wheat varieties when inoculated and grown under conditions favorable for bunt infection. Some varieties of wheat are susceptible to certain races of bunt and resistant to others. For this reason the wheats used to differentiate races are referred to as differential varieties.

The idea of races of bunt was only a year old when the breeding for resistance began at the Utah Agricultural Experiment Station. Little or nothing was known about the number of races or their distribution.

Dwarf bunt is at present considered to be a race of *T. tritici*. *T. levis* was a common mixture in the first collections of dwarf bunt made in 1925, to be used in determining varietal resistance.

During the first four years of breeding for resistance, only inoculum collected from dwarf bunt fields was used in testing varieties and the large amount of hybrid material that had been produced. It was also used for seed treatment studies. The emphasis during these first four years was on breeding for resistant varieties since that was the reason for starting the research.

However, it became evident that one could not develop varieties resistant to all bunts without knowing what races were involved. Breeding had to be modified to the extent of developing resistance to races of bunt. To do this necessitated an investigation to determine the races present.

RACES OF BUNT IN UTAH AND SOUTHERN IDAHO

In determining the number and distribution of races in this area, collections of bunt were obtained from wheat fields in different localities.

The wheat varieties used to differentiate bunt races were Ridit, Hussar, 43e-21 (Relief), White Odessa, Martin, Hohenheimer, Oro, Albit, and Utah Kanred. The latter variety was found susceptible to all collections of bunt. The others had all been reported to possess some resistance to bunt. In 1929, 13 collections of bunt were made and tested, all but one came from dwarf-bunt-infected fields.

In 1930 thirty-one additional bunt collections were made in Cache and Box Elder Counties. While dwarf bunt was found
to predominate, it was evident that other races also were present in the area. Twenty of the thirty-one collections were dwarf bunt. These twenty collections showed little or no infection even on susceptible varieties. These and later studies showed that failure to get high infection from seed inoculation with dwarf bunt was the usual behavior.

Some of the collections were mixed, containing both *T. levis* and *T. tritici*. A number of the mixed collections were purified by a process of screening on differential varieties. From three of these mixtures five races in addition to dwarf bunt were isolated. Three of the races including dwarf bunt, were *T. tritici* and three races were *T. levis*. These races were each given a number with a letter following designating the species.

Out of eighty-three field collections of bunt tested from 1929-33, thirty-seven were dwarf; twenty-three, 2-1; seven, 3-t; eleven, 4-1; one, 5-t, and four, 6-1. Dwarf bunt and race 2-1 made up about 72 percent of the collections. These two races are differentiated by Oro and Hohenheimer, which are susceptible to dwarf bunt and resistant to race 2-1. These two races were nearly always found in the same smutty fields.

In 1936 a field collection of bunt gave rise to one additional race. This race, designated 14-1 was differentiated by Oro, which was susceptible to it. In 1939-40 a study was made of the samples of wheat grading smutty under the wheat loan program. In 1938 there were 34 samples from Utah and 90 from Idaho that graded smutty; in 1939 there were 112 and 359 samples, respectively. Bunt from these samples was increased on a variety susceptible to all races and the inoculum from this was used to inoculate the differential varieties. Increasing these smuts by seed inoculation largely eliminated dwarf bunt; this was intentional as the purpose of the study was to determine if any new races of bunt were present in this area.

All of the races that had previously appeared were recovered, but no new ones. A review of the data again shows race 2-1 to be by far the most prevalent of the bunt races. One of the most striking differences in the two years was the absence of race 14-1 in 1938 and the appearance in 1939 of 90 samples of race 14-1 out of 350. Oro which is susceptible to this race was introduced into southern Idaho from Moro, Oregon, in the early '30's. It was
introduced as a smut-resistant variety but was found to be susceptible to dwarf bunt. The appearance of the large number of collections of race 14-1 indicates that it must have been brought into the state on Oro. It is now well distributed throughout southern Idaho and northern Utah.

Thus, when the writer left to do war work in 1942, the races of smuts as differentiated on winter wheats in Utah were as shown in table 1. Since returning to the breeding project in 1947, collecting and testing of bunts have been resumed, but no new races have appeared. Included in the table are three commercial varieties of wheat developed in the breeding experiments; they are Relief, Cache, and Wasatch. Included also are the additional bunt races that appear on winter wheats but which have not as yet been found in Utah.

Utah races 2-1, 3-t, and 6-1 behave essentially alike so far as the varieties shown in table 1 are concerned; races 4-1 and 5-t behave alike, but differ from the first group; race 14-1 behaves still differently, and dwarf smut differs from all 3 groups. These four groups of races must be recognized in winter wheat breeding in Utah. However, with the likelihood of other bunt races being brought in, which has happened at least once during the course of these studies, there are the 4 groups of races in Utah and 5 other groups of races that must be considered in a breeding program.

BREEDING WINTER WHEATS FOR BUNT RESISTANCE

There are many characteristics to be considered in developing a good commercial variety of wheat, among which are disease resistance, yielding ability, quality, winter hardiness, drought resistance, shattering, straw strength, time of maturity, thresh-ability, grain color, size of kernels, awnlessness, and uniformity of height and maturity. It is not difficult to produce disease resistant strains or strains with any other desirable single character, but when all desirable characteristics must be combined with disease resistance, the problem is more difficult. Breeding is further complicated by the many races of bunt. A knowledge of the number of races and their distribution is basic to breeding. It is a distinct advantage in formulating a breeding program to have some knowledge of the nature of the inheritance of resistance in wheat to races of bunt or to any other character to be improved.
### Table 1. Classification of the 32 races of bunt including the 7 found in Utah, into groups that behave similarly on the differential winter wheat varieties, also the behavior of Relief, Cache, and Wasatch

<table>
<thead>
<tr>
<th>Races with similar behavior</th>
<th>Winter wheat varieties used to differentiate races of bunt</th>
<th>Commercial varieties developed as part of the breeding project</th>
</tr>
</thead>
<tbody>
<tr>
<td>U.S.D.A. No.*</td>
<td>Utah</td>
<td>Kanred</td>
</tr>
<tr>
<td>Dwarf (1-t)†</td>
<td>S</td>
<td>I</td>
</tr>
<tr>
<td>T-1 to 6, 14</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>L-1 to 5, 11, 12, 14</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>T-7, 8</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>L-6, 7, 15</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>L-8</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>T-9, 10, 12</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>L-13</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>T-11</td>
<td>S</td>
<td>S-I</td>
</tr>
<tr>
<td>L-10</td>
<td>S</td>
<td>S</td>
</tr>
<tr>
<td>T-13</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>L-9</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>T-15</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>T-16</td>
<td>S</td>
<td>R</td>
</tr>
</tbody>
</table>

*Key to data in the table based on degree of infection, R=0-10 percent, I=11-40 percent, S=41-100 percent (5). For practical purposes the classification into three groups is probably satisfactory. However, from studies made in Utah there appear to be at least five groups. These are referred to as highly resistant, resistant, intermediate, susceptible, and highly susceptible. It isn’t practical to set limits of infection because the amount of infection in different trials is too variable. It would take years to establish the average infection which would not be of too much value and would, no doubt, vary with different areas.

†Relief used in place of Hussar as a differential variety.

‡Classification for dwarf bunt is based on conditions favorable for high infection, otherwise Hohenheimer and Oro would fall in the I class, Ridit and Cache in the R class.
DIFFERENTIAL GENETIC INHERITANCE OF RESISTANCE TO RACES OF BUNT IN WHEAT

The inheritance of resistance is one of the more difficult characters to deal with. The reason for this is the important part the environment, over which man has little or no control, plays in relation to disease.

Genetic studies on the inheritance of resistance in wheat to races of bunt have been made in a large number of crosses. Some of the most characteristic types of inheritance will be briefly reviewed because of their significance to the breeding program.

In a cross between a sister selection to Wasatch, 122a-394-4 and Oro, the F3 behavior showed a marked tendency for resistance to be dominant to race L8 (14-1). Of the 436 F2's tested, 387 were more like the resistant parent.

Other crosses have shown resistance to be recessive. Relief is susceptible to race 4-1 and resistant to race 6-1. In a Relief x Ridit cross only 6 out of 199 were like the resistant parent. Relief crossed with Hybrid 128 x White Odessa showed a somewhat similar behavior to the preceding cross; there were 47 out of 292 F2's like the resistant parent when inoculated with race 6-1.

In still other crosses, resistance is neither dominant nor recessive but is intermediate. This is shown in a Goldcoin x Ridit cross when the F2's were inoculated with race 6-1. In this cross a large part of the F2 progeny was intermediate in resistance between the two parents.

A number of crosses have shown transgressive inheritance. Crossing two resistant parents has given rise to highly susceptible progeny. The Relief x Ridit cross, where one parent is highly resistant to dwarf bunt and the other intermediate, gave highly susceptible progeny.

In a 53a-37 x Hohenheimer cross, with seed of each F2 plant divided and inoculated in one case with race 3-t and in the other with 2-1, gave a high proportion of the F2 progeny definitely more susceptible than the susceptible parent.

Transgressive segregation has been reported in the other direction, that is, in crossing two susceptible varieties, resistant progeny have resulted. The genetic explanation for these situations is that there are at least two major genetic factors involved and each parent possesses one. Recombination of genes results

Rodenhiser and Holton (5) used the letter of the species ahead of the number which is not the same as the Utah number.
in segregates without any resistant factors in some and with resistant factors in others. This is related to resistance being dominant or recessive. In those crosses where resistant x resistant give susceptible progeny, resistance is dominant, and in those crosses where susceptible x susceptible give resistant progeny, resistance is recessive.

Only one or two crosses have been studied where both parents were highly susceptible, and in these, none of the progeny was resistant. This behavior is explained by assuming neither parent possessed any factors for resistance.

In certain crosses where the two parents were moderately resistant there is evidence that some of the progeny are more resistant than either parent. This can be explained by assuming minor genetic factors that behave in the same way as major factors.

**GENETIC FACTORS CONTROLLING RESISTANCE**

Resistance, being either dominant, recessive, or intermediate, can in some cases be explained on a single factor difference. In others, two factors are required and in still others, the behavior is more complex. In some crosses, it is possible that minor factors are also involved. In one cross the data suggested two factors with linkage.

Transgressive segregation in some crosses is evidence that more than one factor is controlling resistance. It is these different factors for resistance in wheat that makes differential varieties possible.

Although 32 races of bunt have been identified with the differential varieties used, a number of these give identical behavior though they are different species. Inheritance of resistance in wheat to these races could all be accounted for by relatively few genetic factors.

**ACCOMPLISHMENTS IN BREEDING**

The first experiments conducted with dwarf bunt in 1925 (10) demonstrated the resistance of Hussar, Martin, Ridit, and White Odessa; later Albit, Hohenheimer, Oro, and Relief were added to the list. Ridit is actually intermediate in resistance and Hohenheimer and Oro were found susceptible to dwarf bunt. When conditions are not favorable for high infection with the dwarf bunt organism, Hohenheimer and Oro will show little or no
smut. Most of the varieties developed by hybridization and resistant to dwarf bunt have one or the other of the above resistant varieties as a parent.

The varieties grown commercially in Utah during this early period were Turkey, Utah Kanred, Goldcoin, Silvercoin, Jones' Winter Fife, Odessa, and a mixture of varieties locally known as Cache Valley mixed. These were all, with the exception of Odessa, susceptible to dwarf bunt. Turkey and Utah Kanred were grown more extensively than the others since they were higher yielding and had better grain quality.

None of the introduced resistant varieties had been grown in this area and only Ridit showed any promise of being of commercial value. It proved to be less resistant to dwarf bunt than the others, however, and did not yield well.

All these resistant varieties were used in hybridization with local varieties with the aim of combining the desirable characteristics of the local ones with the dwarf bunt resistance of those introduced. Hussar, Martin, White Odessa, and Albit, which were highly resistant to dwarf bunt, were found later to be highly susceptible to some of the other races of bunt in this area. This condition limited their usefulness as parents to be used in crosses.

Careful consideration must be given to various hybrid combinations, always keeping in mind the importance of yield and quality and other desirable characters, besides bunt resistance. Ridit was the only variety that had shown resistance to all races in this area, but to dwarf bunt as indicated and to some of the other races, the resistance was not too high when conditions were favorable for high infection.

At the same time, the number and distribution of races of covered smut were being determined, the breeding work was progressing at a rapid pace even though it was in a way like taking a wild shot in the dark. There was, however, one definite objective and that was to breed for resistance to dwarf bunt. To develop a resistant variety in the shortest time meant using parents as nearly alike as possible. One of the crosses was Hussar x Turkey 26. These varieties are both hard red winter wheats and look alike. It was known that Hussar had grain of poor quality and shattered badly. The cross was made in 1926, and a resistant selection, later named Relief, was released in 1931 in small lots to three farmers. Following its introduction its acreage increased rapidly (9). It had yielded well in two years under a number of different conditions and with the limited seed avail-
able it was possible to obtain two or three additional years' data before it was finally necessary to recommend or reject it for commercial production. Relief continued to yield well, had satisfactory grain quality and high resistance to dwarf bunt; it was however susceptible to two other races of bunt in this area and it had a tendency to shatter.

Shattering has become a vexing problem in the breeding work at the Utah Station. Many of the most promising selections have, under certain conditions that show up only occasionally, a tendency to shatter, and whole families and numerous otherwise good selections have been discarded as a result.

Two races of bunt, 4-1 and 5-t, to which Relief was highly susceptible, had been isolated in this area. From this it was evident that this variety, while valuable in the control of dwarf bunt, would eventually have to be replaced with varieties resistant to these two additional races.

Another selection, later named Cache, was released in small lots for commercial production a few years later than Relief. Cache was selected from a Ridit x Utah Kanred cross made in the same year as the Hussar x Turkey 26 cross. Cache is like Ridit in resistance, it is resistant to all races of bunt in Utah and intermediate in resistance to dwarf bunt. Except when conditions are favorable for high dwarf bunt infection, Cache will get by with little or no smut.

A third selection named Wasatch, from a Relief x Ridit cross, was released for commercial production in 1942. This new variety has yielded slightly less than Relief or Cache, except when they become smutty. It also has a tendency to shatter under some conditions. It is resistant, however, to more races of covered smut. Wasatch is highly resistant to dwarf bunt and to all the other races of bunt that have appeared in Utah and southern Idaho. It is moderately susceptible to two other races that have been isolated in other areas (table 1).

Selections from additional crosses that show resistance to all known bunt races are now well along. With each new variety, the gap is being narrowed between a condition where all commercial varieties were susceptible to all races of bunt to one where the varieties are resistant to all races.

**New Varieties are Grown Extensively**

Only two of the three varieties released are now grown extensively; these are Cache and Wasatch.
During the past two years surveys have been made of dry land wheat grown in Box Elder and Cache Counties to determine to what extent the new varieties are being grown, to get information on the bunt situation, and to make bunt collections to determine if new races have been brought into this area. In 1948, 64 percent and in 1949, 72 percent of the fields were planted to either Cache or Wasatch. The remaining percentage was largely a mixture of varieties. In many cases, a large part of the mixture was Cache and Wasatch.

In 1949, 80.7 percent of the wheat acreage in Utah, according to crop reports, was hard red winter. In 1949, Cache and Wasatch occupied 58 percent of the hard red winter wheat acreage in the state. These two varieties were grown on approximately 215,000 acres, with a production of about 4.4 million bushels at a farm value of nearly 7 million dollars. Similar data are not available for southern Idaho, but if it were comparable to Utah it would add approximately an additional 20 million dollars worth of Cache and Wasatch wheat produced in 1949.

About a third of the dry land wheat fields surveyed in Cache and Box Elder Counties in 1949 contained varietal mixtures. In these fields of mixed wheat, some of the mixture is old smut susceptible varieties, and it is here that most of the bunt is found and especially the higher percentages of infection.

Mixtures in wheat are the result of either carlessness on the part of the farmer or often to volunteer grain. Methods of dry farming are such as to permit wheat from one crop to carry over in the soil and germinate and emerge with the next. This is not serious if it happens to be the same variety, but it is serious if the volunteer variety is bunt susceptible.

THE BUNT SITUATION IN 1948-49

Data from the surveys in 1948-49 compared with those from surveys made in the late '20's and during the '30's show a remarkable change in the amount of bunt in the fields. Surveys made in the earlier period, as previously indicated, showed most of the fields contained bunt, and it was not uncommon to find fields with 30 to 60 percent of the heads infected. In the 1948 survey, 84 percent, and in 1949, 94 percent of the fields visited had no bunt or only a trace. Most of the remaining fields ranged from 1 to 5 percent infection. In 1948, only one field visited had as

*Made by the writer and Dr. E. L. Waldee, associate professor of plant pathology, Utah State Agricultural College.
high as 30 percent, and in 1949, only one field had as high as 20 percent bunt. On one of these fields, the wheat was badly mixed, and in the other Turkey, a susceptible variety, was grown.

The survey also revealed that dwarf bunt, while greatly reduced from what it was, is still about twice as prevalent as ordinary bunt.

**Winter Wheat Breeding in the Future**

Breeding for bunt resistance must be continued. At least two races of bunt are known that will infect Wasatch, the variety with resistance to more of the races than either Cache or Relief. While these races have not yet been found in Utah, it seems reasonable to expect that eventually they will be. Furthermore, new races will undoubtedly be found.

Genetic studies on inheritance in wheat to bunt resistance indicate that higher resistance than anything now available, or even immunity, may be possible.

Hard red winter wheat, the type grown on dry lands, must be of good quality if the milling industries in this area are to be maintained. Good quality includes high protein content of desirable composition. High acre yields must be maintained if wheat farming is to remain a profitable enterprise. To breed dry land wheats of high protein content and yield is a challenge to the breeder. Studies have shown a negative correlation between varietal yields and protein. This relationship has led some to doubt that higher yielding, better quality varieties can be produced. The correlation is not perfect nor is it overly high. Correlation is a measure of an average association and does not mean that among varieties some are not better than others. There is ample proof that this is the case, otherwise, varieties would be either high yielding and low protein content or vice versa. Actually there are all gradations among varieties, and in relation to yield and protein content, they are to a great extent independent.

Utah Kanred is proof that high yield and high protein can be combined in the same variety. Few varieties, regardless of protein, yield higher than Utah Kanred, and likewise few varieties, regardless of yield, have higher protein of better quality. All desirable characters must be combined in a variety to be of greatest value. The raw materials are present among wheat varieties, and hybridization is a means of combining them into the kind of a variety the breeder wants, but to do this requires time and energy.
This paper has summarized some of the more important results of twenty years of breeding winter wheat for resistance to various races of bunt. When the breeding began in 1925, dry land farmers in northern Utah and southern Idaho were confronted with a serious bunt problem. Even though seed treatment with improved methods was generally used, the problem grew progressively worse, and by 1929-30 approximately 75 percent of the grain graded smutty. A survey revealed bunt to be present in most fields, and in many fields a high percentage of the heads was infected. This serious smut situation was found to be caused largely by dwarf bunt through soil infection.

Dwarf bunt was found to differ in a number of respects from other bunt races. Dwarfing of infected culms, increased plant tillering, the production of small, round, hard smut balls and the spreading of the spikelets are the most visible characteristics of plants infected with the dwarf bunt organism. Most of the infection from dwarf bunt was through the soil so that seed inoculation, as used with other bunt, was not satisfactory. Once a soil became infected with the dwarf bunt organism, the infection seemed to remain for a period of years.

Dwarf bunt does not cause smut in spring-sown grain. Furthermore, it causes little or no smut if the grain is sown late and emerges during the winter. This probably results from the fact that dwarf bunt does not infect wheat at as low a temperature as other races. It does, however, cause infection at higher temperatures than the others and infects wheat over a wider range, which includes the entire planting season in this area.

Dwarf bunt, however, was not the only race present in the area. By 1931 five other races had been isolated. In 1936, an additional race was found. Dwarf bunt and race 2-1 were the predominating races throughout the twenty-year-study period and both were nearly always in the same smutty fields.

It is not difficult to breed wheats resistant to races of bunt or other desirable single character, but when all characters required in a good commercial variety must be combined with resistance to all races of bunt, the problem is not a simple one.

Genetic studies on the inheritance of resistance in wheat to dwarf bunt and other races have shown some interesting results. Genetic data suggest the possibilities of developing more resistant varieties than now available. In some crosses, resistance is dom-
inant, in others it is recessive, and in still others it is intermediate. Some crosses have shown transgressive inheritance; crossing two resistant varieties gave susceptible progeny.

Inheritance of resistance in wheat to races of smut can in some crosses be explained on the basis of a single factor pair; in others two factors are required, and in still others, the behavior is more complex.

Three varieties, Relief, Cache, and Wasatch, developed in these studies, have been released for commercial production. Wasatch is the most smut-resistant of the three and is resistant to all bunt races appearing in Utah and southern Idaho. It is susceptible, however, to some races not found in Utah. Cache is higher yielding than Wasatch but less resistant, especially to dwarf bunt. About two-thirds of the wheat grown in northern Utah is either Cache or Wasatch, and they are grown in about equal proportions.

Recent surveys and grading records compared with earlier ones reveal a remarkable reduction in the number of smutty fields and in the percentage of heads infected.

**LITERATURE CITED**

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