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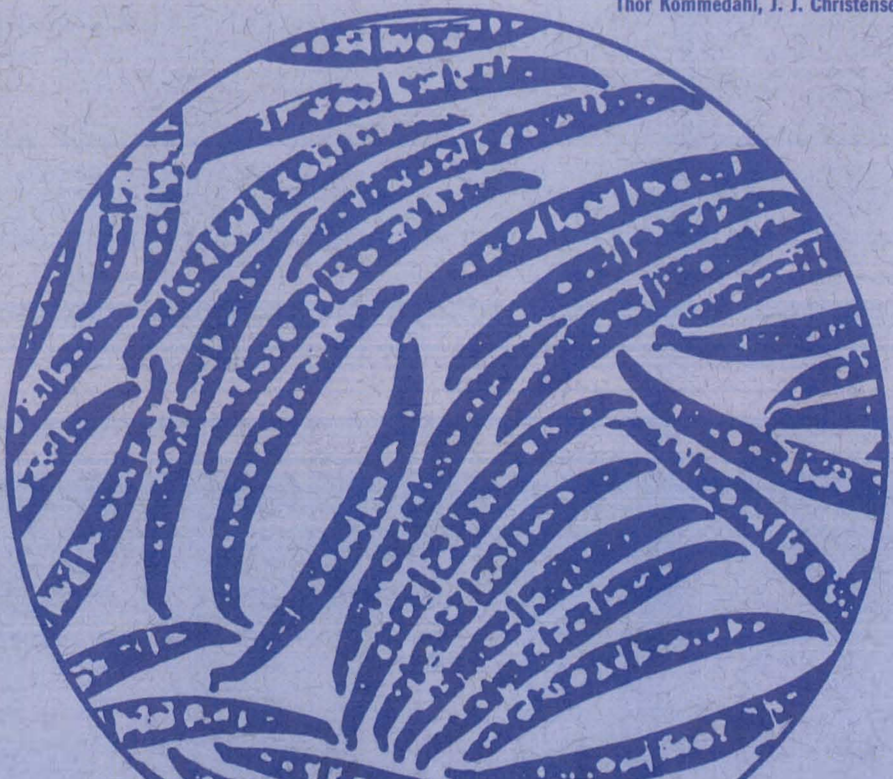
A Half Century of Research in Minnesota on Flax Wilt Caused by *Fusarium Oxysporum*

Thor Kommedahl, J. J. Christensen, and R. A. Frederiksen



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Summary

The early work on flax wilt was started in the United States in 1889 by Otto Lugger, a biologist in the Minnesota Agricultural Experiment Station. Although he wrongly concluded that flax straw, not a fungus, was the cause of wilt, he stimulated work in Minnesota and elsewhere on the cause and control of flax wilt. In 1893, Hiratsuka in Japan and in 1901, Bolley in North Dakota established that flax wilt was caused by a **Fusarium** species, now named **F. oxysporum** f. sp. **lini.**

Four types of wilt symptoms are described: early (seedling), late (wilt after anthesis), partial, and unilateral. Early wilt is potentially the most destructive, since 100 percent of the plants in a stand may be lost. Late wilt has been observed in 20-90 percent of the plants in a given year and generally results in a premature ripening of plants with shriveling of some seed. The yield loss can be 20 percent, based on the weight of 1,000 seeds. Also, late wilt reduces numbers of seeds per boll and thereby per plant. Partial and unilateral wilt are of less importance and averaged 3-5 percent in prevalence during a 3-year observation period of 40 flax varieties in a wilt nursery.

Fusarium oxysporum f. sp. **lini** is limited in its host range to species of flax and survives for decades in infected crop debris in soil. The fungus is seedborne and can be disseminated on infected stem fragments.

F. oxysporum f. sp. **lini** comprises an indefinite number of races that differ from each other in numbers of plants wilted per variety when tested in the greenhouse with single isolates in autoclaved soil. Isolates or races from Arizona and California have proven more pathogenic than races from Minnesota on Minnesota varieties. Differences in wilt from one location to another in Minnesota suggest differences in races in the field. Evidence also may be interpreted to indicate a single common race with minor gene differences among isolates.

Temperature is the single most important environmental factor affecting wilt in flax. Its importance was shown in the field in a 17-year period with 40 varieties and a 3-year test with 39 varieties. There was a direct relationship between the number of hours during the growing season that the soil temperature exceeded 21° C. and the percentage of plants that wilted. The number of days that the soil temperature reached or exceeded 24° C. was not as reliable an indicator as the number of hours the temperature was 21° C. or above would have been.

At low soil moisture the incidence of wilted plants increased among moderately resistant or moderately susceptible varieties in the field. This factor may be an indirect one and may affect soil temperature or numbers of antagonists.

Wilt was found on all the major soil types in Minnesota, but there were fewer wilted plants on peat soil. In greenhouse and field tests, the addition of nitrogen, potash, and possibly phosphate reduced the incidence of wilt in susceptible varieties. However, it was not established whether fertilizers affected host or pathogen, or both. Seven herbicides applied singly did not affect incidence of wilt in the field.

Plants grown from cracked or split seeds were more subject to wilt than plants grown from sound seed of the same variety. The wilt fungus entered seeds through injuries in the seedcoat and invaded cotyledons, hypocotyl, and radicle. Upon germination, the fungus entered seedlings through root hairs or root epidermis.

The first pure line variety (Primost) developed in the United States was selected by plant breeders in Minnesota in 1904, but it proved susceptible to wilt. The varieties Chippewa, derived from Primost, and Winona were released in 1922 as wilt-resistant varieties in Minnesota. In 50 years of breeding, selection, and testing, hundreds of wilt-resistant varieties have been developed in cooperation with plant breeders in the Department of Agronomy and Plant Genetics and the U.S. Department of Agriculture. Most of the testing for wilt resistance was done in a St. Paul "wilt nursery" planted continuously to flax since 1913. Susceptible lines of flax, among the thousands tested annually, are eliminated from the population in the wilt nursery. Only wilt-resistant plants survive the exposure to the mixture of isolates present in the soil. The effectiveness of testing is shown in the predominance of wilt-resistant varieties now grown in the north-central states. The effectiveness also is apparent from tests on the world collection of flax in the wilt nursery at St. Paul. Varieties developed in the United States in that collection (305 varieties) averaged only 27 percent wilted plants, but varieties developed in 28 countries averaged 54 percent. Moreover, of the 59 varieties developed at Minnesota and the 169 developed in North Dakota, the average percentage of wilted plants was 22-23 percent, while the average for varieties developed outside the north-central states (but tested at St. Paul) ranged from 30 to 100 percent. Another measure of effectiveness of developing resistance was shown in a 1954 test comparing varieties of the world collection selected in Minnesota from 1919-30 with varieties developed during 1941-53. Sixty-two percent of the varieties in the first group wilted; only 4 percent in the second group did.

Survival of varieties depends upon disease incidence. Seeds of 10 morphologically distinct varieties were mixed, sown in different fields, harvested, and planted again in the same or different fields for 4-5 years. After 4 years in the wilt nursery, six of the 10 varieties had disappeared from the population and, of the surviving four varieties, Bison and CI 671 comprised 89 percent of the plants. After 5 years in another sequence, Bison, Redwing, and CI 671 predominated. In 3 of 5 years, wilt resulted in predominance of Bison and CI 671, but in a still different sequence the lack of exposure to wilt for the first 3 years and the presence of rust, to which Bison is susceptible, resulted in the predominance of Redwing. In this same study, losses in yield attributable to wilt ranged from 30 to 50 percent.

In another test, six flax varieties were sown in a nursery where flax had been grown for 43 years. The yields of five of these varieties averaged 8-16 bushels per acre for the 3-year period, while yields from the same varieties for the same period on wilt-free soil averaged 19-27 bushels per acre. These differences were due to wilt, but probably also were due to differences in soil fertility.

Studies on inheritance of resistance to wilt showed that wilt resistance in the F_1, F_2, F_3, and F_4 populations from crosses of resistant and susceptible parents usually was intermediate in resistance between the parents. Wilt resistance was not associated with sex of the parent. Of 47 crosses of resistant and susceptible varieties, the F_1 populations usually were intermediate. Two-thirds of 33 F_2 populations were intermediate in resistance, and none of the 33 was appreciably more resistant than the resistant parent or more susceptible than the susceptible parent. In four crosses, 55-96 percent of the F_3 populations were intermediate to the parents in resistance. The resistant parent influenced F_3 progenies more than the susceptible parent did in three of the four crosses. The influence of the resistant parent also was obvious in a cross of a resistant (Bison) and a susceptible (Newland) variety, where only one of 125 F_4 families had more than 50 percent wilted plants. Some varieties wilt early, some late, and some wilt throughout the season. Progenies from crosses of parents that wilt late also wilted late in limited tests.

Resistance to wilt appears to be non-race specific, or field (horizontal), resistance. If it occurs, race-specific resistance probably is of less importance than field resistance, because varieties are exposed to a composite of isolates in the field. Testing for field resistance in a wilt nursery where flax has been grown continuously for many years is an eminently effective method for developing wilt-resistant varieties of flax, and varieties developed in this way remain resistant for a relatively long time. In fact, wilt seldom has been found in commercial fields of flax in Minnesota during the past decade.

A Half Century of Research in Minnesota on Flax Wilt Caused by *Fusarium Oxysporum*

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In 1913, the year the "flax-sick plot" was established at Minnesota, flax wilt, caused by *Fusarium oxysporum* f. sp. *lini* (Bolley) Snyd. & Hans., was the limiting factor in the production of this oil seed crop. Then it was virtually impossible to grow flax successfully on land previously cropped to flax unless the soil had been free from flax culture for 7-12 years. When flax followed flax, there frequently were complete crop failures (6, 7, 43). The production of flax declined substantially from about 1900-19 (67). In fact, flax production failed to increase again until new resistant varieties were developed and distributed to growers.

Today, wilt-resistant varieties of flax can be grown successfully not only on old, cultivated land but also on flax-after-flax land and even on plots continuously cropped to flax for 50 successive seasons.

Fiber flax culture preceded oil flax culture by about 100 years in the eastern United States, and it was not until 1770 that flax was first grown commercially for seed. Flax culture spread westward from New York and New Jersey to Pennsylvania and had reached the Upper Midwest by 1900. Minnesota, North Dakota, and South Dakota became the leading states, producing more than 16 million bushels of flax seed. Currently, Minnesota produces about 6.3 million bushels.

The westward march of flax culture during the 1800's has been ascribed to several causes, but wilt apparently was the primary one, even though it was not the most obvious cause at the time. By 1885 or 1890, flax wilt had become destructive to an alarming degree in Minnesota and North Dakota.

Reports indicate that flax wilt has been by far the most destructive in the United States and Japan and less so in Argentina and Canada. In Europe, long term rotations have been practiced for centuries and may well be the reason that this disease has not become a major problem there. In some parts of the world, flax wilt never has been destructive, perhaps because the soil temperatures are relatively low during the early growth period of flax plants.

This publication, which deals chiefly with seed flax investigations and to a limited extent with fiber flax, embraces over a half century of cooperative work by the University of Minnesota's Department of Plant Pathology and Department of Agronomy and Plant Genetics and the U.S. Department of Agriculture. During this period, 1913-63, many state and federal investigators contributed to the results reported here.[*]

History

Although the cause of flax-sick soil was not established until about 1900, the disease apparently was recognized long before in Europe (15, 43). In fact, Pliny (11), in 29 A.D., stated that "flax has the property of scorching (exhausting) the ground where it is grown and of deteriorating the quality of the very soil itself".

The pioneer work on flax wilt in the United States was begun at Minnesota in 1889 by Otto Lugger, a biologist. According to Lugger (43), "the industry and farmers had suffered greatly during the last 5 years in many regions from a mysterious disease" of flax. These men were greatly concerned about the future success of flax culture. Farmers appealed to the governor of Minnesota, W. R. Merrian, for assistance in solving this "threatening evil". The governor secured the cooperation of the regents of the University of Minnesota, and Lugger was appointed to investigate the troubles that rendered soil unfit for flax culture.

Lugger (43) made his original field experiments on flax-sick soil in the vicinity of Windom, Minnesota. He proved that applications of fertilizers to the soil did not prevent wilting in flax. Even different kinds and amounts of fungicides in soil failed to control wilt. When he added old flax straw, chaff, and water extracts from diseased flax plants, severe wilt developed on hitherto wilt-free soil.

From these experiments, made in 1890, Lugger concluded that flax straw itself, not a pathogen, was the cause of wilt, for no control was obtained with fungicides. Additional experiments made with flax straw and plants in the greenhouse led Lugger to the same conclusions. Although Lugger reached the wrong conclusion, he made a great contribution by creating an interest in the flax wilt problem. Scientists from elsewhere, North Dakota especially, came to see Lugger's experiments, became intrigued with the problem, and returned to their laboratories and field plots to work on this important disease.

By 1896, Snyder, a chemist at Minnesota, had proved beyond doubt that low soil fertility, as then generally

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[*] Plant Pathology: E. C. Stakman, J. G. Leach, O. S. Aamodt, H. D. Barker, A. W. Henry, C. V. Kightlinger, H. A. Rodenhiser, C. C. Allison, J. J. Christensen, T. Kommedahl, and R. A. Frederiksen; Agronomy and Plant Genetics: H. K. Hayes, A. C. Arny, A. H. Moseman, J. O. Culbertson, and V. E. Comstock.

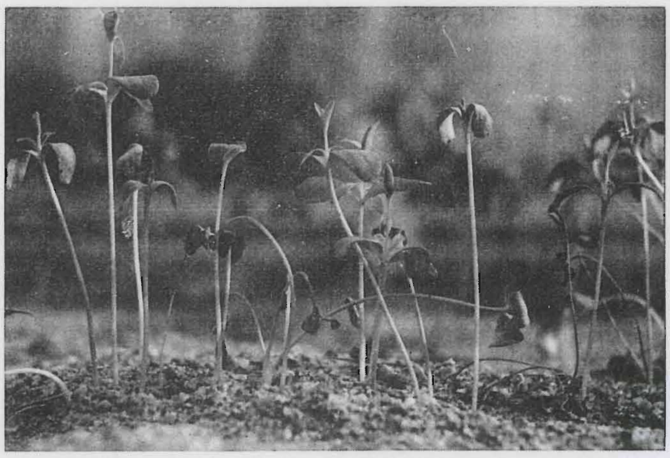

Figure 1. Early symptoms of seedling wilt caused by **Fusarium oxysporum** f. sp. **lini**. Cotyledons curl initially, followed by wilting of the stem. Finally, stems turn brown and the fungus can sporulate on the dead stems.

Figure 2. Complete loss of plants of wilt-susceptible varieties of flax grown on wilt-sick soil as indicated by the absence of plants next to wilt-resistant varieties. Flax had been grown continuously for 50 years in this plot.

assumed, was **not** the cause of flax-sick soil. In fact, he clearly established that a crop of flax extracted less mineral matter from the soil than did a crop of wheat (56).

According to Tochinai (63), Miyabe had concluded in 1892 that a species of *Fusarium* caused flax to wilt. In 1893, Hiratsuka (28) confirmed Miyabe's findings, although his work was not published until 1897. Bolley, unaware of the work done in Japan, demonstrated in 1901 that flax wilt was caused by a fungus, which he named *Fusarium lini* (7). The name was changed in 1940 from *F. lini* Bolley to *Fusarium oxysporum* f. sp. *lini* (57).

In 1893, Broekema (15) had evidence that varieties of flax differed in susceptibility to wilt. However, it was Bolley (7) who first observed in 1901 that some flax plants grown on thoroughly infested soil survived when nearly all other plants died. The following year, these selected plants again were resistant. For a long time, Bolley and others assumed that flax plants had to be grown continuously on such soil to maintain their resistance. As late as 1913, Bolley recommended that farmers should set aside 1 acre of wilt-sick land as a permanent flax seed plot in order to have resistant seed for sowing the next season.

It was not until 1923 that Barker (6) definitely established for the first time that a pure line of flax remained resistant whether it was grown on wilt-free or wilt-sick soil. Others have verified this fact (1, 5, 16).

Although resistant varieties have been released, they have not always remained resistant to wilt. When released by Bolley in 1913, varieties N.D. 52, N.D. 73, and N.D. 114 were highly resistant to wilt, but in 1916 they were susceptible when tested in the flax-sick soil at St. Paul. This development can best be explained on the basis of physiologic specialization.

In 1926, Broadfoot and Stakman (14) and Broadfoot (13) described nine parasitic races of *Fusarium oxysporum* f. sp. *lini*. Since then it has been reported that *F. oxysporum* f. sp. *lini* comprises an indefinite number of races or biotypes that differ essentially in their parasitic capabilities on different varieties of flax (9).

Because resistance to this wilt pathogen is only relative and is modified readily by environmental factors, especially temperature, and because this fungus consists of innumerable pathogenic biotypes, very little is known about the nature of inheritance to wilt. Tisdale (61) in 1917 and Burnham (16) in 1932, among others (1, 33), have suggested that multiple factors are involved in resistance.

Symptoms

Wilt symptoms are classified into four types: early or seedling wilt, late wilt, partial wilt, and one-sided or unilateral wilt. All types of wilt may be found in a wilt-susceptible variety, but seedling wilt usually predominates.

Wilt symptoms may appear at any stage of flax growth and may vary greatly with the age and variety of plant, environmental conditions, and the physiologic race involved. Bolley (7) reported that young seedlings may be killed before they emerge from soil; however, Flor (24) found that seedlings were not infected prior to formation of cotyledons in the field. Diseased plants may occur at random throughout the field or may appear in distinct patches.

Early Wilt

Young seedlings of susceptible varieties can die before they emerge from soil, but they usually wilt and die from the cotyledonary stage until they are 15 centimeters (cm.) tall. At first, infected plants appear sickly, begin to wilt at the top, then slowly die and eventually become dry and brown. The symptoms first become evident when the edges of the cotyledon roll inward and then collapse (figure 1). About this time the stem usually becomes somewhat constricted at the ground level, and the seedling eventually falls over and becomes very brittle. If the soil is moist the dead seedlings may become covered by

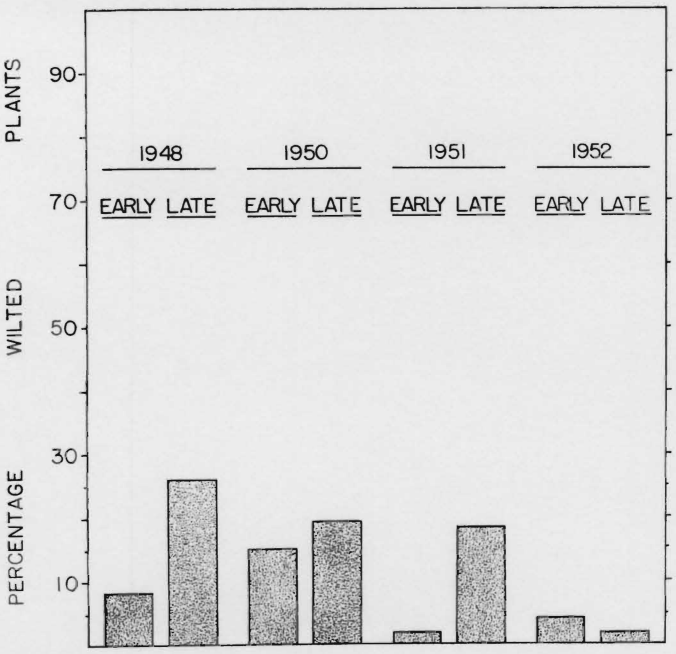

Figure 3. Percentage of plants that wilted early and late in 4 years of testing. Figures are averages of 40 lines and varieties of about 100 plants per variety in a wilt nursery begun in 1913.

mycelium, which then may sporulate. Wilson (71) also observed sporulation on dead seedlings. Symptoms can be seen 6 days after inoculation (18).

Seedlings killed early often are overlooked. The leaves or even the entire plant may be readily washed away by heavy rains or become covered with soil. Consequently, there may be a spectacular loss of plants, such as shown in figure 2.

On older plants the first appearance usually is a slight yellowing or browning of the upper leaves on a green stem. If the temperature is about 22° C. or above the leaves on the tip of the shoot droop, turn brown, and die. Eventually, these leaves fall off and leave a brown but erect stem. The roots of infected plants usually appear healthy, although the cortex can be easily peeled off. The fungus frequently fruits abundantly at the bases of these plants.

Early wilt seems to be less prevalent than late wilt (figure 3). However, varieties apparently differ in resistance to early and late wilt, as seen from comparing prevalence of wilt in 1950 (figures 3 and 4). Comparing average wilt for 39-40 varieties for a 3-year period (1948-50), early wilt averaged about one-third as prevalent as late wilt. This has not always been so, and the situation will vary from season to season with changes in variety and climate.

Because of the emphasis on selecting varieties resistant to early wilt during 1901-40, varieties susceptible to late wilt could have been overlooked (figures 3 and 5). However, notes on wilt resistance sometimes were taken several times throughout the growing season and it was all called wilt, with no distinction between early or late wilt. This fact makes it difficult to compare prevalence of early and late wilt in the early part of the period. Varieties may differ in susceptibility to early or late wilt (38).

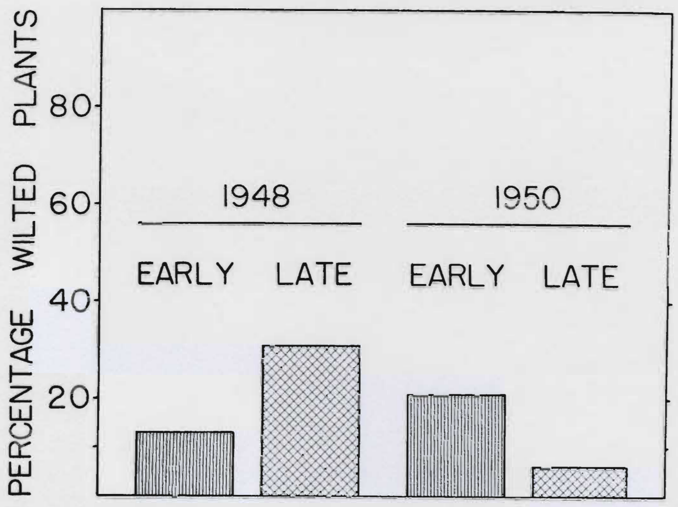

Figure 4. Percentage of plants that wilted early and late in 2 years of tests. Figures are averages of the same 39 varieties of flax tested in a special wilt nursery started in 1946 at St. Paul.

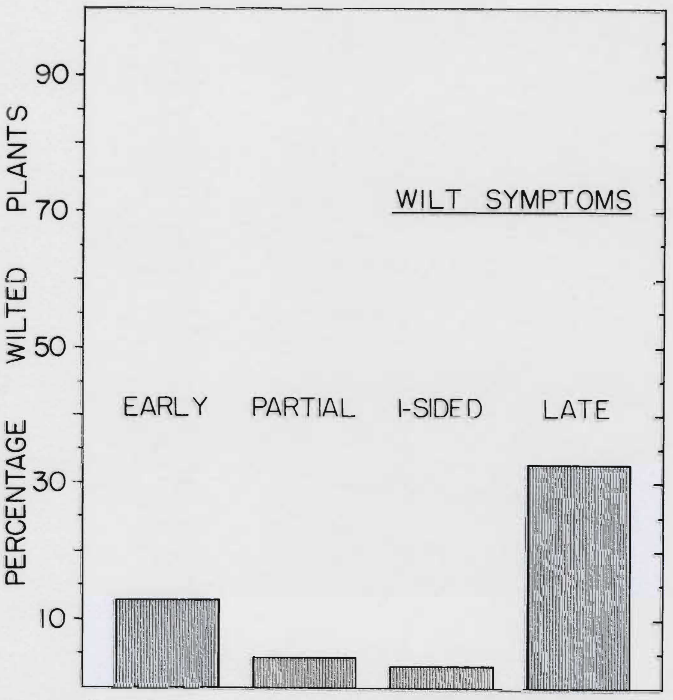

Figure 5. Percentage of wilted plants with the four types of wilt symptoms, based on averages for three seasons (1948-50) with the same 38 varieties of flax, four replicates of about 100 plants per replicate. Results were obtained from a special wilt nursery begun in 1946.

Even though early wilt may be less prevalent than late wilt, early wilt may be more destructive. When a given plant wilts early, it dies and disappears and there is no seed yield. If the plant recovers so that only partial wilt occurs, there still can be some seed yield. If the plant escapes early wilt, either because of heredity or changes in the environment, but then succumbs to late wilt, the seed loss frequently is not complete, as shown by the presence of some reasonably good seed in figure 6A.

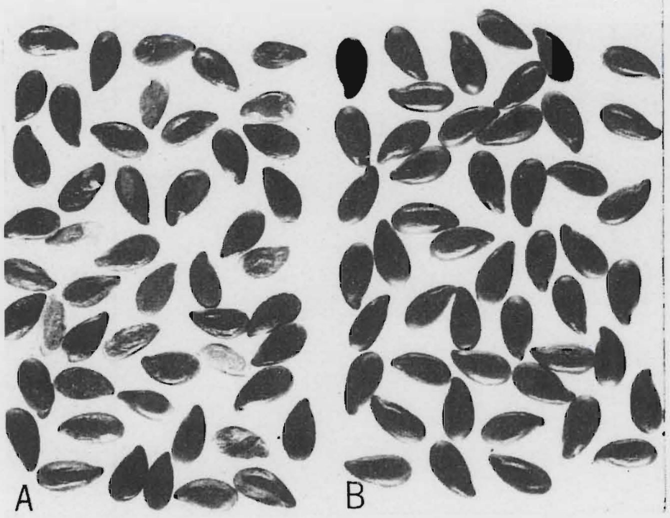

Figure 6. Seed harvested from flax plants with symptoms of late wilt (A) compared with seed from healthy plants (B). There are 50 seeds on each side.

Late Wilt

Late wilt occurs any time from flowering through boll set. A general necrosis of stem tissues, both internal and external, together with an increased rigidity and brittleness of the stem, is characteristic of late wilt. The stem discoloration from late wilt differs from the pasmo disease in that stems discolored by late wilt are a uniform light-brown, while pasmo produces chocolate-brown stems and, at early stages, the stems are banded.

Late wilt can be mistaken for root rot or for any condition that causes premature ripening of the plant. However, late wilt causes a darker coloration of the stems than either root rot or premature ripening does.

Late wilt had been observed for some time and was noted by Barker (6), Bolley (7), Borlaug (9), Flor (24), and Tochinai (63) prior to 1945, but its importance was not generally recognized in the field until that year, when it loomed prominently with the increased use of the variety Crystal in test plots. Late wilt produced prominent areas in the field that resulted in premature ripening of flax.

A visual estimate of the severity of late wilt in the field for seven varieties of flax was made in 1945. The percentages of late wilt infected plants per variety were: Crystal, 90; Biwing, 60; Minerva, 60; Bison, 40; Dakota, 25; Redwing, 25; and Koto, 20. These percentages are averages for four replicates. Crystal appeared to be most susceptible to late wilt, and Dakota, Koto, and Redwing were least susceptible. Subsequent culture on nutrient agar established that the condition was late wilt. Presence of the late wilt pathogen can be ascertained in the laboratory from a cut section of infected stem. A stem section about 1 cm. long is surface disinfected in 1 percent NaOCl for 1 minute and placed on nutrient agar. The pathogen causing late wilt will grow from the stem section after 2-3 days of incubation at about 25° C., as illustrated in figure 7.

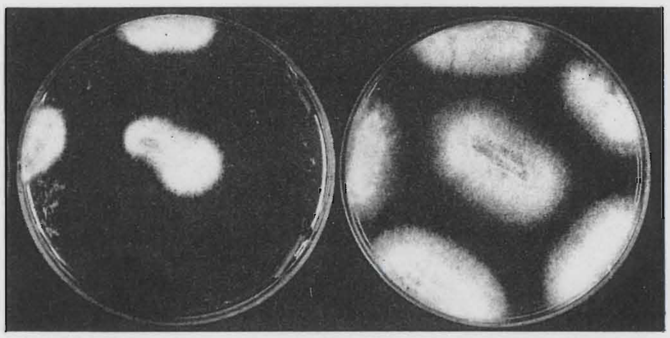

Figure 7. Colonies of **Fusarium oxysporum** f. sp. **lini** isolated from stem sections of flax plants with symptoms of late wilt.

As shown in table 1, the roots and lower parts of stems having late wilt proved to be infected with the pathogen (as determined by isolation and subsequent tests of isolates for pathogenicity to flax). Even the presumably healthy or green plants were infected to a considerable extent with the pathogen, which also was reported by Burnham (16). On the other hand, the variety Arny will discolor in the absence of infection.

Shortly after these results were obtained, all stems turned brown and the pathogen could be isolated from nearly all stems. Even pedicels of the inflorescence were infected, and occasionally seeds also were infected. Apparently, invasion of the stem by the pathogen precedes discoloration of the stem tissues. This situation had been noted earlier by Schuster (55).

When the incidence of late wilt was compared with the incidence of early or seedling wilt (wilt that occurs prior to flowering), late wilt occurred more frequently than early wilt in 1948 and 1951, as shown in figure 3. The figure is based on averages of 40 lines and varieties tested in the wilt nursery, which was begun in 1913. However, when comparisons were made with a different set of 39 varieties tested in a different wilt nursery (started in 1946), the results for 1948 agreed (figures 3 and 4). But late wilt was more abundant in 1950 in the older nursery (figure 3) than in the new one (figure 4). When all types of wilt were considered and averages for three successive seasons (1948-50) were computed, late wilt

Table 1. Extent of infection among flax plants from a field where symptoms of late wilt were apparent but in which discolored (brown) and green stems were observed

Plant part invaded*	Plants infected† Brown	Plants infected† Green
	percent	percent
Root	100	79
Stem 1	100	56
Stem 2	92	37
Stem 3	85	22
Stem 4	70	17
Pedicels	50	6

* The stem of each plant was cut into four parts (between root and inflorescence). Stem 1 represents the lower one-fourth of the stem and stem 4 represents the upper one-fourth.

† Each percentage is based on isolation from 75 plants prior to the turning brown (late wilt) of green plants. Plant parts were harvested and placed on agar media to identify the causal fungus on July 19, when seeds were just forming.

proved to be more important than other types of wilt in the new nursery (see figure 5).

Late wilt results in varying degrees of shriveled seeds from paper thin seeds to functional seeds that are only dimpled (see figure 6). Other causes for blighted seed have been described by Kommedahl et al. (39). The time when the disease strikes apparently determines how much loss will be sustained.

When temperatures are favorable for wilt shortly after flowering, the bolls (capsules) that form are empty. Hundreds of such plants have been observed where there were no seeds in the bolls. There was little loss in seed yields when late wilt appeared shortly before harvest.

From plants grown in a wilt nursery started in 1946, seeds were harvested in 1948 from plants that had late wilt and from plants that appeared healthy in the same wilt plot. One thousand seeds from each of six varieties were weighed. The greatest reduction occurred in Arrow flax, where the weight per thousand seeds was 8.3 percent less from plants with late wilt than from plants without symptoms of it. Five other varieties (Bison, Crystal, Dakota, Koto, and Minerva) ranged from 0-4 percent reduction in seed weights.

These comparisons were made with plants growing in a wilt nursery. When comparisons were made between plants growing on wilt-sick soil and plants not grown on wilt-sick soil, weight per thousand seeds was less by 20 percent for Bison flax, 19 percent for Koto flax, and 17 percent for Dakota flax.

Furthermore, plants with late wilt averaged 3.0 seeds per boll, while plants growing in the wilt nursery but without late wilt symptoms averaged 4.2 seeds per boll, based on 100 bolls of Crystal flax for each average figure. Plants normally produce 6-7 seeds per boll out of a possible 10. Thus, late wilt can reduce seed production per boll and thereby per plant.

Partial Wilt

Frequently a seedling wilts and dies except for the roots and buds at the base of the stem. If cool weather follows hot weather, buds at the base of the stem develop into new shoots following the death of the original shoot. When the weather is more favorable for flax than for wilt, the lateral shoots grow and produce seed. As long as the weather remains cool the new shoots remain free from infection. With a return to hot weather, which favors wilt, the lateral shoots may subsequently wilt and the whole plant may die. This is called partial wilt and is pictured in figure 8.

Lateral shoots from partially wilted plants seldom produce enough seed to compensate for the loss from the wilting of the first shoot.

In 1923, Barker (6) recognized the importance of partially wilted plants, but it has not always been considered in taking notes on wilt nor has it been counted as early wilt in the records. Records of its prevalence were kept for the 3-year period shown in figure 5, when it averaged about 5 percent.

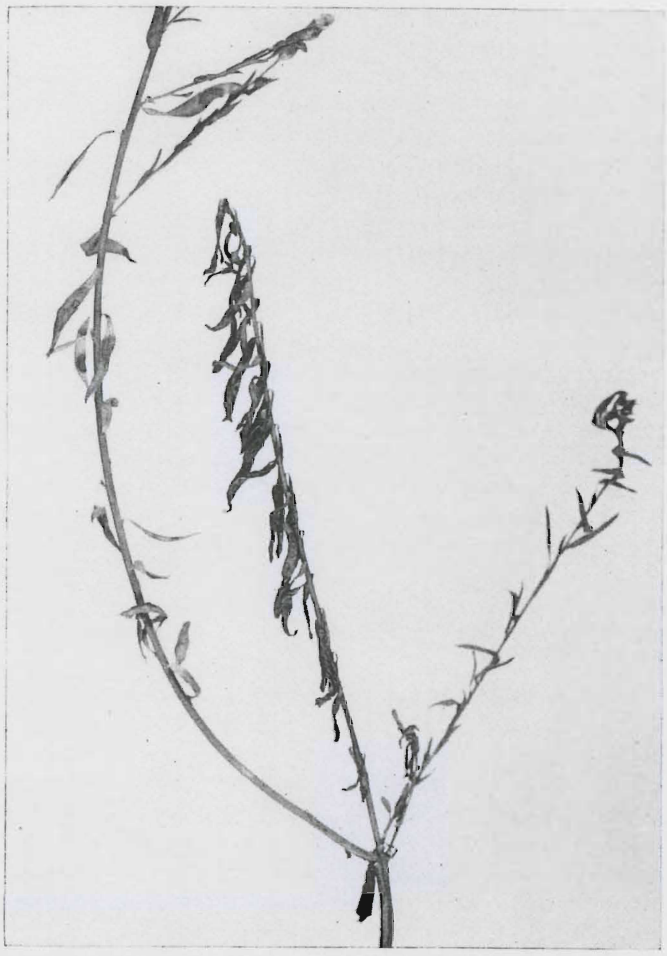

Figure 8. Partial wilt of flax. The middle shoot wilted, but new, noninfected shoots subsequently developed from lateral buds at the base of the plant, and the new shoots produced seed and were free from infection.

Flax plants frequently are slightly chlorotic, as though they were in a stage intermediate between wilting and not wilting. Such plants often do succumb to wilt, but some may persist to maturity. These plants have not actually wilted and are not included as partially wilted plants. Nevertheless, they are not vigorous and do not produce much seed. Such plants prove to be infected with the wilt pathogen. In wilt readings based on plant vigor such as used by Flor (24) of North Dakota, such plants are taken into consideration in evaluating wilt resistance of a variety.

Unilateral Wilt

Unilateral (one-sided) wilt is a variation of late wilt in which only one side of the stem and all branches of the inflorescence whose vascular elements connect to that side are discolored. This type of wilt has been reported previously in flax (6) and vascular wilt diseases of other crops.

One hundred stems with unilateral wilt were split to separate the discolored from the green portion of the stem, and each stem segment was placed separately on nutrient agar. The wilt pathogen was isolated only from the discolored part of the stem, indicating that the pathogen does not grow laterally around the stem.

When plants were examined histologically, discoloration of the vascular elements in the root, stem, and pedicels was apparent. Bolls attached to pedicels arising from the discolored side contained shriveled seed, as found for the late wilt shown in figure 6A.

Unilateral wilt averaged only 3 percent of the wilt in the 3 years of testing (figure 5), making it much less prevalent than either early or late wilt. Unilateral wilt often is counted as late wilt when notes are taken on performance of varieties in a wilt nursery.

We do not know why only some of the vascular elements are invaded by the pathogen; perhaps it is a matter of chance. One-sided wilt was no more prevalent on the south exposure than on north, east, or west, as determined by recording the prevalence of each at cardinal points of the compass. We have observed no difference among varieties in prevalence of unilateral wilt.

Host Range

Apparently *Fusarium oxysporum* f. sp. *lini* can infect all varieties of flax. The world collection of flax varieties has been tested at least twice in wilt-sick soil at St. Paul. All varieties have become infected with the wilt organism. These include varieties of *Linum usitatissimum* and those of *L. angustifolium* Huds. and *L. crepitans* Boemingh. Varieties of the latter two species often are grouped with *L. usitatissimum*. Houston and Knowles (29) reported a wild species of flax as susceptible to wilt.

As far as we know, *F. oxysporum* f. sp. *lini* will not induce wilt in any plant species outside of the genus *Linum*. Borlaug (9) inoculated a wide variety of plants with this fungus, but none developed symptoms of wilt. This finding was confirmed in 1967 by Davis (19).

Causal Organism

Although several *Fusarium* species have been isolated from flax plants and seed, *Fusarium oxysporum* f. sp. *lini* is the only recognized species than can wilt flax (4, 57). In 1932, Bolley and Manns (8) listed *F. russianum* as a cause of wilt in seedling flax, but now that organism is considered to be a race of *F. oxysporum* f. sp. *lini*. Borlaug (9) inoculated flax with nine well-known species of *Fusarium*, but none induced wilt in flax.

Several species of fungi have been reported to contribute to soil sickness and to cause seedling blight and damping off (8, 60). Some of the more common ones are *Asterocystis* sp., *Colletotrichum linicola, Fusarium* spp., *Pythium* spp., and *Rhizoctonia* sp. Tervet (60) postulated that certain soil fungi in association with *F. oxysporum* f. sp. *lini* may help to bring about wilting in flax in some way. However, Tervet's (60) experiments were done in the greenhouse, where flax roots generally are more succulent and susceptible to root infection. Flor (24) made tests in the field and found that other fungi were not important in the soil sickness "complex"; only *F. oxysporum* caused seedling blight or wilt in the field.

With small seedlings, it sometimes is difficult to distinguish wilting by *F. oxysporum* f. sp. *lini* from the blighting produced by other soil-borne fungi. To be certain, the appropriate number of isolations on nutrient media must be made.

Recent work at Minnesota also indicates that nematodes sometimes may be associated with wilting. Schleder (54) found that adding the root knot nematode *Meloidogyne hapla* Chitwood to soil infested with *F. oxysporum* f. sp. *lini* greatly increased the percentage of wilted plants in the flax varieties Marine and B-5128. We do not know how these nematodes increase the percentage of wilted plants; perhaps nematodes create avenues of entrance for the fungus.

Wilt readings sometimes may include damage caused by organisms other than *F. oxysporum* f. sp. *lini*. It seems likely that root rotting organisms such as *Rhizoctonia solani* (24) may contribute to the symptoms recognized as late wilt. But this possibility does not minimize the importance of *F. oxysporum* f. sp. *lini*.

Life Cycle

F. oxysporum is a facultative parasite. It not only parasitizes and kills the flax plant, but it can grow and sporulate on dead, previously infected tissue. Park (52) has described this species as a highly competitive colonizer of fresh organic matter that penetrates tissues rapidly and deeply ahead of other organisms in an ecological succession. In fact, this species is a primitive parasite and pioneer fungus, which probably accounts for its success in maintaining itself for decades in soil. Moreover, it survives passively as chlamydospores or colonizes root surfaces of nonhost plants (3).

F. oxysporum f. sp. *lini* is pleomorphic. It produces three distinct kinds of spores: microconidia 5-12 × 2-3.5 μ and nonseptate; macroconidia 17-50 μ long with one to five septa, three septa being the most common; and chlamydospores, which may be produced in both hyphae and conidia, both terminally and intercalarily. The three-septate macroconidia are 25-40 × 3-4.5 μ. Chlamydospores are ellipsoidal, terminal, or intercalary and are 5-10 μ in diameter. The chlamydospores are double walled and sometimes turn brown (57, 72).

On a nutrient substrate the spore may germinate in less than 2 hours. More than one germ tube usually is produced by a macroconidium, whereas only a single germ tube grows from a microconidium. Penetration of root hairs occurs shortly after germination and up to 2 weeks after germination, depending on the variety.

According to Bolley (7) and Wilson (71), *F. oxysporum* f. sp. *lini* may attack any part of a growing plant (root, stems, leaves, and seed). Work by Tisdale (61) in 1917 and recent work at Minnesota (48, 50) indicate that the initial infection occurs primarily through the roots and particularly through the root hairs of young seedlings. Apparently plants of both susceptible and resistant varieties harbor the fungus in the cortex of their roots. This was reported also by Davis (19) for other forms of this species. In susceptible varieties the fungus can be isolated from any portion of the diseased stem.

During moist weather the fungus may produce an abundance of both macro- and microconidia on any part of the plant, particularly near the ground. The fungus also grows and fruits readily on diverse plant parts in or on soil. In certain types of soil, mycelia can ramify through the soil, and chlamydospores are not uncommon.

The fact that *F. oxysporum* f. sp. *lini* can survive or live saprophytically in soil for 5-10 years is a strong indication that the organism is not readily destroyed by other microorganisms in the soil. Anwar (2) demonstrated clearly that *F. oxysporum* f. sp. *lini* persisted much better in the soil in Minnesota than did *Helminthosporium sativum*, a root rot pathogen of cereals. This he attributed to the difference in the sensitivity of the two organisms to the antibiotic microflora in the soil. Of 86 isolates of bacteria and fungi isolated from soil and tested in petri dishes, 48 were antibiotic to *H. sativum*, whereas none was strongly antibiotic to *F. oxysporum* f. sp. *lini*. Significantly, the population of *F. oxysporum* f. sp. *lini* varied with the season, but the trend was the same as for the other saprophytic organisms present in the soil. Borlaug and Christensen (unpublished data) applied large quantities of grain inoculum containing *Trichoderma lignorum, Pencillium* spp., and other organisms to flax wilt soil plots at flax planting time, but no reduction in percentage of wilted plants resulted. A liberal amount of grain straw also was added to the infested soil and again there was no reduction in percentage of wilted plants. Such results clearly indicate that *F. oxysporum* f. sp. *lini* is an aggressive colonizer of organic matter in soil and survives in soil as well as or better than most pathogens.

The fungus is disseminated by diverse methods utilizing wind, water, and animals to disperse plant parts and soil. The most common and effective method appears to be by means of seed and infected plant parts. Most seed lots of flax carry spores of *F. oxysporum* f. sp. *lini* on the seedcoat. This is especially true of weathered seed, for the spore can adhere to it more readily than to the smooth seedcoats of normal seed. Spores, both micro- and macroconidia, get into the seed from diseased straw during threshing and combining. The inoculum on or in seed is the most effective means of establishing infection in nature, because the inoculum is adjacent to the infection court. Seed, especially seed of susceptible varieties, often harbors the fungus. There is good evidence (unpublished) that the fungus often is introduced into clean fields on infested and infected seed. Furthermore, infected plant parts often are found in uncleaned seed lots. It has been demonstrated that the organism is readily disseminated to other countries by means of infected seed lots (8).

Undoubtedly the spores of *F. oxysporum* f. sp. *lini* and infected plant parts and soil are disseminated to some extent by wind. But this method has not been adequately investigated. Runoff water from infected fields may carry the fungus or infected plant parts and infected soil. Evidence does not indicate a rapid buildup of pathogens by this method (9).

Besides planting infected and infested seed, man also disseminates the pathogen by spreading infested flax straw and soil onto clean soil. Animals, including birds, have been known to spread the pathogen. *Fusarium* spores have been observed on insects, so they too may be agents of dissemination. Since infection can occur through injuries to roots, soil insects as well as nematodes may create avenues of entrance for the pathogen.

Races

F. oxysporum f. sp. *lini* is an outstanding example of a fungus species that comprises an indefinite number of biotypes and physiologic races. It also is an excellent example of great diversity in a species where the sexual stage is not known. We do not know how fast these differences in biotypes arose. Some arose by mutation, since monosporous isolates from microconidia frequently give rise to many distinct types. Perhaps others arose by means of heterocaryosis or parasexualism.

Isolates of *F. oxysporum* f. sp. *lini* differ from each other in many ways; e.g., in the amount and type of sporulation; production of microconidia, macroconidia, and chlamydospores; size and number of septa; pigment production on diverse media; rate and type of growth on substrates and in the host; temperature requirements; alcohol production; antibiotic capabilities; and pathogenicity. The degree of difference obviously depends upon the diversity of the substrate and host plants involved. Some isolates may be alike on one substrate or one variety of plant but quite different on another.

In 1926, Broadfoot and Stakman (14) and Broadfoot (13) demonstrated for the first time that there were distinct parasitic differences in *F. oxysporum* f. sp. *lini*. They recognized nine distinct parasitic races on four varieties of flax. One race was particularly conspicuous because it caused seedlings 2-4 cm. tall to become colorless above the cotyledons. These races also differ in cultural characteristics and in morphology of the conidia. Later, Letcher and Willaman (42) showed that these races differ greatly in their ability to produce alcohol. The more virulent races produced the most alcohol in culture. A similar relationship was reported by Matsui et al. (45).

F. oxysporum f. sp. *lini* consists not only of innumerable cultural races but also of parasitic races (9, 10, 13, 14, 20, 30, 36, 38, 46, 69). Borlaug (9) could not find any variety of flax that was resistant to all isolates of the wilt fungus. He concluded that when a given variety of flax was inoculated with numerous isolates, a wide range in resistance or susceptibility occurred. For example, he reported that on Redwing the range in infection of 15 mass isolates varied from 3-99 percent. He found a range of 2-85 percent wilted plants among 15 mass isolates on Newland flax (figure 9).

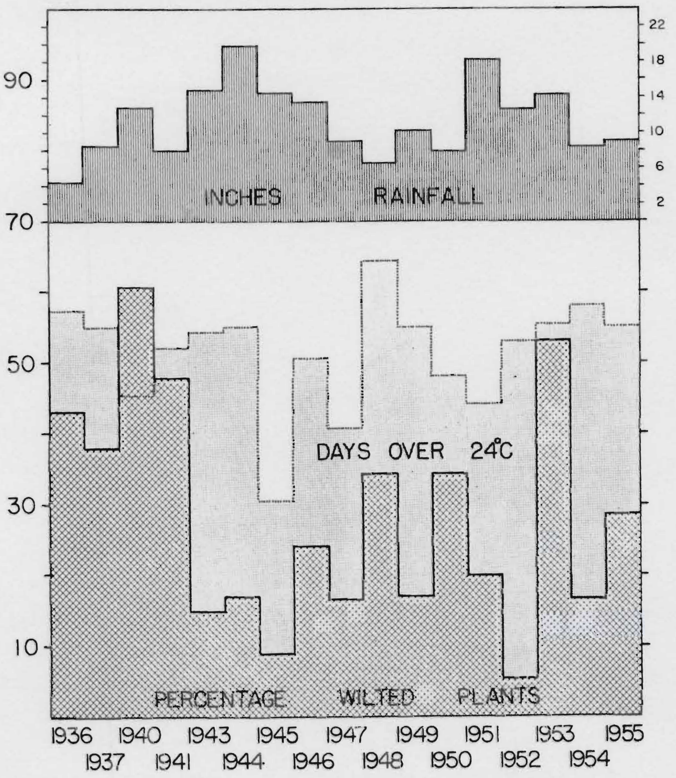

Figure 11. Percentage of wilted flax plants from 1936 to 1955 compared to the number of days when the soil temperature exceeded 24° C. during the period May 15 to July 30, and to the rainfall during the period May 1 to July 30. Wilt percentages are based on averages of 40 lines and varieties and about 100 plants per variety in the wilt nursery started in 1913 at St. Paul.

data reported in figure 10 were with the same 39 varieties, and notes were taken by the same person (Kommedahl) in the same way each year. Some data on either wilt or soil temperature were not available for the whole period (1936-55), which accounts for the missing years.

Other factors may account for differences in wilted plants. For example, high rainfall in any given year might cancel or reduce the effects of high temperature (see figure 11).

Soil Moisture

Inspection of the rainfall data in figure 11 indicates that soil moisture might affect the development of wilt. It is apparent that 1945 not only was a year with a cool growing season, but that the rainfall was high. This combination helped Punjab survive despite its susceptibility to wilt and the abundance of inoculum in the soil.

The period 1943-46 was one relatively high in rainfall and low in incidence of wilted plants, whereas the period 1936-41 was low in rainfall and high in incidence of wilted plants. However, in some years there appeared to be no relationship between number of wilted plants and either rainfall or number of days the soil temperature exceeded 24° C. Perhaps varieties differ in response to moisture as well as to temperature.

To explore further the possible role of soil moisture in the field (as measured by application of water), an experiment was set up in which seeds of three varieties of flax were sown in the wilt nursery. In one series of plots, the soil was sprinkled daily with water. In the second series, no water was applied. Both plots received rainfall that fell normally during the test periods. The results appear in table 3.

Table 3. Percentage of wilted plants in three varieties of flax grown on wet and dry wilt-sick soil in the field

Variety	Wilted plants* Wet	Dry
	. . percent . .	
Crystal	22	41
Punjab	75	88
Koto	16	8

*Based on 400 plants per variety tested in 1950 in the regular wilt nursery started in 1913.

The added water did not affect the incidence of wilted plants for the wilt-susceptible variety Punjab; however, the number of wilted plants was about twice as great on the dry soil (no water added) as on the wet soil (water added daily) when the moderately resistant variety Crystal was tested. Thus, soil moisture may influence wilt with varieties intermediate in resistance to wilt. Since the incidence of wilt in the resistant variety Koto is so low, it is doubtful that this difference is biologically important. Possibly higher moisture favors antagonistic organisms on roots; e.g., it was reported that by increasing soil moisture from 40 to 60 percent the number of mycolytic bacteria antagonistic to *F. oxysporum* f. sp. *lini* increased accordingly (66).

Soil Type

Flax wilt has been found in moderately susceptible to moderately resistant varieties on most soil types, including peat, in Minnesota: on the Waukegan-Withrow soils (silt loam) of Dakota and Washington Counties, on the Carrington-Clyde soils (silty clay loam) of southeastern counties, on the Clarion-Webster soils (silt to clay loam) of southern Minnesota, on the Barnes-Parnell soils (silt to clay loam) in west-central counties, and on the Fargo-Bearden soils (heavy silt loam and clay) of the Red River Valley. These are the major soil types in the flax growing regions of the state. Similarly, Bolley (7) reported wilted plants on all soil types in North Dakota. In fact, flax wilt has been reported on many soils throughout the world, wherever flax is grown. The amount of inoculum in soil need not be high to cause flax to wilt, as was shown in the following experiments.

Soil from the wilt nursery was diluted with an equal amount of a soil consisting of two parts silt loam to one part sand. Half of this diluted mixture was again diluted and this procedure was continued for nine successive dilutions, ending in a final mixture of one part wilt-sick soil in 512 parts of noninfested loam. In another series, sand was the diluent. Punjab flax was sown in each pot in the greenhouse using soil of each dilution. The results are based on two to four replicates of six pots per replicate and 25 seeds per pot.

With successive dilution, the percentage of wilted plants of Punjab flax decreased from 82 (control) to 81, 79, 54, 28, 18, 11, 8, 9, and 7 using sand, and from 82 to 62, 38, 32, 23, 15, 15, 11, 9, and 8 using silt loam soil as the diluent. Thus, even a dilution of 1:512 of wilt-sick soil contained enough inoculum to cause 7-8 percent of the plants of a susceptible variety to wilt.

Also, by sprinkling wilt-sick soil about 3 millimeters (mm.) deep over seeds of Punjab spread on autoclaved soil in pots in the greenhouse, an average of 28 percent of the plants wilted, ranging from 14-41 percent among the 12 pots.

When wilt-sick soil was diluted 50 percent with peat, the percentage of wilted plants of Punjab decreased from 81 in the undiluted soil to 43 in the peat mixture. Nair (48) at Minnesota also illustrated that an increase in inoculum resulted in an increase in incidence of wilted plants. He tested three varieties to three races of the wilt fungus and found that if spores were added to soil in concentrations of 10^3 to 10^6 spores/milliliters (ml.), there was a proportionate increase in incidence of wilted plants, and more so with wilt-susceptible than with wilt-resistant varieties.

Thus the amount of inoculum carried from a flax field on soil attached to tillage equipment or carried by wind or water erosion may spread the fungus to adjacent fields where flax might be grown in succeeding years. However, a high amount of organic matter in peat can support a high population of soil microorganisms, which probably compete with the wilt fungus to hold it in check at least temporarily.

Fertilizer

Lugger (43), in 1890, was the first to make tests in the field on the role of fertilizers in the development of wilt. He did not observe any difference in wilt among fertilized and nonfertilized plants and concluded that exhaustion of soil by previous crops of flax did not cause flax to wilt.

Snyder (56) also made field tests to determine whether flax removed nutrients from soil at a rate different from that of other crops. From his fertilizer trials, he concluded that flax did not remove nutrients more than cereal crops did.

However, these men had different objectives and were not testing whether fertilizer applications influenced the amount of wilt among resistant and susceptible varieties.

Experiments were made in the greenhouse and in the field to determine the effect of nitrogen, phosphorus, and potassium fertilizers on wilt development. Four varieties were used in each test: Bison and Redwing, which were relatively resistant to wilt, and Crystal and Royal, which were relatively susceptible. The plants were tested in the greenhouse using flats filled with soil taken from the wilt nursery. The results are shown in table 4.

In both greenhouse and field tests, nitrate, phosphate, and potassium generally reduced the percentage of wilted plants. The reduction was much greater for the more susceptible Crystal and Royal flax than for the more resistant varieties. Both lime and sulfur generally reduced the number of flax plants that wilted.

Table 4. Percentage reduction in wilt of four varieties of flax grown on wilt-sick soil in the greenhouse and field to which three fertilizers and two amendments were applied

Fertilizer or amendment*	Reduction wilted plants over control				Average reduction of wilted plants
	Bison	Redwing	Crystal	Royal	
Nitrate			percent		
Greenhouse	7	9	7	26	12
Field	10	0	33	12	13
Phosphate					
Greenhouse	0	11	23	13	11
Field	20	8	44	24	24
Potash					
Greenhouse	14	0	36	10	14
Field	15	6	25	18	16
Lime					
Field	16	10	28	25	20
Sulfur					
Field	16	2	30	7	14

*Ammonium nitrate at 100 pounds per acre (32 pounds of nitrogen), superphosphate (0-20-0) at 300 pounds per acre (60 pounds of P_2O_5), muriate of potash (0-0-60) at 100 pounds per acre (60 pounds of K_2O), lime at 320 pounds per acre, and sulfur at 320 pounds per acre. Results in the greenhouse are based on averages of 50-75 plants, and results in the field on averages of two seasons' data: 200 plants in 1949 and 400 plants in 1950 (plants grown in regular wilt nursery).

In contrast, Bolley and Manns (8) found in North Dakota that high applications of sulfur and sodium chloride each year for 4 years failed to influence the number of plants that wilted.

It is impossible to determine from these experiments whether pH is involved, because both superphosphate, which tends to increase soil acidity, and lime, which decreases it, reduced wilt.

However, Nair (48) at Minnesota, using one race in the greenhouse, found that more flax plants wilted in the pH range from 5.5-7.5 than at pH values either side of this range. Wilson (71) found that *F. oxysporum* f. sp. *lini* spread in soil of pH 4.2 but not in soil of pH 7.6 or 8.0, yet stated that the striking difference in soil acidity was not the causal factor in the spread of the pathogen.

In the greenhouse, Nair (48) tested four flax varieties, Marine, Minerva, Punjab, and Redwood, for the effect of fertilizers on wilt development using a single race of *F. oxysporum* f. sp. *lini*. He found that phosphate (P_2O_5, 43 percent) increased significantly the percentage of wilted plants, in contrast to our results in table 4, while ammonium sulfate (22 percent) or potash (K_2O, KCl, 52 percent) alone or in combination significantly reduced wilt.

Nair also reported that three nitrogen compounds (ammonium sulfate, sodium nitrate, and urea) reduced the number of wilted plants of B-5128, Punjab, and Redwood flax in greenhouse tests.

Thus it appears that adding nitrogen, potash, and possibly phosphate fertilizers can effectively reduce wilt in susceptible varieties. However, the fertilizers may promote the growth of the host and make it possible for the host to withstand infection. There may be no direct effect of fertilizers on the wilt fungus.

Table 5. Percentage survival in seedlings of Redwing flax growing in the wilt nursery when subjected to seven different herbicides, 1959

Herbicide and application rate per acre	Survival*
	percent
None (control)	62.0
4(2,4-DB) [4-(2,4-dichlorophenoxy) butyric acid] (1 lb.)	46.6
2,4-D (2,4-dichlorophenoxyacetic acid) (4 oz.)	56.5
Dalapon (2,2-dichloropropionic acid)	56.7
TCA (trichloroacetic acid) (5 lb.)	69.4
MCPA (4 oz.) plus TCA (5 lb.)	72.6
MCPA (2-methyl-4-chlorophenoxyacetic acid) (4 oz.)	74.1
MCPA (1 lb.) plus dalapon (1 lb.)	75.2
HSD at 5%	15.6

* Averages of three replicates.

Table 6. Effect of herbicidal application on yield of six varieties of flax in the absence of weeds in the wilt nursery, 1961

	Herbicide*		No herbicide	
Variety	Yield†	Wilted plants‡	Yield†	Wilted plants‡
	bu./acre	percent	bu./acre	percent
Arny	25	13	27	9
Bison	19	9	20	10
B-5128	22	31	23	29
Marine	21	42§	24	40§
Redwood	26	5	27	8
Punjab	0	100	0	100

* Herbicides used were MCPA (2-methyl-4-chlorophenoxyacetic acid) at 4 ounces per acre (acid equivalent) and TCA (trichloroacetic acid) at 5 pounds per acre (acid equivalent). Flax was hand weeded in the no herbicide plots.
† Based on average yield from rod-row (5 m. long) plots.
‡ Determined from 100 emerged seedlings within the row. All forms of wilt were counted.
§ Much of the wilt occurred late in the season and thus had almost no effect on yield.

Table 7. Effect of injured seed on emergence and incidence of wilt in three varieties of flax tested in a wilt nursery

		Condition of seed	
Variety*	Observation†	Sound	Injured
		percent	
Crystal	Emergence	54	15
	Wilt	77	91
Dakota	Emergence	56	25
	Wilt	71	70
Minerva	Emergence	59	17
	Wilt	64	75

* Samples were farmers' seed lots sent to the Minnesota State Seed Laboratory for germination tests.
† Emergence refers to the number of plants that emerged from the seeds sown. Wilt refers to the number of emerged plants that wilted, expressed in percentage. Data are based on five replicates of 100 seeds per replicate sown in the field.

Herbicides

Because flax generally is found to be a poor competitor with weeds (23, 40, 41), herbicides usually are recommended for good stands of flax. However, flax growers have observed flax damage that is similar to wilt, and it sometimes may be difficult to distinguish herbicide damage from wilt. Thus, seven herbicides were used to spray on weeds among plants of Redwing flax growing in the regular wilt nursery. The results appear in table 5. Obviously, none of the herbicides affected percentage survival significantly.

In a similar experiment 2 years later, two herbicides (MCPA for broad-leaved weeds and TCA for grasses) were applied and compared to results from hand weeding. Then yields and wilt percentages were determined for six varieties. Results appear in table 6. The application of herbicides did not affect yield or incidence of wilted plants among the six varieties that usually vary in their resistance to wilt. It therefore is safe to apply appropriate herbicides in flax without affecting incidence of wilt.

Seed Conditions

Many seed lots of flax produced in the flax-growing area of the United States germinate very poorly in soil. Some lots germinate less than 20 percent, chiefly because of mechanical injuries during harvest, which apparently are due to unusually dry conditions (39).

To test whether injured seed would be more subject to wilt than sound seed of the same seed lot, Crystal, Dakota, and Minerva were chosen. Both sound and injured seeds were selected from the same seed lot by examining them with an ×8 magnifying glass for evidence of external seed injury. These seeds were germinated on blotting paper, then dipped into a suspension of spores and hyphae of a given isolate of *F. oxysporum* f. sp. *lini*, and planted, blotter and all, in flats in the greenhouse.

On the basis of four replicates per variety and 100 seeds per replicate, only 3 percent of the Dakota seedlings grown from sound seed wilted, while 100 percent of the seedlings germinated from injured seed wilted and died. Similar results were obtained with Crystal: 2 percent of the seedlings from sound Crystal seed wilted, while 40 percent of the seedlings from cracked seed wilted and died. From these greenhouse results, it was evident that seed condition can effectively influence the percentage of wilted plants with the varieties tested. The fungus either adheres to the seed surface or in cracks or penetrates the seed through the damaged seedcoat.

In a second experiment, seeds of Crystal, Dakota, and Minerva were tested in the field. Just as in the previous experiment, sound and injured seeds were selected from the same lot with the aid of an ×8 magnifying glass. Seeds of the three varieties, at 100 seeds per replicate, were treated with an organic mercury dust and planted in the wilt nursery, where flax had been grown annually since 1913. The results are given in table 7. Considerable difference between sound and injured seed in the percentage emergence was evident. However, of the plants that emerged, the percentage wilt for a relatively resistant variety like Dakota was about the same for both sound and injured seed, although a difference of 14 percent wilt between sound and injured seed sources of the susceptible variety Crystal was found. Minerva flax usually is intermediate between Dakota and Crystal in wilt reaction. It occupied the same relative position in this experiment, with a difference of 11 percent wilt of injured seed over sound seed of the same seed lot.

Sometimes the coat of flax seed appears to be rough, although no cracks or injuries can be detected. Such rough or weathered seeds were picked out from a given seed lot of Minerva for comparison with sound seed of the same lot. Sixty-four percent of the seeds produced seedlings in soil, but of the plants that emerged wilting was no more severe than that from sound seed of the same lot. However, it was 15 percent less than that from injured seed from the same lot. Thus injured seed (seed with cracked and split seedcoats) can result in increased incidence of wilt, whereas weathered seed appears to be relatively unimportant. On the other hand, the fungus can adhere more readily to the surface of weathered seed and frequently is isolated from such seed (39). According to Tochinai (63), Hiura also showed that the wilt fungus can penetrate the seedcoats and remain dormant there for a long time.

When Punjab was injured artificially, hyphae of *F. oxysporum* f. sp. *lini* entered through the wound (a in figure 12), invading the cotyledons (b), hypocotyl (c), and radicle (d). Thus, injured seed can become invaded by the wilt pathogen as described earlier by Nair and Kommedahl (50). By culturing naturally infected flax seeds, it was found that about three seeds per thousand were infected with the wilt organism (36). *F. oxysporum* f. sp. *lini* previously had been shown to be seedborne (7). Nair and Kommedahl (50) also reported that the pathogen can enter through the micropyle of sound seed.

The pathogen also can invade the root hairs of the germinating seedling and the epidermal cells of the root (figure 13). This possibility was shown by Tisdale (61) in 1917. The microconidium of *F. oxysporum* f. sp. *lini* germinates and the hyphal tip may adhere tightly to the root hair of flax as shown in "a" in the camera lucida drawing (figure 13A). The hypha can be pulled away only with considerable force, suggesting that a mucilaginous material has been produced or that an enzyme has digested part of the root hair and the hyphal tip is held to the hair.

Hyphae subsequently enter the epidermis from the root hair (b) or enter cells directly as shown at the right in figure 13A. From here, hyphae invade the cortex (figure 13B) and the vascular elements as pictured by Tisdale (61) and by Millikan (47), as well.

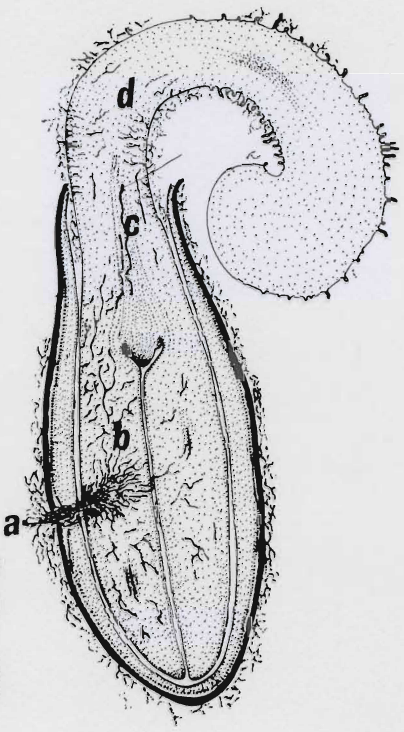

Figure 12. Hyphae of **Fusarium oxysporum** f. sp. **lini** enter injured flax seed (a), and invade cotyledons (b), hypoctoyl (c), and radicle (d). (Drawn by P.N. Nair.)

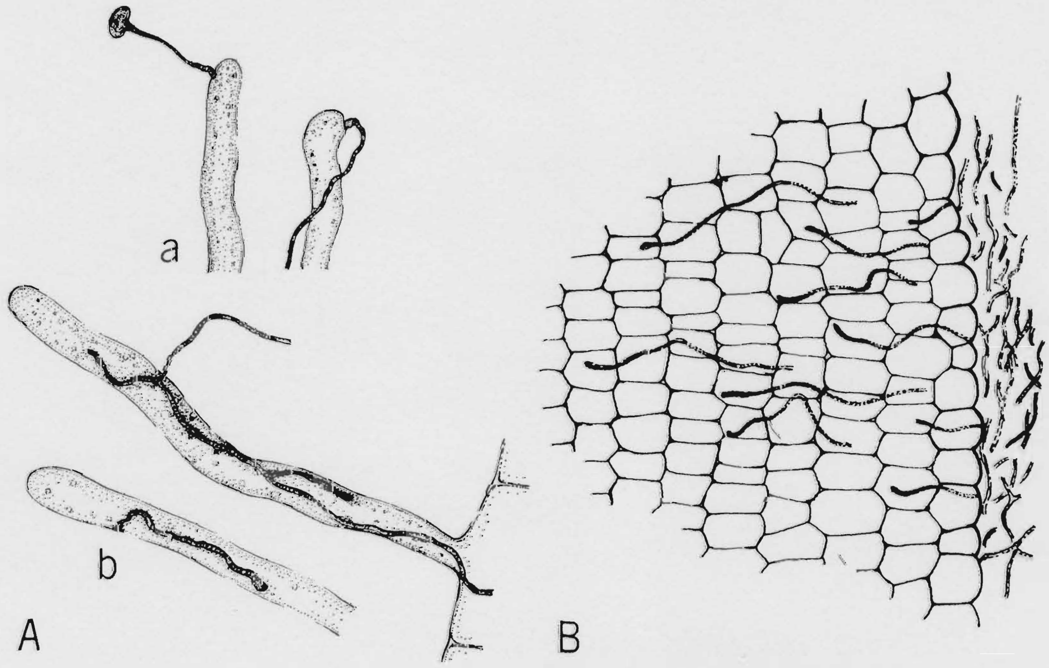

Figure 13. Infection of flax roots by **Fusarium oxysporum** f. sp. **lini** as shown by microconidium that germinated to penetrate root hairs (A) and by hyphae that penetrated epidermis of the root (B), with subsequent invasion of the cortex and vascular elements. (Drawn by P.N. Nair.)

Testing for Wilt Resistance

Although Bolley made his original selections of flax (N.D. 52 and N.D. 114) for resistance in 1902, the varieties were not distributed to growers until 1908 and 1912, respectively. Buda, another resistant variety produced in North Dakota, was distributed to farmers in 1921.

Flax improvement began in Minnesota in 1896 (5). By 1904, Primost (Minn. No. 25), the first pure line variety in the United States (21), was being distributed to Minnesota farmers. But Primost was not wilt resistant. In 1922, Chippewa, derived from Primost, and Winona were developed and released as wilt-resistant varieties (5) in Minnesota. Since then, many wilt-resistant varieties have been produced. Consequently, wilt seldom is an important disease in the upper Mississippi Valley today.

Results from 50 years of testing many new and old varieties of flax clearly proved that most varieties, if not all, have some degree of field resistance. This definitely is true if one considers physiologic races. Even a susceptible variety like Punjab has some resistance to a given race. The results further indicate that it is possible to select plants on infested soil that have varying degrees of resistance to *F. oxysporum* f. sp. *lini*. The extent to which the degree of resistance can be isolated in a line of flax depends upon the heterogeneity of the parental variety. The data also indicate that wilt resistance is not linked with agronomic characters.

Although Bolley (7) was the first to prove that it was possible to select resistant and semi-resistant lines of flax out of a susceptible variety, he believed that lines did not remain resistant unless they were grown on flax-sick soil. In 1923, Barker (6) first demonstrated that a selfed line of flax did not become susceptible even after being grown on "clean" soil for 3 years. He proved definitely that resistance to wilt was an inherent characteristic in the plant. Today this well-known fact (17) is the basis for selecting wilt-resistant lines.

The earliest wilt-resistant varieties were developed at North Dakota (N.D.R. No. 52, 73, and 114) and are credited with saving the flax crop of northwestern agriculture (21). Shortly after came the wilt-resistant variety Linota, then Bison and Buda, from North Dakota, and Redwing from Minnesota in 1904. By 1938, 85 percent of the flax grown in Minnesota, the Dakotas, and Montana was descended from wilt-resistant Bison flax.

With the establishment of "wilt disease gardens" at North Dakota in 1893 and at Minnesota in 1913, wilt-resistant varieties were developed and, at the present time, all varieties recommended by experiment stations in the north-central states are wilt-resistant. The early history of flax wilt has been reviewed in detail by Barker (6), Bolley (7), and Dillman (21) and recent history by Christensen (17) and Millikan (47).

Disease Garden In North Dakota

Shepperd set up cropping systems at North Dakota State University in 1893 and included plots of continuous flax culture, so that by 1900 the continuous flax plots had enough ripe plants to make only two normal sheaves from the 1 acre plot (7). This plot, designated plot 30, was taken over by H. L. Bolley in 1900 as a "wilt disease garden" for additional testing of flax varieties for wilt resistance. It is the oldest "flax-sick" experimental plot in North America, if not the world.

On July 4, 1900, Bolley scattered soil from plot 30 onto non-flax soil and sowed flax in it. The seedlings wilted and died. He demonstrated that the wilt-sick soil contained a fungus that caused wilt. Plot 30 has been in continuous flax culture from 1900 to the present and has served as a plot for screening new lines for resistance to wilt. The susceptible lines or selections wilt and die, thereby eliminating themselves from the population. Resistant lines survive, produce seed, and after harvest are tested for other characteristics.

Disease Garden In Minnesota

In 1913, a plot of land was set aside on the farm at the University of Minnesota, St. Paul, in which flax followed flax continuously. This plot also has been used to the present time. After selecting seeds of wilt-resistant lines and varieties in the nursery, the straw is plowed into the soil to increase the inoculum of *F. oxysporum* f. sp. *lini*. Straw from infected flax stems from other parts of the state and adjoining regions also has been added from time to time to introduce possible new races of the pathogen into the wilt nursery. Sometimes soil from infected flax fields has been mixed with soil in the wilt nursery. Many cultures of *F. oxysporum* f. sp. *lini* also have been added to the soil at planting time. Of course, we do not know whether all or any of the added cultures survived and became part of the inoculum in the soil.

Seed of varieties from all over the world has been introduced into the plot and, since the pathogen can be carried on or in flax seed, new races may have been introduced into the nursery. The wilt nursery in St. Paul probably harbors a greater diversity of races of the wilt fungus than any other plot of soil in the world. Isolations made from the soil and infected plants have given a vast array of biotypes that differ in many ways, including pathogenicity (figure 9).

For many years, particularly during the early thirties and forties, several thousand lines of flax were tested annually for resistance to wilt. All new or improved varieties of flax developed at Minnesota were tested for wilt resistance in this nursery. After plant breeders from the Department of Agronomy and Plant Genetics made crosses, the progenies, beginning with the F_2 generation, were tested each year until a variety either was released by the experiment station or rejected for reasons such as susceptibility to rust or pasmo or because of undesirable agronomic or biochemical characteristics.

The susceptible lines and varieties wilt, die, and eliminate themselves from the flax population. Only resistant lines remain, as illustrated in figure 2. This early testing eliminates many lines of flax in the early generations and

Table 8. Percentage of wilted plants of 827 varieties of the world collection of flax tested in the wilt nursery in St. Paul, 1954

Country of origin	Varieties	Varieties with 100 percent wilted plants	Average wilted plants
	.......number.......		percent
North America			
Canada	24	2	29
Guatemala	1	1	100
United States	305	43	27
South America			
Argentina	137	35	49
Brazil	6	4	83
Uruguay	12	3	44
Europe			
Bulgaria	6	4	78
Eire	2	0	53
France	1	0	20
Germany	7	2	67
Greece	2	2	100
Netherlands	22	9	58
Portugal	5	5	100
Sweden	3	0	43
Eurasia			
U.S.S.R.	85	45	78
Asia			
Afghanistan	2	2	100
India	43	23	67
Iran	3	3	100
Japan	4	0	18
Korea	1	0	20
Manchuria	1	1	100
Syria	1	1	100
Turkey	107	102	98
Africa			
Egypt	7	5	94
Ethiopia	31	21	90
Kenya	2	0	65
Morocco	2	1	60
Australia	5	1	65
Totals and average	827	315	54

Table 9. Percentage of wilted plants of 305 flax varieties developed in nine states tested in the wilt nursery in St. Paul, 1954

State	Varieties*	Varieties with 100 percent wilted plants	Average wilted plants
	.......number.......		percent
North Carolina	5	4	80
Michigan	2	0	20
Minnesota	59	9	23
North Dakota	169	16	22
South Dakota	3	1	73
Montana	58	7	30
Oregon	1	1	100
California	7	4	75
Texas	1	1	100

* Varieties tested were those included in the world collection of flax.

Table 10. Comparison of the wilt reaction of 59 flax varieties produced at Minnesota and grouped into three groups according to time of introduction

Year of introduction	Varieties*	Varieties with 100 percent wilted plants	Wilted plants	
			Range	Average
	....number....		.....percent.....	
1919-30	19	9	5-100	62
1931-40	24	0	1-60	9
1941-53	16	0	1-25	4

* All varieties tested were those included in the world collection of flax and were tested at the same time in the St. Paul wilt nursery.

thereby not only has simplified the job of selection, but has saved vast sums of money.

The terms "wilt nursery", "wilt-sick" soil, and "disease garden" all describe a plot of land in which the soil is thoroughly infested with the wilt pathogen and in which varieties can be tested for wilt resistance.

Two Minnesota wilt nurseries are described in this bulletin, one started in 1913 and one started in 1946, but ended in 1950. The latter nursery was used for special studies on late wilt.

Varietal Behavior

The effectiveness of testing for wilt resistance has been illustrated in past decades by the selection and release of wilt-resistant varieties. When 827 varieties in the world collection of flax were tested at one time in the wilt nursery, varieties developed in the United States averaged only 27 percent wilt, compared with higher percentages for other countries (see table 8).

The 305 flax varieties from the United States shown in table 8 are shown again in table 9. Most of the varieties developed in North Dakota, Minnesota, and Montana had lower average percentages of wilted plants than varieties developed elsewhere and tested in St. Paul, The differences might be explained either by different collection of races of the pathogen or by different environmental conditions in the states.

Another measure of the effectiveness in testing for wilt resistance was shown for 59 varieties developed in Minnesota over a 34-year period when varieties were selected for successively greater degrees of resistance. When varieties selected during 1919-30 were tested in 1954, an average of 62 percent of the plants wilted, but for those varieties selected during 1941-53, only 4 percent wilted (table 10).

The varieties in the wilt nursery differed from decade to decade. The continuously planted varieties were Bison, Punjab, and Redwing. These varieties were sown every 50 rows as a check on the uniformity of inoculum in the plot. Punjab wilted 100 percent each year. The results for Bison and Redwing appear in figure 14. As shown in the figure, wilting was uniformly low for Bison, but wilt percentages were high for Redwing in the decade 1930-39. Low rainfall during this decade might have favored susceptibility to wilt of Redwing more than Bison, as it did for the variety Crystal (see table 3).

Varieties are not genetically uniform populations. Some are made by bulking sister selections; others become mixed by natural crossing in the field. Flax is self-pollinated, but 0-5 percent natural crossing occurs in the field (16, 22), averaging about 1 percent (16).

This genetic variation among varieties manifests itself in variation in resistance to wilt also. This fact was illustrated for a number of selections made from single plants

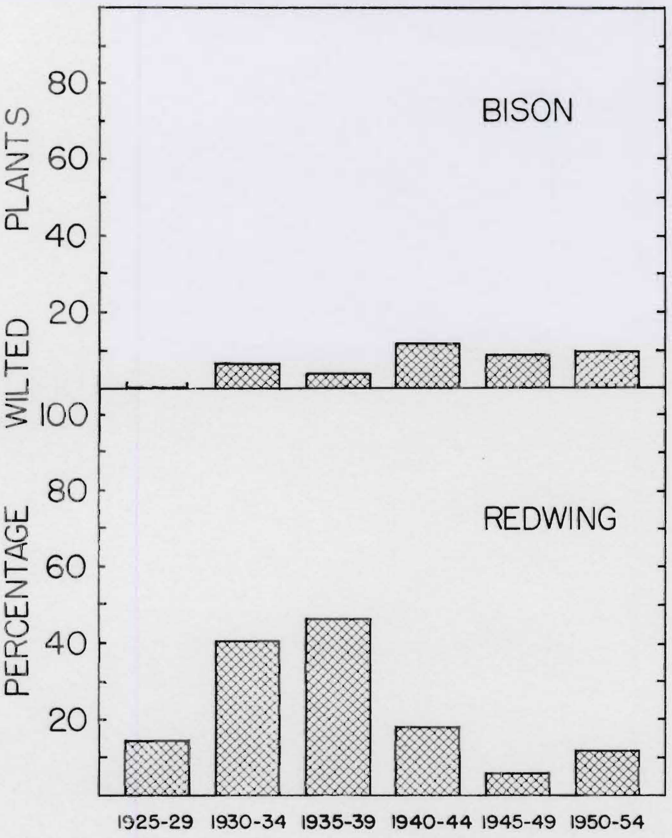

Figure 14. A comparison of the two flax varieties Bison and Redwing in percentage of wilted plants in a wilt nursery begun in 1912. Figures are averages of 5-year periods with about 1,000 plants of each variety per year.

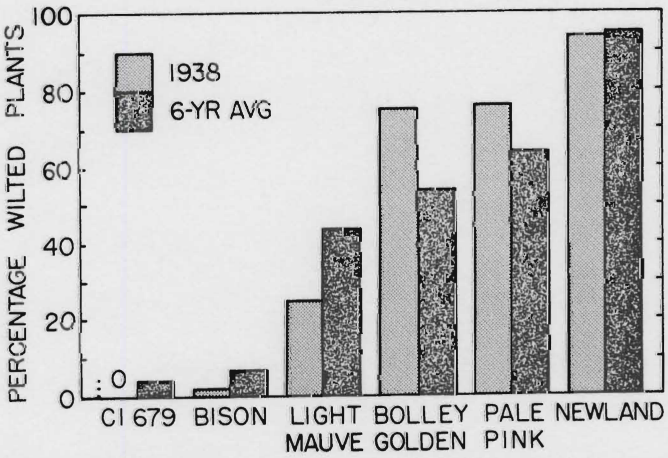

Figure 15. Average percentage wilt of six varieties of flax grown in the regular wilt nursery in 1938 and for the period 1933 to 1938. Data for each year are averages of three replicates of about 100 plants per replicate.

of seven varieties in 1936 (table 11) and for three varieties in 1955 (table 12). Note, for example, that one selection from Argentina had 3 percent wilted plants, while another had 50 percent (table 11). Others were uniformly resistant (Minnesota selection) or susceptible (Pale Blue). In table 12, Redwood was quite uniformly resistant, while B-5128 and Marine were mixtures of wilt-resistant and wilt-susceptible plants.

Although changing environmental conditions can alter the resistance of a given variety to wilt somewhat, that variety will behave fairly consistently from season to season. This was shown in 1938 when the reaction to wilt of six varieties was compared (figure 15). Both Bison and CI 679 had low incidences of wilt in 1938 and for a 6-year period, whereas Newland was consistently very susceptible to wilt for the same time. This kind of resistance appears to be nonspecific resistance. Intravarietal variation is a factor to be considered in a program of testing for wilt resistance. This consideration was emphasized by Houston and Knowles (30) in California.

Table 11. Variation in wilted plants among single plant progenies from seven varieties of flax grown in the wilt nursery, 1936

Variety	Plant number	Wilted plants*
		percent
Argentine selection (CI 712)	1	3
	2	8
	3	31
	4	50
Argentine selection (CI 416-3)	1	17
	2	42
	3	61
	4	93
Bison	1	2
	2	6
	3	9
	4	14
	5	17
Light Mauve	1	10
	2	35
	3	71
Minnesota selection (CI 679)	1	1
	2	2
	3	3
	4	5
Pale Blue	1	67
	2	74
	3	87
	4	96
Pale Pink	1	22
	2	42
	3	67

* Seeds from each plant were divided into two or three lots and each lot was planted in one row. Percentages are averages of two or three rows (replicates).

Table 12. Variation in wilted plants among 140 to 200 single plant selections from each of three flax varieties tested in the wilt nursery, 1955

Percentage wilted plants	Single plant selections per wilt class*		
	B-5128	Marine	Redwood
		number	
0-10	23	22	52
11-20	8	28	57
21-30	9	24	29
31-40	8	12	0
41-50	14	12	0
51-60	19	9	0
61-70	9	13	0
71-80	8	11	0
81-90	31	9	2
91-100	71	20	0
Total	200	160	140

* Results are averages of duplicate nonadjacent rows of approximately 100 seeds per row.

Table 13. Disease reaction of 10 flax varieties to three diseases

Variety	Reaction*		
	Rust	Wilt	Pasmo
Abyssinian Yellow (CI 300)	MS	VS	S
Bison (CI 389)	S	R	MS
Bolley's Golden Sel. (CI 976)	I	MS	VS
Common Pink (CI 479)	MR	MS	MR
Long × E. (CI 697)	R	MS	S
Punjab (CI 20)	R	VS	S
Redwing (CI 320)	S	MR	S
Smokey Golden (CI 1002)	R	MS	VS
Willamette	MS	MS	S
CI 671	R	R	MS

* I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible, VS=very susceptible.

Table 14. Effect of rust and wilt on survival of yellow- and brown-seeded varieties and on blighted seed after one generation on each of four soil types

Disease	Soil type	Seed coat color*		Blighted seed
		Yellow	Brown	
		percent		
Wilt	Silt loam	5	95	47
Rust	Peat	12	88	8
None†	Sandy loam	35	65	10
None	Clay loam	19	81	13

* The mixture of 10 varieties sown at each location originally had 40 percent yellow and 60 percent brown seed.

† None means that no artificial epidemics were created. Scattered infection from rust and pasmo was present but was not epidemic.

Table 15. Prevalence of 10 varieties after 4 years in a wilt nursery at St. Paul after mixing equal amounts of seed of each variety and sowing the mixture in the field

Variety	Stand
	percent
Bison and CI 671	89
Common Pink	6
Redwing	5
Abyssinian Yellow	0
Bolley Golden	0
Long × E.	0
Punjab	0
Smokey Golden	0
Willamette	0

Table 16. Effect of wilt and rust on the number and dominant varieties of flax over a 5-year period starting with a seed mixture of 10 varieties equally mixed

Disease per year*					Final Stand		
1941	1942	1943	1944	1945	Varieties	Dominant variety	Prevalence
					number		percent
Wilt	Wilt	None	Wilt	Wilt	4	Bison, CI 671	90
Wilt	None	None	Wilt	None	4	Bison, CI 671	97
None†	None	None	Wilt	Wilt	5	Redwing	80
Rust	None	None	Wilt	Wilt	5	Redwing	96
None†	Rust	Wilt	Wilt	None	8	Redwing	66

* Wilt was tested on a silt loam soil at St. Paul, and rust was tested on peat soil at Coon Creek. Plots where no epidemics occurred were on clay loam except where indicated.

† Plots on sandy loam soil with no epidemics.

Varietal Survival Affected by Disease

Experiments were made to study population trends when seeds of different flax varieties were mixed and sown on different soils. Seeds of 10 morphologically distinct varieties of flax, identifiable in the field on the bases of seed and flower color, plant height, and growth habit, were selected. The mixed seeds were sown in one of these locations: the silt loam of the wilt nursery at St. Paul, the clay loam free from wilt at St. Paul, the sandy soil usually free from disease at Hastings, or the peat soil in the rust nursery at Coon Creek.

Twenty seeds of each of 10 varieties were mixed, making 200 seeds sown per row. Ten rows were planted to each mixture on each soil type. Seeds were treated with ethyl mercury phosphate prior to sowing.

After each growing season, each row was harvested in bulk, and the bulk sample was sown again the following spring on the type of soil from which the sample was harvested. Random samples were taken during the winter to ascertain the resulting percentage of each variety in mixtures where seed characteristics were used to establish varietal identity.

At the end of 4 years, bulked seeds from each soil type were planted on all other soil types. Disease notes were taken for each lot on each soil type each year.

When seeds of the 10 varieties were mixed, 40 percent of the seeds were yellow and 60 percent were brown.

The 10 varieties used are listed in table 13, together with their reaction to rust (*Melampsora lini* (Pers.) Lev., wilt, and pasmo (*Septoria linicola* (Speg.) Gar., the three major diseases of flax during the time of this study.

After one generation on wilt-sick soil, the percentage of yellow seed dropped from the original 40 percent to 5 percent (table 14), with an increase in the more wilt-resistant brown-seeded plants. The percentage of blighted seed also was highest in the wilt-sick soil, using the term blighted as described by Kommedahl et al. (39). On the plots without disease epidemics, the percentage of yellow seed dropped 5 percent on sandy loam and 21 percent on clay loam after one generation (table 14).

After 4 years in a wilt nursery, only four of the 10 varieties of flax remained (table 15). Bison and CI 671 made up 89 percent of the total remaining, while six varieties were eliminated by wilt and disappeared from the population.

After 5 years, Bison, Redwing, and CI 671 were the dominant varieties of the 10 tested (see table 16). Wilt in 1941 and in 1944 or 1945 resulted in Bison and CI 671 being predominant. The absence of wilt for the first 3 years resulted in predominance of Redwing, which was accentuated when rust occurred in the 1st year. This sequence probably eliminated the rust-susceptible Bison. On the other hand, a different combination of rust and wilt resulted in Redwing predominance, but to a lesser extent (see table 16).

The relative effect of wilt and rust on stands of flax and on weight of seed harvested from 2,000 seeds sown in the field is shown in table 17. The seeds of the 10 varieties were sown either as mixtures or as separate varieties.

Table 17. Effect of wilt and rust on stand and yield of seed of 10 varieties of flax grown separately and as mixed stands*

		Stand		Seed yield	
Disease	Soil type	Mixture	Separate	Mixture	Separate
		..percent..		....grams....	
Wilt	Silt loam	37	35	1.8	2.1
Rust	Peat	80	71	5.3	11.0
None	Sandy loam	72	70	23.0	22.0
None	Clay loam	49	48	25.0	23.0

* Stands and yields are based on 2,000 seeds planted for each treatment. Germination on blotters prior to sowing seed was 93 percent. Stand is expressed as percentage emergence of seeds sown. Seeds of 10 varieties were mixed prior to sowing and also were planted separately.

As shown in table 17, the results were about the same, whether seeds were sown separately or in a mixture. Seeds sown on wilt-sick soil produced only about one-tenth the harvest of seeds sown on soil not infested with the wilt organism. The stand of flax on wilt-sick soil was about half that on the sandy loam soil and about one-third that on the clay loam.

Thus it is apparent that soil infested with the wilt fungus has a selective effect on survival of varieties that are mixed, and the wilt-resistant varieties have a greater survival value. Also, losses in seed yield attributable to wilt can range from 30-50 percent, based on yields from 18-foot (5.5-meter) rows in the field.

Yield Affected by Continuous Flax Culture

Seed of six flax varieties was sown in the regular wilt nursery for 3 consecutive years (1956-58). The same varieties were grown on wilt-free soil during the same

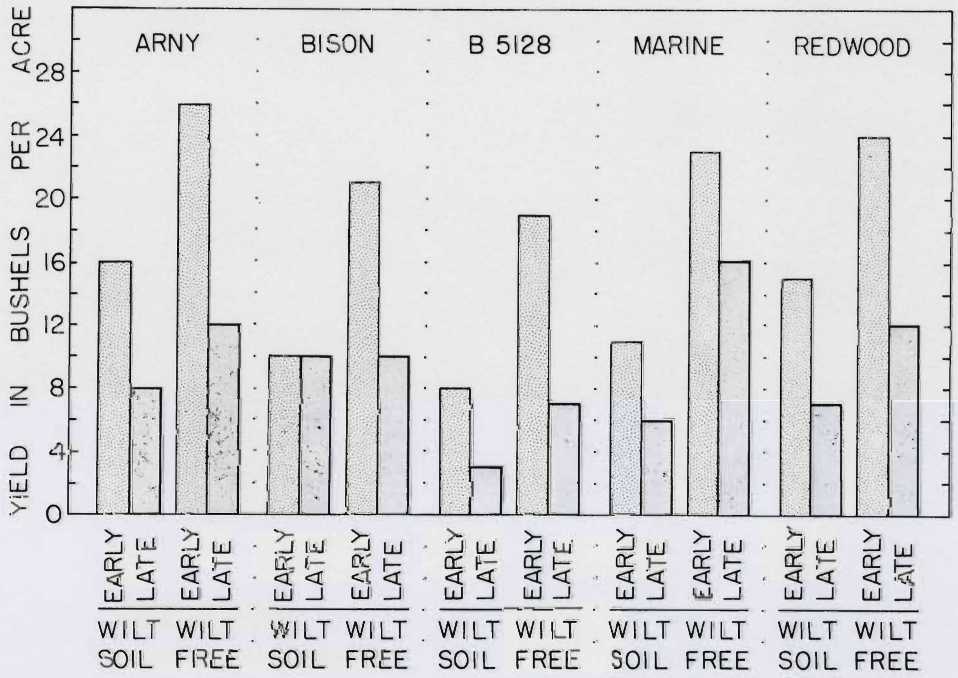

Figure 16. Seed from five varieties of flax in 1958. Varieties sown on the wilt-sick soil of the regular wilt nursery, on which flax had been grown since 1913, and on a nearby wilt-free plot. There were two plantings, one early and one late, on each plot. Results are based on an average of all entries in the wilt nursery for each variety.

Table 18. Comparison of yields and wilted plants of flax grown in a flax wilt nursery and flax in a wheat disease nursery for early and late plantings, 1960

	Yield* and wilted† plants from early and late plantings							
	Flax nursery				Wheat nursery			
	Early		Late		Early		Late	
Variety	Yield	Wilt	Yield	Wilt	Yield	Wilt‡	Yield	Wilt‡
	bu./acre	percent	bu./acre	percent	bu./acre	percent	bu./acre	percent
Arny	26	12	14	1	30	1	22	3
Bison	18	8	13	2	24	2	23	8
B-5128	21	26	14	17	28	6	19	5
Marine	21	34	17	34	27	8	27	12
Redwood	31	13	18	2	35	1	24	7
Punjab	0	100	0	100	22	4	15	8

* Based on average yield from rod-row (5 m. long) plots.
† Determined from 100 emerged seedlings within the row. All forms of wilt were counted.
‡ Plants apparently wilted but, from isolations made, many fungi, including **Fusarium** spp., accounted for the wilt, seedling blight, or root rot of flax.

time for the early planting and for 1956 and 1958 for the late planting. Seeds were harvested from 40th-acre plots in the wilt nursery and from wilt-free soil nearby. The results appear in figure 16.

After 43-45 years of continuous flax culture, the yields of five flax varieties were 8-16 bushels per acre, which is about that of the state average for a 10-year period in Minnesota (10 bushels per acre for the same 3-year period). On the other hand, it is about half of what the same varieties yielded during this period on wilt-free soil (19-27 bushels per acre). Thus, the wilt disease probably reduced yield: There was 100 percent loss with the susceptible variety Punjab and some reduction with the moderately susceptible varieties B-5128, Marine, and Redwood. B-5128 averaged 50 percent wilted plants and had the lowest yield even when planted early. Marine averaged 38 percent and Redwood averaged 31 percent wilted plants. Their yields were considerably lower than those obtained on wilt-free soil. Whether planted early or late, Arny with 7 percent and Bison with 10 percent wilted plants yielded better on wilt soil than B-5128 and Marine, but not better than Redwood. Apparently, differences in yield may be due to varietal characteristics other than resistance to wilt, and probably also to differences in soil fertility.

A similar study was made in 1960 for the same varieties. The results appear in table 18. Redwood had the highest yield, but wilt probably accounted for some loss in yield on the wilt-sick soil. Similarly, an increase in wilt was accompanied by a decrease in yield in the early plantings with other varieties. Other factors have to be considered, since soil fertility might also be different when flax and wheat soils are compared. Nevertheless, fairly good yields were obtained with wilt-resistant varieties on wilt-sick soil, illustrating the substantial progress made in the development of wilt-resistant varieties of flax over the years.

Inheritance of Resistance to Wilt

Crosses were made to study the inheritance to wilt of a number of common varieties of flax that differed widely in resistance. The varieties are listed in table 19. Crosses were made of these varieties, and the progenies in the F_1, F_2, F_3, and F_4 generations were tested for wilt resistance. The varieties were arbitrarily placed into five classes of wilt resistance for study purposes. A variety was considered resistant when 0-20 percent of the plants wilted, moderately resistant when 21-40 percent wilted, moderately susceptible when 41-60 percent wilted, susceptible when 61-80 percent wilted, and very susceptible when 81-100 percent wilted. These categories are not used in practice. Varieties in which more than 25 percent of the plants wilt would be regarded susceptible in a wilt nursery and would not ordinarily be considered further in a program of breeding for wilt resistance.

F_1 Generation

The incidence of wilted plants in the F_1 generation of crosses between varieties that were the same or different in wilt resistance is shown in table 20. The wilt resistance of the F_1 generation usually was intermediate in reaction to wilt, which had been reported previously (1, 16). In all the combinations tried and even though reciprocal crosses were not made, wilt resistance did not appear to be associated with the sex of either parent (table 20). In only eight of the 47 crosses was the percentage of wilted plants in the F_1 generation greater than for either parent, and in only four of these eight crosses was the difference enough to place the F_1 generation in the next highest category of wilt susceptibility.

In only four of the 47 crosses listed in table 20 was the F_1 generation more resistant than the more resistant parent and in only one of the four was the resistant F_1 generation appreciably more resistant than the more resistant parent (Ottawa 770B × Bison).

F_2 Generation

Segregation for wilt susceptibility in the F_2 generation is shown in table 21. Seed of the F_2 generation was tested in each of 2 years and compared with the parents. It also was tested for wilt resistance during the same time peri-

Table 19. Relative susceptibility of 23 varieties of flax to Fusarium oxysporum **f. sp.** lini

Variety or CI number	Wilted plants*
	percent
Resistant	
Bison (CI 389)	8
CI 438	7
652	2
658	3
669	8
679	7
697	16
712	19
Moderately resistant	
Argentine (CI 416-3)	40
Bolley Golden (CI 644)	31
Ottawa 770B (CI 355)	39
Moderately susceptible	
Light Mauve (CI 379-1)	57
Pale Pink (CI 479)	59
Redwing (CI 320)	48
Susceptible	
Rio (CI 280)	63
CI 387-1	72
421	74
423	77
673	63
Very susceptible	
Abyssinian Yellow (CI 300)	98
Newland (CI 188)	99
Ottawa 829 (CI 391)	88
Pale Pink (CI 649)	88

* Percentages are averages of three seasons (1934-36), except for CI 652, 658, 669, and 673, which are averages for 2 years (1932-33).

Table 20. Reaction of parents and F_1 generations derived from flax varieties with different degrees of susceptibility to Fusarium oxysporum **f. sp.** lini

Type of reaction*	Cross	Wilted plants		
	♀ × ♂	Parents†		F_1 generation‡
		♀	♂	
		percent		
R × R	CI 679 × Bison	9	5	0
	(Long × E) × CI 438	4	12	25
	CI 712 × (Long × E)	5	6	3
	CI 712 × CI 438	0	2	18
	CI 438 × Bison	13	3	8
	CI 416-3 × (Long × E)	8	6	19
	CI 421 × Bison	9	2	16
MR × R	CI 416-3 × CI 438	25	9	18
MS × R	Ottawa 770B × CI 712	57	6	42
	Light Mauve × Bison	43	2	7
	Ottawa 770B × (Long × E)	46	4	38
	CI 423 × CI 679	47	9	52
S × R	CI 387-1 × Bison	67	0	37
VS × R	CI 423 × Bison	98	2	40
	CI 421 × CI 679	94	4	74
	CI 391 × Bison	100	0	36
	CI 649 × Bison	98	2	13
	CI 479 × Bison	100	14	56
R × VS	CI 679 × Newland	2	100	67
	CI 438 × Newland	14	100	98
	Bison × Newland	4	100	18
	(Long × E) × Newland	2	100	81
	CI 712 × Newland	15	95	100
	CI 416-3 × Newland	14	98	72
VS × S	Ottawa 770B × Redwing	100	80	100
	CI 391 × Redwing	86	71	71
	CI 479 × CI 387-1	100	62	75
S × VS	CI 387-1 × CI 300	75	100	92
VS × VS	Redwing × Light Mauve	100	100	100
	CI 300 × Newland	100	100	100
	CI 391 × CI 649	83	100	100
	Ottawa 770B × CI 387-1	100	100	100
	CI 649 × Redwing	100	83	100
	CI 423 × CI 300	89	100	100
S × S	CI 391 × Light Mauve	75	67	100
	Bolley Golden × CI 387-1	70	75	70
MR × MR	CI 416 × CI 712	38	37	31
	Ottawa 770B × CI 479	23	31	53
	Ottawa 770B × CI 438	38	39	61
MR × VS	Ottawa 770B × Newland	29	100	81
	Bolley Golden × CI 300	25	93	94
VS × MR	CI 391 × Bolley Golden	100	36	73
	CI 649 × Light Mauve	91	37	61
MS × S	CI 423 × Newland	58	100	100
MS × MR	Ottawa 770B × CI 416-3	45	26	17
S × MR	Ottawa 770B × Bison	80	40	17
	Redwing × Bison	62	33	45

* R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible, VS=very susceptible.

† Based on averages from 1934-35 in the regular wilt nursery.

‡ Percentages are based on stands of 10-35 plants in the regular wilt nursery.

od. The difference in incidence of wilted plants in the F_2 population for the 2 years of testing can be attributed to differences in the environment that favored more wilting of plants in 1936 than in 1935.

Of the 33 F_2 populations listed in table 21, only two were more resistant than the more resistant parent. However, the greater resistance, no more than 4 percent, was negligible.

In eight of the 33 progenies, the F_2 populations were more susceptible than the more susceptible parent. But the greatest increase in susceptibility was only 13 percent, hardly an appreciable difference. However, six of these eight crosses were between resistant varieties and another one was between a resistant and a moderately resistant variety.

Thus, about two-thirds of the F_2 populations from the 33 crosses were intermediate between the two parents in wilt susceptibility and none of the 33 F_2 populations was appreciably more resistant than the more resistant parent or more susceptible than the more susceptible parent.

Table 21. Reaction of parents and F_2 generation of 32 crosses derived from flax varieties with different degrees of susceptibility to *Fusarium oxysporum* f. sp. *lini*

		Wilted plants				
		Parents (1935-36)		F_2 generation†		
Type of reaction*	Cross ♀ × ♂	♀	♂	1935	1936	Weighted average
		percent				
R × R	CI 679 × Bison	9	4	7	20	13
	(Long × E) × CI 438	0	12	11	..	11
	CI 712 × CI 438	6	12	12	18	15
	CI 438 × Bison	6	0	19	..	19
	Ottawa 770B × CI 712	11	3	20	18	19
	Ottawa 770B × (Long × E)	17	12	17	26	21
	CI 416-3 × CI 438	0	0	1	..	1
	Light Mauve × Bison	15	3	5	10	7
MR × R	Ottawa 770B × CI 438	28	8	36	..	36
	CI 416-3 × CI 712	35	5	36	11	23
	CI 712 × (Long × E)	24	7	0	7	3
MS × R	CI 479 × Bison	44	4	..	19	19
	Ottawa 770B × Bison	44	0	11	..	11
	CI 416-3 × (Long × E)	49	5	7	25	16
VS × R	CI 423 × CI 679	87	6	17	56	36
	CI 423 × Bison	95	4	18	31	24
	CI 421 × CI 679	96	5	81	39	60
	CI 421 × Bison	96	4	6	4	5
	CI 649 × Bison	98	10	24	34	29
R × VS	CI 679 × Newland	5	100	46	77	61
	CI 438 × Newland	0	100	95	..	95
	Bison × Newland	4	100	13	65	39
VS × R	(Long × E) × Newland	7	100	94	80	87
R × VS	Ottawa 770B × Newland	15	99	34	84	59
MR × VS	Bolley Golden × CI 300	29	99	90	59	74
VS × MR	CI 649 × Light Mauve	95	29	67	63	65
VS × VS	CI 300 × Newland	95	99	99	85	92
	CI 423 × CI 300	90	97	100	96	98
	CI 423 × Newland	87	100	99	100	99
MR × S	Ottawa 770B × CI 479	21	64	32	66	49
	Ottawa 770B × CI 416-3	27	76	52	60	56
MS × VS	CI 416-3 × Newland	46	99	75	87	81
	CI 712 × Newland	47	100	95	90	92

* R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible, VS=very susceptible.
† Percentages for each year are based on 300-400 plants per year in the regular wilt nursery.

As seen in table 21, it made little difference whether the resistant variety was the maternal or paternal parent in crosses with **very susceptible** varieties of flax.

F_3 Generation

The F_3 populations were tested for wilt resistance in 1933, 1936, and 1937, although different crosses were tested in each of these 3 years.

Table 22 shows that in crosses of the resistant varieties CI 652, 658, and 669 with the susceptible variety Rio, more than half of the F_3 families had fewer than 40 percent wilted plants when CI 652 was the parent. However, only one-third had fewer than 40 percent wilted plants when CI 658 was the maternal parent, while one-third of the families had more than 90 percent wilted plants. Similarly, one-third of the families had fewer than 40 percent wilted plants when CI 669 was the maternal parent, but only about 10 percent of the families had 90 percent or more wilted plants.

When the same three resistant varieties were crossed with the resistant variety Golden, more than half of the families had fewer than 30 percent wilted plants when either CI 652 or CI 669 was the maternal parent. However, when CI 658 was crossed with Golden, about one-third of the families had fewer than 40 percent wilted plants and about one-third had more than 90 percent wilted plants—the same result as when CI 658 was crossed with Rio.

Thus, in crosses with different paternal parents differing in wilt resistance (Rio and Golden), the inheritance of wilt resistance in CI 658 was about the same.

The F_3 generations of seven different crosses are shown in table 23. When wilt-resistant varieties were crossed with wilt-susceptible varieties, most of the F_3 families were intermediate in wilt resistance: 65 percent of the F_3 families for CI 423 × Bison; 76 percent for CI 423 × CI 679; 94 percent for Bison × Newland; and 96 percent for CI 679 × Newland. Moreover, in three of the four crosses, the resistant parent appeared to influence

Table 22. Distribution of F_3 families into 10 percent classes for percentage of wilted plants, 1933

Cross or variety	Families	Families per percentage class									
		0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
	number										
CI 652	1	1	..	..	..	..	..	..	..	..	..
652 × Rio	93	22	5	9	11	16	8	6	7	3	6
Rio	1	..	..	..	..	..	..	1	..	..	..
CI 658	1	1	..	..	..	..	..	..	..	..	..
658 × Rio	351	71	13	7	10	16	25	33	27	33	116
Rio	1	..	..	..	..	..	..	1	..	..	..
CI 669	1	..	1	..	..	..	..	..	..	..	..
669 × Rio	127	25	6	4	9	17	13	9	10	21	13
Rio	1	..	..	..	..	..	..	1	..	..	..
CI 652	1	1	..	..	..	..	..	..	..	..	..
652 × Golden	124	35	16	12	16	8	8	9	4	4	12
Golden	1	..	1	..	..	..	..	..	..	..	..
CI 658	1	1	..	..	..	..	..	..	..	..	..
658 × Golden	78	12	6	3	5	10	2	1	8	7	24
Golden	1	..	1	..	..	..	..	..	..	..	..
CI 669	1	1	..	..	..	..	..	..	..	..	..
669 × Golden	103	48	5	0	5	6	4	8	10	6	11
Golden	1	..	1	..	..	..	..	..	..	..	..

Table 23. Reaction of F_3 families and parents to wilt, 1936

Variety or cross	Plants tested	Classification of families					Wilted plants	
		Total	Resistant as resistant parent	Susceptible as susceptible parent	Intermediate	Over 50 percent wilt	Range	Average
	number						percent	
Bison	..	..	..	..	..	..	..	13
B × N	13,836	160	19	0	151	37	3-75	38
Newland	..	..	..	..	..	..	..	95
Bison	..	..	..	..	..	..	..	4
479 × B	4,397	58	29	23*	6	2	0-61	18
CI 479	..	..	..	..	..	..	..	20
Bison	..	..	..	..	..	..	..	2
B × 679	25,255	257	241†	16‡	0	0	0-25	4
CI 679	..	..	..	..	..	..	..	4
Newland	..	..	..	..	..	..	..	100
679 × N	6,343	74	3	0	71	37	7-85	48
CI 679	..	..	..	..	..	..	..	5
Bison	..	..	..	..	..	..	..	2
423 × B	5,895	74	18	8	48	12	0-94	26
CI 423	..	..	..	..	..	..	..	81
CI 423	..	..	..	..	..	..	..	87
423 × 679	7,065	78	19	0	59	10	0-74	25
CI 679	..	..	..	..	..	..	..	1
CI 423	..	..	..	..	..	..	..	90
423 × N	10,749	103	17§	86	0	103	64-100	93
Newland	..	..	..	..	..	..	..	99
Totals	73,540	804	346	133	335	201	..	..

* Sixteen families were more susceptible than either parent.
† As resistant as either parent.
‡ More susceptible than either parent.
§ More resistant than either parent.

the F_3 progenies more than the susceptible parent did, and each parent exerted about equal influence in the fourth cross. These results might have been expected, since selection was made on wilt-sick soil where resistance to wilt was favored and susceptible lines were eliminated from the population.

Crosses of two **very susceptible** varieties (CI 423 and Newland) resulted in 17 of 103 F_3 families that were more resistant than either parent.

Crosses of two resistant varieties (Bison and CI 679) resulted in 16 of 257 F_3 families that were more susceptible than either parent.

In tests of F_3 seed made the next year (1937), the influence of the resistant parent in favoring resistant progenies in the F_3 generation was again apparent (table 24), but only when the F_2 generation was produced on wilt-sick soil. When the F_2 (and F_1) seed was produced on wilt-free soil and the F_3 population tested for wilt re-

Table 24. Distribution of F_3 families into 10 percent classes of wilted plants when F_2 seed was produced on wilt-sick and wilt-free soil, 1937

Soil for growing F_1 and F_2 seed	Cross or variety	F_3 families	Families per percentage class*									
			0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
							number					
Wilt-sick	CI 479	..	..	..	1	..	..	1	1	1	1	1
	479 × Bison	42	35	2	3	1	1	..	..	..	..	..
	Bison	..	6	..	..	..	..	..	..	..	..	..
	CI 697	..	2	..	..	..	..	..	..	..	..	..
	697 × 712	4	1	..	..	1	..	..	1	..	..	1
	CI 712	..	2	..	..	..	..	..	..	..	..	..
	CI 421	..	..	..	..	..	..	..	..	..	..	2
	421 × 679	2	2	..	..	..	..	..	..	..	..	..
	CI 679	..	2	..	..	..	..	..	..	..	..	..
	CI 421	..	..	..	..	..	..	..	..	..	..	2
	421 × Bison	4	4	..	..	..	..	..	..	..	..	..
	Bison	..	2	..	..	..	..	..	..	..	..	..
	CI 416-3	..	2	..	..	1	..	..	..	..	1	..
	416-3 × Bison	15	14	..	..	..	..	1	..	..	..	..
	Bison	..	3	..	..	..	..	..	..	..	..	..
	Ottawa 770B	..	1	1	..	..	..	..	..	..	..	..
	770B × Bison	7	5	1	1	..	..	..	..	..	..	..
	Bison	..	2	..	..	..	..	..	..	..	..	..
Wilt-free	CI 416-3	..	..	2	..	1	..	..	..	..	1	..
	416-3 × Newland	29	..	..	..	..	1	2	..	3	9	14
	Newland	..	..	..	..	..	..	..	..	..	..	4
	Ottawa 770B	..	2	1	..	1	..	..	..	..	..	..
	770B × B.G.	26	..	3	4	3	6	3	..	4	2	1
	Bolley Golden	..	1	1	..	..	1	..	..	..	..	1
	CI 712	..	2	..	1	..	..	..	..	1	..	..
	712 × N	14	..	..	..	..	..	..	..	..	2	12
	Newland	..	..	..	..	..	..	..	..	..	..	4
	CI 649	..	..	..	..	..	..	..	..	..	2	1
	649 × Bison	11	1	4	3	2	..	..	..	..	..	1
	Bison	..	4	..	..	..	..	..	..	..	..	..
	CI 479	..	..	..	..	..	..	..	..	..	3	2
	479 × B.G.	38	1	7	5	5	6	5	..	4	3	2
	Bolley Golden	..	2	..	1	..	1	1	..	..	..	..

* Results are based on randomized duplicate rows.

sistance on wilt-sick soil, many more families proved to be highly susceptible to wilt. Growing two previous generations on wilt-free soil had perpetuated wilt-susceptible plants in the F_3 population.

In table 25, progenies from three crosses are compared on both wilt-sick and wilt-free soils. It is apparent that there were more susceptible families in the F_3 generation when the F_1 and F_2 generations were produced on wilt-free than on wilt-sick soils.

The continued selection of wilt-resistant lines from a cross is possible only by growing each generation of seed on wilt-sick soil to eliminate wilt-susceptible segregates from successive generations. This necessity was apparent also in the F_4 generation where, for example, only one of 125 F_4 families of Bison × Newland had more than 50 percent wilted plants when each generation was grown on wilt-sick soil, while 18 of 92 F_4 families had more than 50 percent wilted plants on wilt-free soil (see table 26). In this cross, Bison is resistant and Newland is susceptible to wilt.

When two susceptible varieties (CI 423 × Newland) were crossed, all of the F_4 families proved to be highly susceptible to wilt when previous generations were grown on wilt-free soil. One-fourth of the F_4 families were highly resistant to wilt when previous generations of this cross were grown on wilt-sick soil. Thus, wilt-resistant plants increase in a population where susceptible plants are eliminated by wilt.

It has been briefly reported (38) that Newland and Punjab tend to wilt as seedlings, while Linota and CI 423 tend to wilt late in the season. Varieties like Crystal and Redwing are variable. Also, progenies from crosses involving Newland tend to wilt early, whereas progenies containing CI 423 tend to wilt late. As shown in table 27, varieties like Abyssinian Yellow, Newland, Pale Blue, and Punjab wilt early, while Light Mauve, Linota, Pale Pink, and Rio tend to wilt late in the season. Others, such as Chippewa and Redwing, wilt throughout the season.

Because data shown in tables 27 and 28 were collected in different years, when wilt reactions might have varied with environmental differences, only tentative conclusions can be drawn from comparing them. For example, Light Mauve (CI 379-1) tended to wilt late in the season (table 27) and also tended to wilt late in the progenies of a cross with CI 649 in both F_1 and F_2 generations (table 28). CI 679 was wilt resistant (table 27), and

Table 25. Distribution of F_3 families into 10 percent classes of wilted plants when F_2 seed was produced on wilt-sick and wilt-free soil, 1937

Soil for growing F_1 and F_2 seed	Cross or variety	F_3 families	Families per percentage class*									
			0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
		number										
Wilt-free	Bison	..	6	..	..	..	..	..	..	..	..	..
	B × N	35	4	6	3	5	2	3	1	..	2	9
	Newland	..	..	..	..	..	..	..	..	..	..	6
Wilt-sick	Bison	..	..	4	..	..	..	..	..	..	..	..
	B × N	8	4	1	..	..	..	..	..	..	1	2
	Newland	..	..	..	..	..	..	..	..	..	..	4
Wilt-free	CI 697	..	5	..	..	..	..	..	..	..	..	..
	697 × N	36	3	5	4	3	3	2	1	3	4	8
	Newland	..	..	..	..	..	..	..	..	..	..	5
Wilt-sick	CI 697	..	3	..	..	..	..	..	..	..	..	..
	697 × N	2	1	..	..	..	..	..	1	..	..	..
	Newland	..	..	..	..	..	..	..	..	..	..	3
Wilt-free	Light Mauve	..	2	..	1	..	..	1	..	..	..	..
	L.M. × B	29	25	1	..	1	..	..	..	..	..	2
	Bison	..	5	..	..	..	..	..	..	..	..	..
Wilt-sick	Light Mauve	..	1	..	1	..	..	..	..	..	..	..
	L.M. × B	5	4	1	..	..	..	..	..	..	..	..
	Bison	..	2	..	..	..	..	..	..	..	..	..

* Results are based on randomized duplicate rows.

Table 26. Distribution of F_4 families into 10 percent classes of wilted plants when F_1, F_2, and F_3 seed was produced on wilt-sick and wilt-free soil, 1937

Soil for growing seed of F_1, F_2, and F_3	Cross or variety	F_4 families	Families per percentage class*									
			0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
		number										
Wilt-sick	Bison	..	23	2	..	..	..	..	..	..	..	..
	B × N	125	52	30	17	19	6	..	..	1	..	..
	Newland	..	..	..	..	..	..	..	..	..	..	25
Wilt-free	Bison	..	23	2	..	..	..	..	..	..	..	..
	B × N	92	27	17	15	11	4	5	1	..	2	10
	Newland	..	..	..	..	..	..	..	..	..	..	25
Wilt-sick	CI 423	..	..	..	..		..	..	..	..	..	4
	423 × N	8	2	..	..		..	1	..	1	..	4
	Newland	..	..	..	..	..	..	..	..	..	..	4
Wilt-free	CI 423	..	..	..	..	..	..	..	..	..	..	2
	423 × N	16	..	..	..	..	..	..	..	..	..	16
	Newland	..	..	..	..	..	..	..	..	..	..	2
Wilt-sick	CI 679	..	5	..	..	..	..	..	..	..	..	..
	679 × N	37	23	7	1	4	2	..	..	..	..	..
	Newland	..	..	..	..	..	..	..	..	..	..	5
Wilt-sick	CI 679	..	6	..	..	..	..	..	..	..	..	..
	679 × B	51	49	2	..	..	..	..	..	..	..	..
	Bison	..	6	..	..	..	..	..	..	..	..	..
Wilt-sick	CI 479	..	..	..	2	..	1	1	1	..	..	..
	479 × B	19	15	2	1	1	..	..	..	..	..	..
	Bison	..	4	1	..	..	..	..	..	..	..	..
Wilt-sick	CI 423	..	..	..	..	..	..	..	..	..	..	4
	423 × B	6	1	2	3	..	..	..	..	..	..	..
	Bison	..	3	..	..	..	..	..	..	..	..	..
Wilt-free	CI 479	..	..	2	..	..	..	..	1	..	..	2
	479 × B.G.	13	3	5	1	..	..	1	1	2	..	..
	Bolley Golden	..	2	..	2	..	..	..	..	..	..	..
Wilt-free	CI 697	..	3	1	..	..	..	..	..	..	..	..
	697 × N	16	..	..	..	5	..	1	1	3	2	4
	Newland	..	..	..	..	..	..	..	..	..	..	4

* Results are based on randomized duplicate rows.

Table 27. Relative susceptibility of 21 varieties of flax to *Fusarium oxysporum* f. sp. *lini* at five dates after sowing flax in the wilt nursery, 1937

Variety	Cumulative percentage of wilted plants at indicated dates after sowing*				
	June 4	June 12	June 24	July 6	July 15
	percent				
Abyssinian Yellow (CI 300)	50	86	86	86	100
Argentine selection (CI 712)	0	3	3	3	3
Argentine selection (CI 416-3)	4	4	19	32	32
Bison (CI 389)	0	0	0	0	0
Bolley Golden (CI 644)	0	2	12	26	26
Buda (CI 326)	13	19	19	19	19
Buda selection (CI 737)	0	0	3	3	3
Chippewa (CI 178)	27	40	62	70	70
Dehiscent Ukraine (CI 759)	0	1	1	1	1
Light Mauve (CI 379-1)	0	5	5	41	41
Linota (CI 244)	38	50	61	61	100
Long × E (CI 697)	0	6	6	6	6
Minnesota selection (CI 679)	0	0	2	2	2
Newland (CI 188)	60	82	91	91	100
Ottawa 770B (CI 355)	0	4	8	16	16
Pale Blue (CI 423)	52	84	92	98	100
Pale Pink (CI 479)	11	22	66	100	100
Punjab (CI 20)	65	87	87	87	100
Redwing (CI 320)	30	47	47	47	82
Rio (CI 280)	0	10	10	15	65
Walsh (CI 645)	0	0	0	0	0

* Flax seeds were sown on May 10. Data are based on randomized duplicate rows of 100 seeds per row. Notes were taken June 4, 12, and 24 and July 6 and 15.

Table 28. Relative susceptibility to wilt of F_1 and F_2 populations from 11 crosses of flax at five intervals when grown on wilt-sick soil, 1935

Cross	Cumulative percentage of wilted plants at different dates*									
	June 20		June 30		July 8		July 19		Aug. 2	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
	percent									
CI 679 × Bison	0	0	0	0	0	0	0	0	0	7
CI 649 × Bison	14	9	14	20	14	24	14	24	14	24
Bison × Newland	0	1	0	1	0	1	0	8	0	13
CI 423 × CI 679	0	0	0	0	0	0	0	1	50	17
CI 679 × Newland	0	2	0	2	0	2	37	19	58	46
CI 423 × Newland	8	6	8	19	8	19	100	98	100	99
Ottawa 770B × CI 416-3	0	0	0	6	0	6	0	33	11	52
Ottawa 770B × CI 712	0	0	0	1	0	1	0	4	26	20
Ottawa 770B × Newland	0	3	33	17	33	17	44	22	78	34
CI 712 × CI 697	0	0	0	0	0	0	0	0	0	0
CI 649 × CI 379-1	0	6	35	35	57	67	57	67	57	67

* Percentages based on 350-450 plants.

wilted plants, few as they were, appeared late. In progenies of crosses with Bison, CI 423, and Newland, plants wilted only late in the season, if at all (table 28). So it might appear that progenies wilt late from crosses of parents that wilt late.

On the other hand, while Ottawa 770B had few wilted plants that wilted late and Newland had many wilted plants, most of which wilted early (table 27), a cross of these two varieties gave progenies (F_1 and F_2) that wilted throughout the growing season (table 28). Also, both F_1 and F_2 progenies from crosses involving CI 423 (Pale Blue) tended to wilt late (table 28), even though the other parent (CI 679 or Newland) was not more susceptible to late wilt (table 27).

Obviously, much more extensive work must be done before we understand the inheritance of early and late wilt.

Discussion

At the turn of the century, wilt was the limiting factor in flax production. In fact, flax was known as a "new land" crop because flax stands were so poor when flax followed flax or even when flax was planted in a 3-5 year rotation. Today, flax wilt is almost unknown in Minnesota and neighboring states and has been found only occasionally in the past decade. This astonishing success story is the result of experiment station research, first by station botanist Otto Lugger, then by chemist Harry Snyder in Minnesota, and, in later years, by plant pathologists and plant breeders in North Dakota and Minnesota who worked cooperatively on developing wilt-resistant varieties. Their results have been so successful that when varieties such as Arny and Redwood were planted in the wilt disease nursery in St. Paul, where flax had been grown continuously for 45 years, they yielded 26 and 31 bushels per acre, respectively. In old flax varieties, entire stands were lost to flax wilt caused by *F. oxysporum* f. sp. *lini.*

Checking for wilt resistance among new varieties is necessary because this fungus is a soil inhabitant that can survive in soil by growing saprophytically on fresh organic matter (2, 52, 63, 71). It also can inhabit root surfaces (3) or damaged roots (51) of nonhost plants, and it can survive passively by producing chlamydospores (52). It is a primitive parasite in that it can infect root tips of young and old plants and can colonize cortical tissues of roots of both wilt-resistant and wilt-susceptible varieties. Resistance to wilt apparently resides in the vascular system and not in the cortex (4, 12, 16, 19, 38, 50, 61). Resistance is not wholly related to root exudates (37, 48) or to the microbiological population of roots; however, fungi have been reported to be more numerous on roots of the susceptible variety Novelty than on the wilt-resistant Bison (53). Attempts to link pathogenicity with the production of fusaric acid (25, 44) and host resistance to HCN (65) or with respiration inhibitors (49) have indicated no clear-cut relationships.

Although wilt-resistant varieties have been selected and grown commercially for many years, the nature of resistance is not well understood. Part of the difficulty is related to the concept of physiologic races that is applied to the wilt-inducing forms of *F. oxysporum.* With other forms of wilt fungi, resistance of the host is race specific. With pea wilt, for example, one pea variety may be resistant to race 1 but susceptible to race 2 (27, 70). This apparent lack of race specificity in the flax wilt fungus led Armstrong and Armstrong (4) to conclude that races in the flax wilt fungus are not clearly defined. Borlaug (9) indicated that races were described on the basis of the number of plants that wilt with a given isolate and that on this basis an indefinite number of races exists. Since flax varieties always have been selected in the field for resistance to a composite of an indefinite number of isolates collected from all parts of the state, the resistance obtained probably is not specific and is field resistance. Or, in Van Der Plank's terms (68), the resistance is horizontal rather than vertical.

On the other hand, Deshpande and Jeswani (20) have reported experiments on inheritance of resistance to wilt in which resistance appeared to be governed by a pair of duplicating genes, with resistance being dominant over susceptibility. This possibility might suggest that race specificity exists. However, their studies were made in the greenhouse, and this type of resistance might not be demonstratable in the field. Resistance to some clones of the fungus was found to be due to two complementary genes (34, 35).

Extensive work indicates that resistance is governed markedly by environmental factors. The way in which varieties are selected points to the conclusion that the resistance obtained is field, not race-specific, and that multiple factors probably are involved. Consequently, wilt-resistant varieties of flax tend to remain resistant. It also explains why it is not likely that races of the fungus can be selected in the same way as for pea wilt or other wilts (4). Probably the differences among races of the flax wilt fungus are too small to be classified. Or perhaps there is only one common race that comprises many genotypes that vary in minor degrees of pathogenicity.

It is not difficult to show that isolates of the flax wilt fungus can cause wilt in one variety of flax and not in another when tests are made in the greenhouse using single isolates of the fungus in autoclaved soil. Borlaug and Christensen (10) and Schuster (55), for example, demonstrated that Bison was susceptible to race 6 and resistant to race 11 and that Punjab was susceptible to both races. Borlaug (9) also showed that Linota was resistant to race 6 but susceptible to race 8. Millikan (46) compared pathogenicity of isolates from Minnesota, Australia, and New Zealand and found differences in reaction among varieties. As reported in table 2, Koto was resistant to two isolates from Minnesota but was susceptible to an isolate from Arizona, and Buda was resistant to one Minnesota isolate and susceptible to a California isolate. But all these tests were made in the greenhouse with single isolates tested singly.

Borlaug (9) reported, however, that a variety of flax susceptible to two races when tested singly may be much less susceptible when tested in combination, indicating some competition between isolates or races. This result may explain why varieties that are resistant to wilt when tested in the field can be very susceptible to individual isolates from that same field when tests are made in the greenhouse in autoclaved soil. Not only is there no competition among isolates, but the inoculum potential is high in greenhouse tests, which favors wilt development. Moreover, roots of greenhouse plants are more succulent than roots of plants grown in the field. Consequently, races identified on differential varieties in the greenhouse may have little or no meaning in the field. We believe that flax varieties are exposed to a mixture of races or isolates in soil and that selection pressure does not favor the kind of resistance that is race-specific.

On the other hand, races may be important in the field, as suggested by Stakman et al. (58), who reported that varieties resistant in North Dakota were susceptible in St. Paul, and by Vanterpool (69) in Canada, who found that the wilt-susceptible variety Crown had more wilted plants in Saskatoon than in Ottawa soil, whereas the moderately wilt-susceptible Royal had more wilted plants in the Ottawa than in the Saskatoon soil.

Van Der Plank (68) states that varieties initially were selected on the basis of race-specific (vertical) resistance, but that these varieties contained weak genes for resistance. This possibility could explain the results of Stakman et al. (58) and Vanterpool (69), who reported that varieties resistant at one location were susceptible at another. Van Der Plank (68) continues to argue that field (horizontal) resistance was incorporated with vertical resistance to delay the development of an epidemic, once race-specific (vertical) resistance had been overcome.

If homozygous host varieties were selected and tested for resistance to specific isolates, possibly clear-cut races of the pathogen could be identified. But identifying them would have little meaning in practice, since varieties are exposed to a mixture of races in the field. And wilt-resistant varieties of flax can be developed by utilizing nurseries where flax wilt occurs and by exchanging germplasm between locations. Of course, all new varieties developed for agronomic characteristics should be tested for wilt-resistance to prevent the possibility of losing the genes for it.

Clearly, not only are multiple factors involved in wilt resistance and not only does temperature play an important role, but changing agronomic practices in the host environment can predispose plants to wilt. Major changes in herbicide applications, plant nutrition, and other practices will need testing before new varieties can be adopted or new practices can be commercially adapted. The development of varieties that apparently contain field resistance has been so eminently successful that testing in wilt nurseries should be continued to provide growers with wilt-resistant varieties of flax.

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