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Developing Wheats Resistant to

Snow is beneficial in most winter wheat (*Triticum aestivum* L.) areas of the world as protection against cold and as a source of water. Snow is a hazard, however, when it falls early in the season on unfrozen or lightly frozen soil and persists until spring. Certain fungi with the ability to grow at low temperature may destroy the wheat under deep snow when conditions are favorable. In the Pacific Northwest of the United States, snow molds are most severe in Douglas and Okanogan counties, Washington, and in the dryland areas of eastern and southern Idaho. Winter wheats were grown for about 40 years in these areas before snow mold fungi were recorded.

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0191-2917/82/11109006/$03.00/0

Snow Mold, Scald, and Rot

Gray snow mold or speckled snow mold is caused by *Typhula idahoensis* Remsberg (reported by Hungerford in 1923 [8]), *T. incarnata* Lasch ex Fr. (reported by Young in 1929 [8]), and *T. ishikariensis* Imai (reported by Bruehl and Cunfer in 1975 [6]). Pink snow mold is caused by *Fusarium nivale* (Fr.) Ces. = *Gerlachia nivalis* var. *nivalis* (17) (reported by Blodgett in 1946 [8]), snow scald by *Sclerotinia borealis* Bub. & Vleug. = *Myriosclerotinia borealis* (17) (reported by Sprague, Fischer, and Figaro in 1961 [8]), and snow rot by *Pythium iwayami* Ito and other *Pythium* spp. (reported by Lipps and Bruehl in 1978 [14]). All these fungi are probably native to the Pacific Northwest. Some pathogens known in adjacent parts of Canada (17) have not yet been identified in the region.

T. idahoensis and *T. ishikariensis* are restricted to areas with deep snow. In contrast, *T. incarnata* not only is prevalent in deep snow areas but also attacks the roots and crowns of winter wheat and barley in the absence of true snow mold in the mellow, well-aerated soils of Adams, Lincoln, and Spokane counties. Holton (11) first observed this wider adaptation of *T. incarnata*. When winter wheat near Harrington in Lincoln County was sprayed with triadimefon (Bayleton) in two successive seasons, a 4–5 bushel per acre (269–336 kg/ha) increase in yield was obtained because the crown and root rots caused by *T. incarnata* were controlled (D. Gertenbach, *unpublished*). The chronic losses in wheat in the absence of true snow mold are not considered in this paper.

In typical *Typhula* snow molds, the older leaves in contact with soil under

Fig. 1. Nugaines winter wheat destroyed by *Typhula idahoensis*. Early seeding before winter resulted in extensive growth. The leaves were digested by the fungus and collapsed to the soil surface by the weight of snow. Bleached leaves are typical after attack by *Typhula* spp.

Fig. 2. Appearance on 27 April 1962 of winter wheat nursery seeded by Roderick Sprague in the fall of 1961. The nursery contained over 5,000 short rows; only a few wheat lines survived.

now Mold in Washington State

snow are attacked first (20), with the pathogens progressing to the crown with time. If snow lasts long enough, the crown is rotted and the plant is killed (Fig. 1). A grayish aerial mycelium develops over the plants, the snow adjacent to the plants may become green as chlorophyll released from the rotted leaves diffuses into the snow, and sclerotia of the pathogens are abundant in the leaves. These diseases are usually called gray snow mold or speckled snow mold. When the dead leaves are bleached by the sun, the sclerotia are easily seen.

In pink snow mold, mats of pink-salmon mycelium form in rotted crowns. Blodgett (8) observed that the leaves of wheat killed by *F. nivale* did not bleach as did those killed by the *Typhula* spp., were not so digested, and remained brownish after death. *F. nivale* occurs throughout our cereal area. It is not dependent on snow because it is a parasite of roots and lower leaf sheaths of many grasses, including spring cereals.

S. borealis occurs in Washington in northern Okanogan County near the Canadian border (8) only at or above 1,300 m elevation. The permanent snow line is near 2,000 m in this part of the state, so 1,300 m is relatively high and only a few hundred acres of wheat are grown at this elevation.

The conditions favoring Pythium snow rot are poorly defined but include snowmelt water running or standing under snow and ice (14). Most wheat is produced on well-drained soil, so this disease is limited to spots within fields.

Because of their limited significance, *S. borealis* and Pythium snow rot are not included in the wheat breeding program for snow mold control. From this point on, references to snow mold include only diseases incited by the *Typhula* spp. and *F. nivale*. The *Typhula* spp. and *F. nivale* coexist in Douglas and Okanogan counties, and to be dependable, wheats must survive attacks by both. *T. idahoensis* dominates in most seasons on most sites. *F. nivale* is restricted when the soil is frozen (5) and has a longer incubation period.

Ideal conditions for snow mold include early snowfall on unfrozen or lightly frozen soil. The snow cover should increase to a depth that prevents significant freezing of the soil, regardless of how cold the air temperature becomes. The snow-soil interface is like a constant temperature chamber. Snow protects aerial hyphae growing over the surface of the host from direct rays of the sun, maintains high humidity, and reduces light below the threshold of effective photosynthesis. The snow cover should last until late March or early April. The host respires at a slow but significant rate throughout the prolonged darkness, gradually depleting its carbohydrates. Snow molds develop under the most uniform terrestrial environment known: near 0 C, high humidity, and darkness.

Losses from Snow Mold

Sprague (18) reported that 169,000 acres (68,394 ha) of winter wheat were destroyed in Douglas County, Washington, in the winter of 1955–1956 and had to be resown to spring wheat. Winter wheat normally will outyield spring wheat by about 10 bushels per acre (670 kg/ha), so Douglas County lost about 1,690,000 bushels (46×10^6 kg) of wheat from mold that year. Added to this were the costs of buying and transporting spring wheat seed from as far away as Montana, the extra expenditures on fuel and labor, machinery depreciation, and, in some cases, increased herbicide and fertilizer costs. In ordinary snow mold seasons, only 20,000–50,000 acres in Douglas County and about 5,000 acres in Okanogan County require reseeding.

Under certain conditions, losses from snow mold can be overestimated. If the wheat is seeded early and enters the winter in a vigorous, well-hardened state, there are times when all the leaves can be destroyed with little yield loss. We have documented this with fungicide trials. We obtained little measurable yield reduction with 100% loss of leaves one year but a 35% yield loss another season under what appeared to be a similar attack. The difference was attributed to conditions favoring rapid recovery after snowmelt in the former case, and to protracted cool, wet, poor growing conditions following snowmelt in the latter case (8). Iwakiri (20) in Japan observed the same thing. He reported zero loss when less than half the leaves were killed, 3% loss when over half were killed, and 5% loss when all were killed. Significant losses began when the tillers in the crown were attacked.

Control Measures

Crop rotation would reduce losses materially, especially production of alfalfa or sweet clover (8,16). Spring grains are not attacked by the *Typhula* spp., so their production adds no sclerotia to the soil. The major deterrent to rotation, other than use of spring grain, is the rainfall distribution of dryland Washington. Precipitation in July and August in Douglas and Okanogan counties averages less than 1 cm per month, inadequate to sustain any crop requiring summer rain. The area uses the summer fallow system (10) in which a crop is produced once every 2 years on a field. Crop rotations are not economical.

Seed treatments have been tried but none has proved useful. In Washington, *F. nivale* is not seedborne.

Holton (11) and Sprague (18) tried foliar fungicides. Organic mercuries controlled mold and were recommended by Sprague for years. Their use was almost nil. Fungicides must be applied in the season before snowfall when there is no way to predict whether economic losses will occur. The winter is yet to come. Wheat yields are low in most of the mold region, with little margin above actual expenses. If economic losses occur sporadically, the farmers cannot chance the use of expensive preventive foliar sprays.

Benomyl (Benlate) controls *F. nivale* but not the *Typhula* spp., and it reduces winterhardiness. Thiabendazole (Mertect 340-F) also controls *F. nivale* but not *Typhula*. Bayleton controls *Typhula* but not *F. nivale*. These fungicides are also expensive.

Farming methods such as moldboard plowing versus stubble mulch tillage and deep-furrow drills versus standard drills (16) have little influence on snow molds. Mechanical operations offer little help.

Fertilization adequate to sustain a dryland wheat crop is recommended, but no dramatic control has been observed other than maintaining vigor and supporting recovery after injury (8,16).

Farmers in Douglas County learned by experience that seeding date was an important factor in survival and subsequent recovery of winter wheat. Holton (11) confirmed and described these observations. Wheat seeded in late July became very large and robust before winter and usually survived, but yields were reduced because of excessive fall vegetation and loss of water. Seeding in early August became the general practice. The robust plants often survived to make an acceptable crop, even with up to 100% loss of leaves. In Washington, these early seedings were not devastated by wheat streak mosaic, but the risk from *F. culmorum* and stripe rust were increased.

The association of snow with losses led to experiments with blackeners to hasten snowmelt. Coal dust was flown on snow by a few farmers, and some dusted snow with a ground rig for a few seasons, but this method of reducing losses was abandoned in Washington. Dusting snow with fly ash from a coal-burning power plant is practical to some extent in Utah (W. Dewey, *personal communication*).

Discovery of Resistance

Early efforts of county agents, farmers, and researchers to find useful levels of resistance in the Pacific Northwest were unsuccessful. During 1944–1945, Holton tested 15 wheats; the next season he tested 16 (11). Wheats were tested in Idaho at the Tetonia Agricultural Experimental Station. Sprague tested 33 varieties during 1954–1955, and 98–100% of the plants of all varieties were killed. All introductions, official and unofficial, were unsatisfactory and offered little hope (8). Nevertheless, during 1960–1961 both Sprague in Washington and Sunderman (USDA) made extensive efforts to find resistance to snow mold. Sunderman obtained all the winter wheats of the USDA World Cereal Collection, mixed them into a bulk, and planted them at the Tetonia Agricultural Experiment Station on a slope where snow accumulates. Mold was extreme, but a few plants survived. Seed of the survivors were saved and Sunderman retested them and saved those with real resistance. The bulk method of selection makes it impossible to identify the origin of his selections, but they are remarkably resistant. Two were placed in the cereal collection (CI 14106, CI 14107) for posterity. Sel. 7437, 7439, and 7449 are maintained by Sunderman.

In August 1960, Sprague seeded 5,200 wheats of the world collection on a farm in western Douglas County. Mold was moderate, but the results were encouraging. In September 1961, 173 of the most promising wheats of the 1960–1961 season plus 4,000 from the world collection were seeded. Mold was severe. None of the 173 of the previous season survived, but several of the 4,000 did (Fig. 2). Sprague died before he could see the results of his second test. All the good sources of resistance subsequently identified in Washington came from his second nursery. In 1962, a total of 12,000 wheats plus promising previous selections were seeded with the help of C. J. Peterson. In that season, no mold developed. The winter cold killed most of the 12,000 new wheats, but the hardy ones were harvested for further testing. By 1966 (8), we had listed several wheats that had survived in field nurseries in which both *T. idahoensis* and *F. nivale* were severe. All exploration of cereal collections was discontinued to permit us to work with what we had.

CI 9342 from Russia; CI 14106 and 14107 selected by Sunderman; PI 166797, 167822, 172582, 173438, 173440, and 173467 from Turkey; and PI 181268 from Afghanistan are our best sources of resistance. We were surprised no wheats from Japan or Scandinavia were sufficiently resistant to be placed in this category.

Field Testing Techniques

Because seeding date strongly influences resistance to snow mold (Fig. 3), we took a conservative approach, seeding between August 15 and 26 (7). This was fortunate because we still know of no agronomically acceptable selections resistant enough to survive under severe mold conditions if sown between September 7 and 15.

All field tests are on summer-fallowed land. The land is fertilized and sprayed with herbicides by the farmer. We select level fields with no effort to identify areas where snow drifts occur. We obtain both disease and yield data from these plots. Advanced selections are planted in four-row plots, 4 m long, with four replications on each of two different farms.

One border row of each four-row plot is inoculated in each trial. Dead leaves with sclerotia are gathered after snowmelt from the test area, dried, then ground through a Wiley mill with a coarse screen. Many sclerotia are injured, but most remain intact. This dry material is mixed with screened dry sand, five parts of sand to one part of ground leaf. In October this material is distributed on the row of wheat with a Planet Jr. seeder with the planter shoe removed. A stream of sand plus inoculum is dropped on the crowns of the wheat in the row. This method is effective and cheap. In some nurseries the natural inoculum level is so high the inoculated row is no different from the other three rows; in others the inoculated row is much more severely diseased (Fig. 4). We may, in this way, have two levels of severity in the same nursery.

The plot is left undisturbed throughout the winter. Meaningful tests occur when mold destroys 100% of the leaves. The most valuable tests are those in which 70–100% of the plants of known suscepts are dead.

Resistance is judged by recovery, ie, new growth from the crown. The most meaningful readings are made about 6 weeks after snow melt (Fig. 5). The wheats are scored visually by rating the thickness of the stand and the vigor and color of new growth. Some wheats in some years survive but have little vigor and yield poorly even from a good stand. These are discarded.

Segregating populations are seeded and treated the same as selections, except for a seeding rate one-fourth or less of normal.

We have used low-temperature (0.5 C) incubation chambers (3–5,8) for many purposes, but we do not rely on them to identify small differences in resistance that are important in evaluating sister lines of a breeding program. We rely completely on field tests in the breeding program. Bloomquist and Jamalainen (2) report good correlation of known field reactions and results in a snow mold chamber.

The Nature of Resistance

The resistance to snow mold reported in Washington is nonspecific and multigenic according to all observations. The field nurseries are dominated by *F. nivale* in some seasons but by *T. idahoensis* in most. Wheats have to survive attacks by both organisms to be

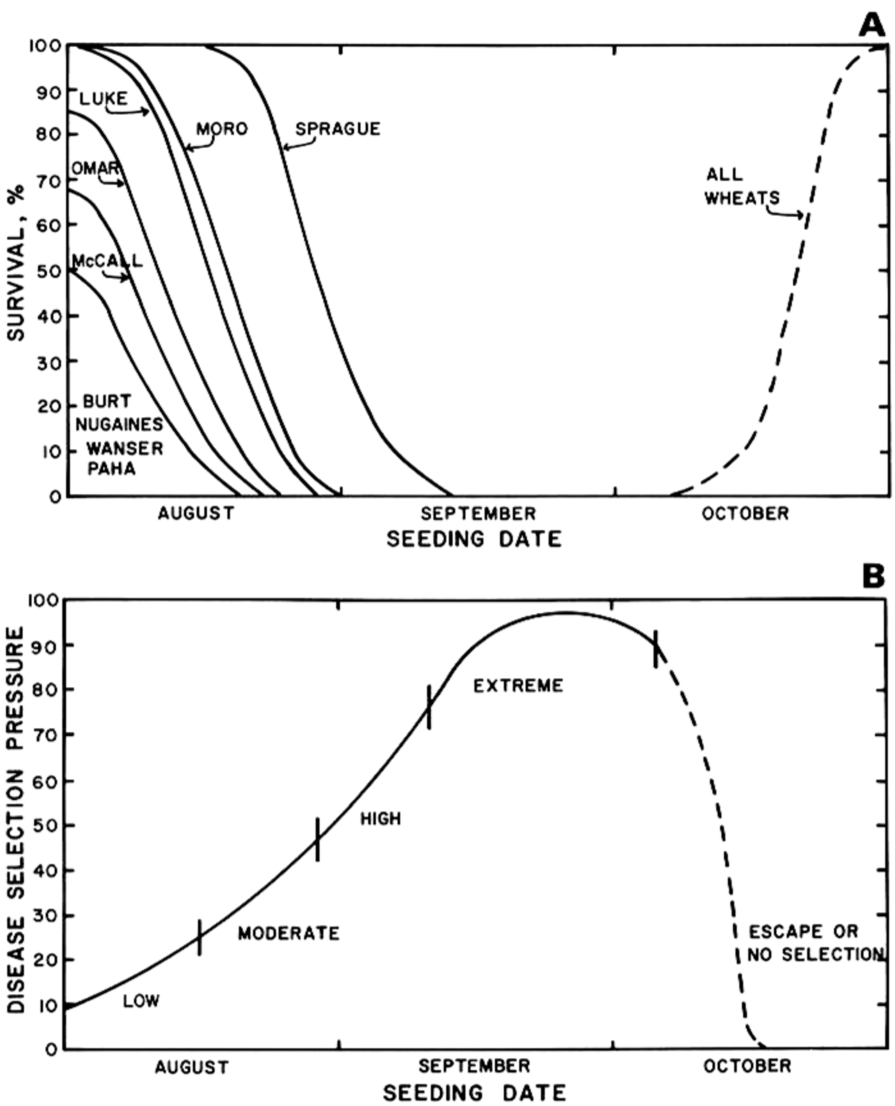


Fig. 3. Seeding date strongly influences survival under snow mold attack. (A) August seeding favors survival, mid to late September seeding favors death, and very late seeding favors escape. (B) Breeding nurseries use the relationship of seeding date to survival in attempts to regulate the severity of selection pressure.

dependable. Attempts to discover pathogenic specialization within *F. nivale*, *T. incarnata*, and *T. idahoensis* sufficient to threaten our sources of resistance have failed (3) (Fig. 6). Advances in resistance to snow mold should be lasting. Safety is also derived from the fact that *T. idahoensis* reproduces as well on leaves of resistant as on those of susceptible wheats (5), resulting in little or no selection pressure on the fungus to adapt to the resistant wheats.

The discovery that resistance resided in the crowns led to attempts to increase the crown tissue by seeding the wheat deeper. Deep seeding did not increase resistance (5).

Early studies of wheat under snow by the Russians and Japanese (cited by Tomiyama [20]) reported that leaf carbohydrates were depleted, followed by hydrolysis of proteins under extreme predisposition. Older leaves were attacked quicker than young leaves. Old leaves of early seedings are pressed onto the soil surface by the weight of the snow, placing them in contact with soilborne inoculum. (Sunderman [19] improved the snow mold chamber test by weighting leaves down to contact the inoculum.) Young leaves of late seedings (1–2-leaf stage) do not become senescent under snow because they are sustained by food reserves in the seed. When wheat is seeded very late, all plants survive because they enter winter in the 1-leaf stage or emerge under the snow. They escape. Yields from such plantings are low, however, making this practice unacceptable in Washington.

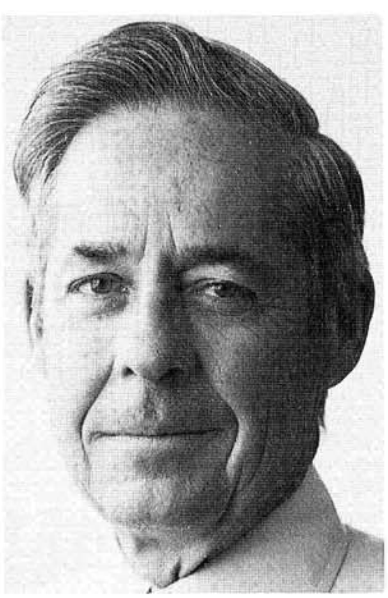
In general, resistant wheats accumulate substantial food reserves before winter and, more important, they use carbohydrates sparingly at 0.5 C in the dark (5,13). Carbohydrates of the crowns are utilized more rapidly when the leaves are attacked than when they are healthy (13), evidence of an active struggle between host and pathogen.

Another observation of significance is that CI 9342, resistant in Washington trials, was poor in Sunderman's trials in Idaho (*personal communication*). Sunderman seeds his trials later than we do. CI 9342 develops resistance slowly (4,13) and accumulates carbohydrates relatively slowly. Therefore, it does better from early seedings. CI 14106, selected by Sunderman, is excellent in both Idaho and Washington; it accumulates higher levels of carbohydrates and it accumulates them earlier (13).

During 1979–1980, two nurseries were seeded within 1 day of each other, and one-fourth of each nursery was inoculated within 1 day of the other. One nursery had good soil moisture in the fall, the other had minimal moisture. The inoculated rows in the nursery with good moisture gave the expected disease reaction. In the drought-stressed nursery, even wheats known to be resistant died. The wheats could not withstand severe mold when weakened by drought.

In conclusion, resistance involves plant size, carbohydrate storage and utilization, and unknown factors. The ability to sustain a certain low level of metabolic activity in the dark near 0 C is vital to resistance.

Tolerance "has long been used to denote the capacity of a plant line or cultivar to endure a given level of disease infection with less loss of value than that commonly sustained under equal infection" (9). According to this concept, the "resistant" wheats, as plants, are probably "tolerant." Under severe attack all their foliage is destroyed and as many sclerotia are produced on "resistant" as on susceptible wheats (6). Despite this, the term "resistance" is preferable to "tolerance" in relation to snow mold of wheat. The rot does not progress deeply into the crowns of the resistant wheats even though the leaves are destroyed. The vital crown tissues are not invaded, and vigorous regrowth (recovery) from the crown is what we call "resistance." The wheats from early seedings have extensive root systems and several tillers. If the crown is undamaged, recovery and subsequent yields are satisfactory.



George W. Bruehl

Dr. Bruehl received his training at the University of Arkansas (B.S.A.) and the University of Wisconsin (Ph.D.). He served with the USDA at Brookings, South Dakota, from 1948 to 1952 and at Rio Piedras, Puerto Rico, from 1952 to 1954. He has worked at the Department of Plant Pathology of Washington State University, Pullman, since 1954. His studies have included anthracnose of grasses, Pythium root rot of spring cereals, diseases of sugarcane, barley yellow dwarf, foot rots, snow molds, and Cephalosporium stripe of winter wheat.

Development and Acceptance of Sprague Winter Wheat

When a few wheats survived the severe mold of 1960–1961, plants of the best lines were transplanted to the Dryland Research Unit, Lind, Washington, and M. Nagamitsu and W. Nelson crossed them with local adapted wheats. Sprague (CI 15376) resulted from the cross PI 181268 × Gaines. Gaines is a high-yielding semidwarf soft white winter wheat. PI 181268 has good resistance to snow mold, has good soft white quality, and emerges well and quickly from relatively deep seeding. The F_2 seed was planted in Douglas County and the progeny exposed that season to a moderate attack. The F_2 looked promising. Subsequent experience has shown that resistance is inherited and that F_1 plants are intermediate in resistance between the resistant and the susceptible parent (13).

Yield, disease, and quality tests proved that Sprague was suitable for use on the farm. When released, it was the best emerging semidwarf known (1). Emergence is important because in dryland fields moist soil sufficient for germination may be deep, requiring deep seeding.

Sprague was first seeded on farms in the fall of 1973. That season, summer fallow moisture was deficient and only a few fields were seeded early. Some fields were seeded after mid-September rains. Nevertheless, the only good fields of winter wheat that year were the early-seeded fields of Sprague. No plants died in fields seeded between August 1 and 15, but 39% died in fields seeded August 26 and all died, even the resistant parent lines, in fields seeded September 26 (7). The fact that Sprague survived in the early-seeded fields during the 1973–1974 season is significant. Snow fell October 30 on unfrozen soil and remained until early April—more than 150 days. That is the most severe exposure on record in Washington.

In 1977, about 150,000 of the 200,000 acres in Douglas County and 26,000 of the 34,000 acres of Okanogan County were seeded with Sprague. Since its release, to my knowledge, snow mold has not destroyed a single acre—when Sprague was well established before winter. This wheat is recommended only in the snow mold region because of its weak straw. It is hardy, emerges well, yields well, but lodges severely under high production conditions. Cook (10) reported that Sprague is moderately

Fig. 4. In this site with a low natural level of inoculum, every fourth row was inoculated with *Typhula* spp. sclerotia the previous fall.

resistant to Fusarium foot rot. This may contribute to its ability to yield well from early seedings in a dryland region.

Conclusions and the Future

A combination of early seeding and moderate resistance enables winter wheat to survive severe attacks by *Typhula* spp. and *F. nivale*. Wheats resistant to the *Typhula-Fusarium* complex are not necessarily resistant to Pythium snow rot (15), and nothing is known about resistance to *S. borealis* in Washington. Luckily, we have only had to contend with the *Typhula-Fusarium* complex.

No wheat has been developed that combines strong straw and mold resistance. For years we crossed our strongest-strawed selections with each other, hoping for greater strength. This recurrent selection did not work. We have started over, going to Sturdy and Cappelle-Desprez for stronger straw than that available in locally adapted cultivars.

A hard red wheat, Sel. 77-99, with Sturdy, Itana, and CI 9342 in its parentage, has strong straw and acceptable yield and quality but is less resistant to mold than Sprague and is susceptible to stripe rust. It is the closest approximation of an acceptable hard red winter wheat resistant to snow mold.

Dwarf bunt (*Tilletia controversa*) is adapted to our snow mold region but has not been a problem in the Washington mold area for years. We attribute this to the widespread practice of seeding early. Some of the sources of resistance to snow mold carry resistance to dwarf bunt, but J. Hoffmann has tested our selections, and mold and bunt resistance are inherited independently of each other.

If carbohydrate metabolism is a key factor in surviving long exposures under snow, wheats from Finland (12) may have been handicapped in Washington by interactions with photoperiod. The difference between 48° north latitude in Washington and 61° north latitude in southern Finland is a major one.

Fig. 5. A snow mold nursery dominated by *Fusarium nivale* (pink snow mold) 6 weeks after snow melt. The leaves of the wheat in the green plots were rotted, and the new growth is from the crowns; the plants will recover.

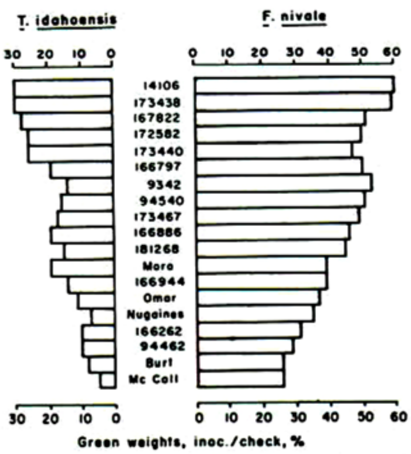


Fig. 6. Resistance to *Typhula idahoensis* and *Fusarium nivale* is roughly correlated, as judged by the green weight produced after attack by the pathogens. Length of the bar represents vigor of the plant (recovery) after attack. Named varieties had a shorter incubation period than numbered wheats and so are more susceptible than indicated.

The grain of the snow mold-resistant parents has little after-harvest dormancy. Against recommendations, farmers have harvested Sprague and planted it the same season, even within a week of harvest—harvest in August, plant in August. It is possible that in the high elevations of eastern Turkey, northern Iran, and Afghanistan, harvest and seeding are sometimes close together, and farmers during the evolutionary period of these wheats may not have stored their wheat to seed the following year, so they selected for little postharvest dormancy. Their farming methods also favored emergence from deep seeding.

Research on snow molds has been supported continuously for 25 years by farmers through the Washington State Wheat Commission. The farmers saw a need, and they did not expect quick results or miracles. Progress has been slow, but it has been real.

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