

## Smutting Patterns in Barley and Some Plant Growth Effects Caused by *Ustilago hordei*

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### ABSTRACT

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Barley plants (*Hordeum vulgare* 'Hannchen') inoculated with *Ustilago hordei* were observed to determine the position of smutted and nonsmutted spikes within the plant as well as the effect of inoculation and smutting on plant growth. Distribution of smutted (77%) and healthy (23%) heads on smutted plants was nonrandom according to position. Tillers arising from a single node of the principal culm (tiller families) tended to be either all smutted or all healthy. When families were differentially smutted, older tillers were most

frequently nonsmutted. Older families contained one or more smutted tillers less frequently than did younger families. The principal culm, which always was oldest, did not fit this age-frequency pattern; it was frequently smutted. Irrespective of the subsequent occurrence of smut in a plant, inoculation caused reduction of tillering, and changed the pattern of tillering such that inoculated plants produced lateral tillers from nodes higher up on the principal culm.

*Additional key words:* resistance, virulence, barley covered smut.

Faris (5) and Johnston (13) both reported that following inoculation of barley (*Hordeum vulgare* L.) with *Ustilago hordei* (Pers.) Lagerh., the first heads to appear in a group of plants were usually healthy, and that smutted heads usually appeared later. Johnston concluded that diseased culms were slower to mature than healthy culms whether the latter were from healthy or smutted plants. Faris (5) reported that the earliest healthy culms were from plants that subsequently proved to be healthy. In neither case was the explanation supported by data. An alternate possibility is that older culms of smutted plants more frequently remain healthy. Little information is available concerning the exact location of healthy and diseased culms in partially smutted or bunted cereals. Churchward (4) found that the resistant wheat cultivar Hope had a low percentage of bunt in late tillers when inoculated with *Tilletia caries*. Disease symptoms and signs, when present, usually occurred on the fifth or sixth tiller. Reed (20) found that *Avena brevis* showed smutted lateral tillers but healthy principal culms in nearly all of the 20-30% of diseased plants that resulted from inoculation with race I of *U. kolleri*. None of the previously named workers reported exact tiller age or position.

According to Hector (11), information on growth patterns in wheat also applies to barley. A brief account of the pattern of growth in barley, given by Sarvella et al. (24) compares closely with the more thorough description for wheat given by Percival (17). In general, the pattern of

tillering can be called monopodial; a central unbranched culm (the principal or apical culm) produces lateral culms (primary laterals) from several of its lower nodes. Each of the primary lateral culms is likewise capable of producing secondary lateral culms. Plants can produce over 100 culms if the environment is sufficiently favorable.

Partial, or incomplete, resistance occurs frequently in barley infected with *Ustilago hordei* (8). The purpose of this study was to determine whether, within smutted barley plants, the smutted and healthy tillers occur randomly or in an age-related pattern. In addition, the effect of inoculation with and smutting by *U. hordei* on the pattern of growth of the plant was studied.

### MATERIALS AND METHODS

Since all plants were grown in the greenhouse, the susceptible barley cultivar Hannchen was chosen because of its high tillering capacity in the greenhouse. The single smut dikaryon composed of haploids E<sub>3</sub>a and I<sub>4</sub>A (7) was used throughout. Seed treatment and inoculation were as described earlier (7). Noninoculated seeds were treated exactly as inoculated seeds, except that sterile complete broth (7) followed by a distilled water rinse was substituted for inoculum.

Pots 15 cm in diameter were used in all plantings after the first. Three plants were grown in each pot. One of the three plants was noninoculated in most of the pots; these plants served as controls to detect possible effects of latent infection in nonsmutted inoculated plants. To obtain profusely tillering plants in the last planting, inoculated seeds were planted singly in pots and fertilized well.

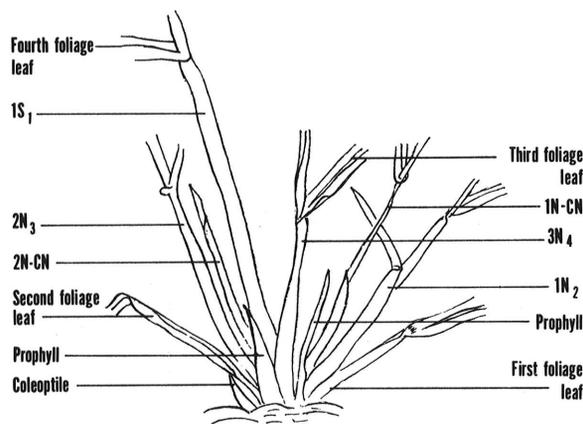
When culms appeared on the plants, the tillers were tagged with paraffin-dipped paper tags to establish a record of their age relationships. Without tagging, it was nearly impossible to determine with assurance the tillering patterns of mature plants. Even though a culm died, its exact position still could be determined. When all culms had headed, their position, sequence, and fate (headed, smutted, or dead) were recorded. To aid in data analysis, diagrammatic sketches were made of hypothetical plants, in which the internodes were greatly lengthened and all leaves excluded. Tiller production and tiller fate were easily indicated on such diagrams by inking the smutted heads, circling the name abbreviations of healthy heads, or crossing out heads which had died after initially being produced. A diagram of this sort was produced for every plant studied.

### RESULTS

A total of 528 barley plants were labeled and recorded, of which 183 were noninoculated. Of the 425 inoculated plants, 209 became smutted. The smutted plants produced 1,198 culms or 5.73 culms per plant. Of these culms, 927 (77.4%) were smutted.

**Growth of the Hannchen barley plant.**—Figure 1 is a line drawing of a typical 1-mo-old Hannchen barley plant with six young culms, which have been labeled along with some of the early normal and modified leaves (coleoptiles and prophylls). Tiller names are followed by symbols which were used in tagging the plants. Early leaves, which subtended the tillers, were important in accurately identifying tiller position.

Some qualitative statements can be made about the general pattern of growth of Hannchen barley in these



**Fig. 1.** The pattern of early tiller proliferation as illustrated by a drawing, based on a photograph, of a 1-mo-old plant of Hannchen barley. Six young culms are visible along with their subtending foliage leaves, coleoptile, or prophylls. Coded symbols: 1N = Primary lateral tiller arising from node of first foliage leaf, 1N-CN = secondary lateral tiller arising from coleoptile (prophyll) node of the 1N primary lateral tiller, etc. A primary lateral tiller has not been initiated from the coleoptile node in this plant. Subscripts indicate order of appearance of primary lateral tillers.

studies. Plants invariably produced the principal culm (1S or "first shoot") as the first and oldest culm. If this culm died early, the next oldest culm assumed its role. If a lateral culm was separated early from a plant, it also acted as a 1S; its lower nodes produced more lateral culms than if it had remained attached to the original plant. Only one primary lateral culm (the first lateral culm produced from the node) was produced from each node of the principal culm in this cultivar. With rare exception the lateral tiller arising in the axil of a lower leaf was older than one arising in the axil of a higher leaf, so that, for example, the tiller associated with the second vegetative leaf (2N) appeared before the tiller associated with the third vegetative leaf (3N) in nearly all plants (Fig. 1). Exceptions to the typical pattern were often in the form of later primary lateral culms from the axils of lower leaves, usually the CN (coleoptile node) or 1N nodes. These lateral culms nearly always died before heading. In only one plant was an exceptional order of appearance of primary lateral culms observed on a partially-smutted (and hence important) plant. Because this exception may not reflect relative tiller bud age in the embryo, this plant was excluded from the analyses.

Plants produced lateral culms from the coleoptile node as high as the eighth vegetative leaf node. In general, however, about three to four nodes were involved, most commonly 1N through 5N. Each lateral culm produced its own (secondary) lateral culms in the same manner that the primary lateral culms arose from the principal culm. For convenience, a primary lateral culm together with all of its lateral culms was referred to as a tiller family, where the sequence did not vary from the expected (e.g., 2N followed by 2N-CN followed by 2N-1N). No attempt was made to compare relative ages of secondary laterals arising from different primary laterals (for instance 1N-CN with 2N-CN). Occasionally, laterals also were produced in tertiary or higher positions (not shown in Fig. 1). At all degrees of tiller production there was an occasional absence of expected tillers. Probably this was due to injury in the meristematic region.

**Distribution of smutted and healthy heads in smutted plants.**—Statistical tests were devised to allow definite conclusions regarding the randomness or nonrandomness of location of healthy and smutted heads in smutted plants. The first of these tested whether or not the distribution of smutted and nonsmutted heads among tiller families was random (Table 1). Each family was classified according to whether all culms were smutted, or all were healthy, or whether some were smutted and some healthy (mixed). From these results, the probability of a culm in that family group being smutted ( $p$ ) and the probability of a culm remaining healthy ( $q$ ) were obtained for each family size. If smut distribution was random, the proportions of families showing the various degrees of smutting should fit the expanded binomial  $(p + q)^n$ , where  $n$  is the number of culms in the family. A chi-square test for goodness-of-fit revealed that the observed numbers do not fit the expected; i.e., the observed frequency of mixed families was too low and that of the other two classes was too high ( $P < 0.001$  in each case). Hence, there was a strong tendency for tiller families to be composed entirely of either smutted or healthy spikes.

Next, the 19 tiller families that were mixed were

TABLE 1. Chi-square test for randomness of occurrence of smutted culms in tiller families of Hannchen barley plants inoculated with *Ustilago hordei*. Separate tests for two, three, and four or more tiller families are presented. Frequencies of mixed families, containing both smutted and healthy culms, are added to give three classes in each test

Family size	All smutted	Mixed	All healthy	Total
Two-tiller families:	81	9	25	115
Expected <sup>a</sup>	(p <sup>2</sup> )	(2pq)	(q <sup>2</sup> )	
	63	44	8	115
p = 0.74 <sup>b</sup>				
q = 0.26				
Three-tiller families:	37	5	14	56
Expected	(p <sup>3</sup> )	(3p <sup>2</sup> q+3pq <sup>2</sup> )	(q <sup>3</sup> )	
	21	34	1	56
p = 0.71				
q = 0.29				
Four- or more-tiller families: (average 6.2 tillers)	33	5	9	47
Expected <sup>c</sup>	(p <sup>6</sup> )	(1-p <sup>6</sup> -q <sup>6</sup> )	(q <sup>6</sup> )	
	4	43	0	47
p = 0.65				
q = 0.35				

<sup>a</sup> assuming random smut distribution according to position, and occurring as (p+q)<sup>n</sup> where n is the number of culms per family.

<sup>b</sup> p = the probability, based on the observed data for the family size, of a single culm being smutted.

  q = the probability of a single culm remaining healthy.

<sup>c</sup> approximate values.

classified according to whether the nonsmutted spike(s) were the oldest, youngest, or neither. If smutting is randomly distributed among tillers in relation to age, the ratio of oldest to youngest healthy tillers should be 1:1. Samples sizes were small, so the Yates correction factor for continuity was applied (27). The oldest member of the family was found to be nonsmutted in 15 of the 19 families. This is a significant deviation from 1:1, and hence there was a clear tendency for older spikes within mixed smutted families to remain healthy.

A test, similar to the one described above, was applied to data on smutting among families to determine whether or not a relationship existed between age (position) of a tiller family and its probability of being smutted. A tiller family was considered smutted if any of its spikes were smutted. Nonsmutted families on all smutted plants were classified according to their age relative to the smutted families. A nonsmutted family (or a series of them) thus could be classified as older or younger than the family or families showing smut, or of intermediate age, depending on when the primary laterals of the families has appeared. Two different results were tested; one ignored the principal culm (1S), and the other included the 1S as the oldest culm (and hence considered only plants in which the 1S survived). In the former there was a highly significant difference between the actual oldest:youngest ratio obtained (55 oldest to 25 youngest with eight occurring at an intermediate position) and 1:1 ( $P=0.001$ ). There was a strong tendency for older tiller families to remain healthy in partially smutted plants. When the 1S culm was included, however, the tendency was no longer found using the simple test (31 oldest to 25 youngest with 30 occurring at an intermediate position,  $P=0.45$ ). Fates of the tiller families also were obtained (Table 2), and a portion of the data plotted (Fig. 2). Data for the 1S culms

and, to a lesser extent, for the CN and 1N families, are affected by the relatively high death rates of these groups; had these culms all survived to heading, the percentages of smut may have been changed. The data (Table 2 and Fig. 2) show that the CN and 1N positions (bulked) were smutted significantly less frequently than the 2N position, which was in turn smutted significantly less frequently than the 3N, 4N, or higher positions. The latter three groups were not significantly different. The frequency of death of a tiller family was directly proportional to its age. Culms that developed later grew faster than those that developed earlier.

TABLE 2. The production and fate of tiller families (groups of lateral tillers arising from a single node of the principal culm) in Hannchen barley plants infected with *Ustilago hordei*

Nodal position <sup>a</sup>	Tiller family fate			Surviving families smutted <sup>d</sup> (%)	Sample size (no. plants)
	Headed (%)	Smutted (%)	Dead (%)		
1S	14.6	50.2	35.2	80.4 bc	213
CN and 1N	29.0	46.0	25.0	61.3 a	124
2N	17.6	61.7	20.7	77.8 b	188
3N	10.3	68.5	21.2	86.9 c	184
4N	14.8	74.7	10.5	83.4 c	162
5N and above	12.5	72.2	15.2	85.3 c	184

<sup>a</sup> Code symbols: 1S = principal culm, CN = lateral tiller from coleoptile node, 1N = lateral tiller from first vegetative leaf node, 2N - lateral tiller from second vegetative leaf node, etc.

<sup>d</sup> Values in the same column not sharing the same letter are significantly different ( $P=0.05$ ).

**The effect of inoculation and of smutting on plant growth.**—Three main effects were examined: stunting, effects on extent of tillering, and effects on the pattern of plant growth.

Three wk after they were planted, seedlings of one season's greenhouse crop were examined for stunting. Of 206 inoculated seedlings, 25 exhibited some stunting in the form of short, narrow, dark-green leaves. None of 83 noninoculated plants were stunted. Of the 25 stunted plants, 16 became smutted and nine did not. This sample is too small for statistical treatment. However, the

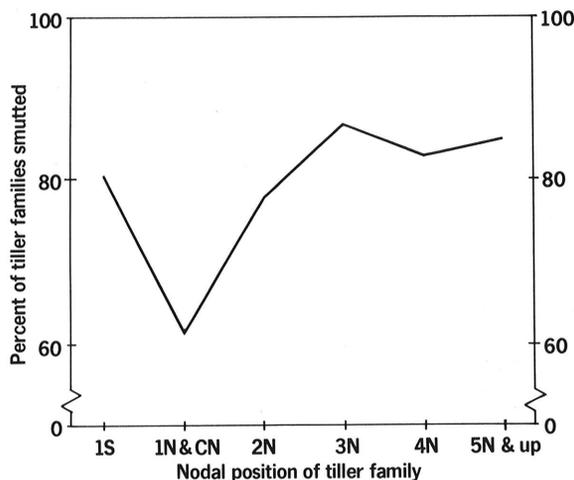


Fig. 2. The frequency of occurrence of visible covered smut in tiller families (all tillers produced at a single node of the principal culm) and in the principal culm of Hannchen barley plants. Order of appearance of families is from left to right. Smutted families have one or more smutted members. Coded symbols: CN = family arising at coleoptile node, 1N = family arising from first foliage leaf node, etc.

TABLE 3. Paired comparisons for the mean number of culms initiated per Hannchen barley plant, and their fates (headed, smutted, or dead), when plants were noninoculated, inoculated with *Ustilago hordei* but failed to become smutted, or inoculated and smutted

Treatment comparisons	Paired observations	Culms per plant <sup>1</sup>		
		Headed (no.)	Dead (no.)	Total (no.)
Noninoculated	68	5.56	2.93	8.49
Inoculated nonsmutted		4.91	2.47	7.38
Inoculated nonsmutted	63	4.97 a	2.13	7.10 b
Smutted		4.63 a	2.81	7.44 b
Noninoculated	48	6.33	2.87	9.21
Smutted		4.10	2.35	6.46

<sup>1</sup> Means not sharing the same letter are significantly different ( $P=0.05$ , paired  $t$  analysis). Statistical comparisons involved paired means only.

stunting probably was smut-related, even though no clear relationship between stunting and subsequent smutting was seen (i.e., stunted plants were not always smutted).

Because of rather large among-pot variation observed in 1972-1973, plants of different treatments were paired, each pair being from the same pot, in order to measure the effects, if any, of inoculation and smutting on tillering. Whether plants showed smut or not, there was a significant reduction in the number of tillers per inoculated plant, both of tillers initiated and of those surviving to maturity, when such plants were compared with noninoculated plants (Table 3). There was no significant difference between smutted and nonsmutted inoculated plants in total tillers initiated or those surviving. Noninoculated plants had significantly more dead tillers than inoculated plants. This is probably a reflection of the overall higher tiller production of noninoculated plants. Smutted plants had significantly more dead tillers than nonsmutted inoculated plants.

To examine the effect of inoculation and smutting on the pattern of plant growth, smutted, nonsmutted inoculated, and noninoculated plants were analyzed with regard to the percentages of plants attempting to produce tillers from each node (Fig. 3). Smutted and nonsmutted inoculated plants differed in growth patterns only in that smutted plants initiated tiller family production with a significantly higher frequency at the CN and 6N nodes. This may relate to the higher death rate of culms in smutted, as opposed to nonsmutted, plants, whereby dead culms are replaced by new ones. A marked effect of smutting and inoculation on the pattern of plant growth is seen when inoculated and noninoculated plants were compared. The noninoculated plants produced more lateral tillers from lower nodes than either of the inoculated groups; i.e., inoculation had the effect of decreasing lateral tiller production at the 1N node and increasing it at the 5N and 6N nodes. The CN did not

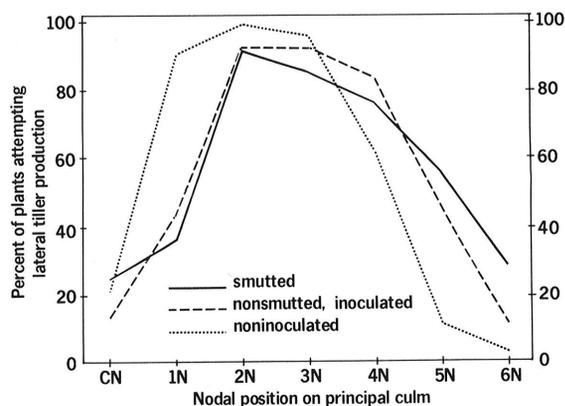


Fig. 3. The percentage of Hannchen barley plants (noninoculated, nonsmutted but inoculated, and smutted) initiating lateral tillers at different nodes of the principal culm. Coded symbols: CN = coleoptile or lowermost node, 1N = first foliage leaf node, etc. Significant differences in percentages exist between noninoculated and inoculated plants at the 1N, 4N, and 5N nodes and between smutted and nonsmutted inoculated plants at the 6N node.

conform to this pattern, although it might have been expected to do so.

Finally, emergence of heads was delayed about 1-2 wk on smutted plants. In each planting, the healthy plants were the first to be recorded and harvested, whereas those which emerged last were invariably smutted plants. Heads of nonsmutted inoculated plants did not emerge later than those of noninoculated plants.

#### DISCUSSION

In both two- and six-rowed barleys, Bonnett (2) found that two bud primordia are present in dormant seeds. One is the apical bud, which gives rise to the principal culm, the other is in the axil of the coleoptile, and becomes the lowermost lateral culm. In wheat, it is not until 10-15 days after germination that bud primordia in the axils of the oldest vegetative leaves can be detected (17). There is a clear difference in development among bud primordia at initiation of smut infection. Extent and kind of variation in early development among individual plants has never been determined. Histological studies necessarily have involved only a small number of embryos, so that the rare case of atypical development, if it exists, would have gone undetected.

**The distribution of smutted and healthy heads in smutted plants.**—The pathway by which smut fungi spread to various parts of the crown has not been conclusively determined by histological studies because of too few observations of smutted embryos. It is likely, although not supported by evidence, that considerable variability exists, so that the mycelium does not move precisely through the same tissues in each seedling. From the limited evidence available, however, it appears that smut hyphae enter the crown from below, so that older leaf sheaths and nodes are infected first. Mycelium is then more abundant in the lower part of the crown than in the upper (10, 15, 23, 29). This evidence does not provide a ready explanation of the observed distribution of smutted culms. On the contrary, if the location of the hyphae within the crown were the determining factor, one would expect the older culms to be more frequently smutted.

In a few plants, the oldest and youngest primary lateral culms were smutted and one or more intermediate tiller families were healthy. This may be the result of multiple infections (infection of a seed with more than one dikaryon). Such multiple infections have been conclusively demonstrated by Person and Cherewick (18) in oats infected with *U. kolleri*. They did not determine smutting patterns based on tiller relationships, but they showed that different dikaryons can occur in different culms of the same plant. The similarity of *U. kolleri* and *U. hordei* is such that it would seem likely that multiple infections also occur with the latter fungus. With *U. kolleri*, genotypic mosaics indicate that how and when smut hyphae spread throughout the crown region are variable. A thorough study of the multiple-infection phenomenon in the barley-*U. hordei* interaction is still needed.

Sampson (23) observed a barrier of lignified cells between the nodal tissues containing *U. kolleri* mycelia and the apical growing point in resistant oat plants. She concluded that if the plant could produce this barrier before the fungus reached the growing point, the culm or

culms would not become smutted. Retardation of fungal growth might account for resistance under this hypothesis. Whether or not lignification is the critical event, the idea that degree of smutting depends on relative rates of growth or development of the embryo and the smut mycelium is promising, particularly in explaining high levels of resistance. Ohms and Bever (16) found that the mechanism of resistance to *U. tritici* in one wheat cultivar seemed to be simply that the seedlings outgrew the smut mycelium. This could also apply to studies such as those of Popp (19), who found that embryos of resistant wheat cultivars were infected as frequently with *U. tritici* as those of susceptible cultivars. Swinburne (29) believed that with wheat infected with *T. caries*, once hyphae reached the shoot apex smut always was expressed in the resultant culm. If a barrier such as lignification or physical distance develops before the mycelium reaches the shoot apex, smut will not occur. This is the key to the observed pattern. Presumably the barrier would be produced first in older culms whose primordia are more developed initially, and thus allow less time after germination for the mycelium to reach the shoot apex than in younger culms. This effect seems to prevail over the apparent closer proximity to the advancing hyphae of lower, older culm primordia.

A phenomenon similar to the above occurred within individual spikes. Occasionally, spikes were found with both smut teliospores and healthy seeds. Invariably, the healthy seeds were found on the upper part of the spike and the smut on the lower part. The same observation was recorded by Faris (5). Meiosis in barley begins at the top of the spike and proceeds downward (1), so that upper seeds are slightly older. Thus, the within-spike smutting pattern is the same as that seen at the within- and between-tiller family level; i.e., older portions are more likely to be smut free.

The principal culms did not fit into the same age/smut frequency pattern as the lateral culms, and the above hypothesis cannot apply to them. Although there is no doubt that the 1S culm is the oldest culm on the plant (the first to appear) and that it arises from the most-developed shoot apex in the embryo, it is not the least frequently smutted culm. Hence the observation that healthy culms emerge before smutted culms in a group of inoculated plants is probably not due to the smutting/age relationship of culms. The 1S culm seems to occupy a special place with regard to smutting. Its shoot apex could perhaps be considered the "target" of the fungal hyphae. From the standpoint of pathogen fitness, this is logical since the principal culm is the most likely to be produced by the plant.

Deep sowing and cooler growing temperature, which tend to slow germination and plant growth rate, have been shown to increase the frequency of smut (14, 29). This is explainable on the basis that these conditions lengthen the period during which seedlings are subject to the fungus.

**The effect of inoculation and smutting on plant growth.**—Inoculated seeds grew into plants with fewer surviving culms than seeds not inoculated, regardless of whether or not inoculated plants became smutted. This represents, as far as we are aware, the first report of any effect of smut inoculation on nonsmutted plants when a

compatible host-smut combination is involved. It is also the first report of such an effect in either compatible or noncompatible combinations of barley and *U. hordei*.

Reports of effects on nonsmuted hosts, such as blasting (sterility of heads) (9, 21), reduced stands (12, 28), and reduced height and yield (30, 32) have always involved incompatible or low-compatible host-parasite combinations. Surprisingly, the effects observed in this work were much more subtle than any of those reported previously. Neither blasting, reductions in seedling stand, nor increased tiller mortality were observed in nonsmuted inoculated plants in our work. The only other effects observed on nonsmuted, inoculated Hannchen barley plants were the infrequent stunting of seedlings and the shift in the pattern of tillering. All of these effects could be caused by the presence of mycelium in the plant during no more than the seedling stage. Under crowded greenhouse conditions the differences between treatments were probably magnified by plant competition. One can safely conclude that in this particular host-parasite combination, smut fungus mycelium is present for at least a short period in inoculated seedlings of ultimately "healthy" plants. A different line of evidence supporting this same conclusion was presented earlier (7). This is not the situation in some resistant combinations of host and smut, where the pathogen was unable to penetrate beyond the pericarp (19, 31). It seems doubtful that the pathogen could have had a significant effect on plant growth were exclusion so effective. The literature indicates that such resistance is probably not as frequent as that which allows penetration of the embryo. One cannot generalize, however, from the present findings, that all resistance in barley is of the nonexclusive type, particularly since the host and parasite combination studied did not exhibit resistance in the usual (economic) sense. Results from three other studies support "nonexclusive" resistance in smut-free, *U. hordei*-inoculated barley (13, 25) and in the similar *U. kolleri* in oats (3). No evidence for "exclusive" resistance has been found in the barley-*U. hordei* system.

Smuted plants exhibited other symptoms which nonsmuted, inoculated plants did not exhibit. Chlorotic streaking and distortion of upper leaves of smuted culms, but never of healthy culms, was usual. Occasionally, probably because of high temperatures (26), stripe smutting occurred in the upper one to two leaves of smuted culms. Such symptoms were absent from nonsmuted inoculated plants. Numbers of tillers initiated and of tillers maturing were both reduced in smuted and nonsmuted inoculated plants when these were compared with noninoculated plants. The only other report on this phenomenon in barley-*U. hordei* was made by Ruttle (22), who observed that smuted plants produced fewer mature tillers than nonsmuted plants (which were also inoculated). This contrasts with results of the present work in which there was no difference in tiller production between smuted and nonsmuted inoculated plants. It is possible that Ruttle employed an inoculation procedure which allowed a large proportion of plants to virtually escape infection.

Death of initiated culms before maturity is not confined to smuted, or even inoculated plants. Even under the best of growing conditions in the field, such dead culms always were observed. Percival (17) noted

them in wheat and speculated that they were probably the result of an insufficient number of adventitious roots coupled with periods of dryness. Their increased frequency in smuted plants might be explained on the basis that they are further deprived of water or nutrients because of physiological or physical changes in the plant harboring the developing smut fungus. There is evidence that such changes occur in *U. tritici*-infected wheat (6).

Finally, the change in pattern of plant development represents further evidence for the presence of smut mycelium in nonsmuted, inoculated plants. In this respect, as in others, nonsmuted inoculated and smuted plants have more in common than either group does with noninoculated plants. To speculate on the basis of the change in pattern, it is possible that the presence of smut inhibits tiller production at the earliest, lowermost nodes. The plants so affected then produced their lateral tillers from higher nodes. This is clear despite the fact that inoculated plants initiated fewer culms than did noninoculated plants. Whether the inhibition of lower nodes was due to actual death of primordia or to some other, more subtle, effect, is not clear.

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