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To the Graduate Council:

I am submitting herewith a thesis written by Richard Harold Mullenax entitled "Plumular Morphology and Seedling Morphogenesis of Irradiated and Nonirradiated Embryos of Barley (Hordeum vulgare L.)." I recommend that it be accepted for nine quarter hours of credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Agronomy.

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PLUMULAR MORPHOLOGY AND SEEDLING MORPHOGENESIS OF
IRRADIATED AND NONIRRADIATED EMBRYOS OF
BARLEY (HORDEUM VULGARE L.)

A Thesis
Presented to
the Graduate Council of
The University of Tennessee

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Richard Harold Mullenax

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CHAPTER I

INTRODUCTION

Barley (Hordeum vulgare L.) is frequently used as an experimental organism in radiation biology. Considerable information has been accumulated about the dormant barley embryo, but most of the work has little bearing upon plumular ontogeny. Furthermore, there is a paucity of data available relevant to varietal differences in numbers of leaves and axillary buds present in the dormant embryo.

The developing seedling has received some attention regarding date of leaf and tiller emergence (macroscopic observations); however, there is little information in the literature pertaining to the sites of origin and chronological initiation of primary and secondary tiller meristems.

The purpose of this study is to describe the embryonic and seedling morphology of several varieties of barley. Histological examinations were made of dormant embryos and developing seedlings from irradiated and nonirradiated grains, with the prospect of determining the effects of gamma radiation on the growth of meristems from the dormant embryo following germination. Other meristems which differentiated during the ten-day post-sowing period were also studied in relation to their number and origin.

CHAPTER II

REVIEW OF LITERATURE

I. DORMANT EMBRYOS

Eames (8) stated, "The monocotyledonous embryo has long been a morphological puzzle and the subject of much controversy" Esau (10) related ". . . Whereas a voluminous literature deals with the early stages of embryonic development, only scanty information is available on the late stages during which the tissue systems and the apical meristems attain their final embryonic organization." She further stated that, "The development and structure of the grass embryo are so complex that this embryo may be said to raise more morphological problems than any other embryo."

Avery (2) considered the coleoptile to be homologous with the first foliage leaf and to be the second leaf of the plant with the leaf distal to it being the third leaf. He described the scutellum to be the first leaf and the epiblast to have little morphological significance. He also interpreted the coleoptile as a single leaf rather than the result of fusion of two stipules. Arber (1), however, reasoned that the epiblast might possibly be the vestige of a second cotyledon with the scutellum being the first. Her work with barley embryos dealt primarily with the scutellum, epiblast, and coleoptile, giving little emphasis to the dormant plumule. However, she did observe the presence of axillary

buds in the coleoptylar axils of Avena sativa and Leersia oryzoides.

Boyd (6) presented the coleoptile as a plumular organ equivalent to the first foliage leaf; she also concluded that the "first leaf" is actually the second plumular leaf of the seedling. Worsdell (26) regarded the scutellum to be the lamina of the coleoptile, corresponding to that of the foliage leaf of the grass, with the coleoptile and epiblast being the cotyledons.

McCall's (16) interpretation of the dormant wheat plumular bud agreed with Avery's (2), since they both observed three leaves in the dormant embryo exclusive of the coleoptile. Avery, however, observed the presence of a tiller bud, while McCall made no mention of a tiller bud. The dormant corn plumule as seen by Sass (24) contained three embryonic leaves, while Avery (2) found four well developed leaves. Avery's description of the oat embryo did not correspond to Bonnett's (5). Avery showed the embryo contained three leaves, whereas Bonnett only observed two. Both showed development of the axillary bud in the coleoptylar axil. Reeder (21) presented drawings of twenty-one grass embryos, each having only one leaf and showing no evidence of axillary meristems.

Fisk and Millington (11) portrayed a cross-section of an entire barley grain but the embryo structures lack clarity and the leaf number cannot be ascertained. Cook (7) showed the dormant barley embryo, but again, details were not clear enough to distinguish leaf number and axillary structures. Lunden (14) found the dormant barley embryo to contain four leaves and two differentiated lateral buds. Sarvella et al.

(23) presented still another interpretation from Lermer and Holzner (13), showing the barley embryo to possess an axillary bud designated as axillary bud 2 in the axil of the coleoptile and another, axillary 3, in the first leaf axil. Axillary bud 4 was on the flank of the shoot apex, and the shoot apex was labeled axillary bud 1. According to their interpretation, the variety Hulless Haisa had three axillary meristems. Bonnett (4) found the dormant barley embryo to contain three leaves and one tiller bud. Nostog (18) and Merry (17) found the dormant barley embryo to have four and three leaves, respectively, yet neither noted the presence of axillary buds.

Esau (10) described the scutellum to be a cotyledon and stated that the epiblast, opposite the scutellum, is often considered to be a rudimentary cotyledon. She defined the coleoptile as the sheath enclosing the apical meristem and leaf primordia in the embryo. The areas of interest in the present study do not include any structures below the epiblast (coleorhiza, root cap, etc.); the scutellum and the epiblast will not receive emphasis. The main plumule, as used here, will include the structures above the juncture of the coleoptile with the exception of the axillary buds, which are synonymous with lateral branch and tiller buds. As development progresses the lateral branches will also produce leaves and secondary branches (Figure 1).

II. DEVELOPING SEEDLINGS

Bonnett (4) noted that by the time the second leaf was well along in development nearly all the potential leaves or leaf initials of the main stem had been initiated.

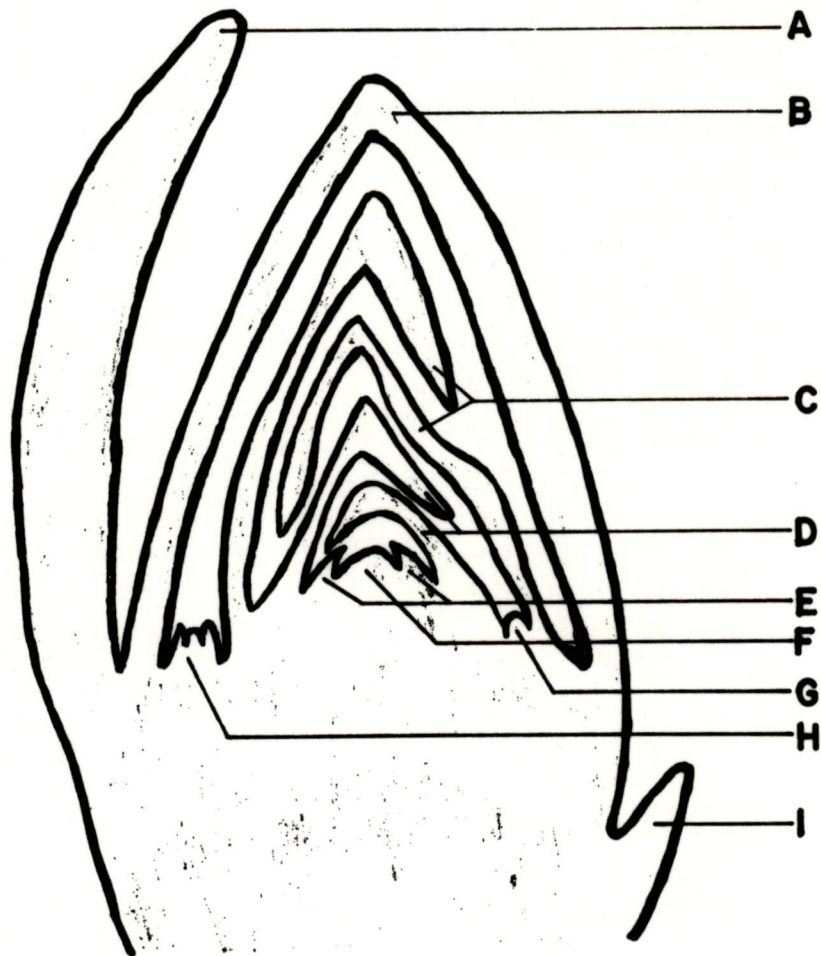


Figure 1. Drawing of median longisection of a typical barley embryo omitting structures below the epiblast. A, scutellum; B, coleoptile; C, first leaf; D, second leaf; E, third leaf; F, apex; G, second primary tiller primordium; H, first primary tiller primordium; I, epiblast.

Tillering is important in the development of many grasses, but the sites of origin and the chronological order of appearance have received little attention. Enyi (9) concluded that the first and second primary tillers of a swamp rice variety (BG78) together contribute more than fifty per cent of the total shoot or tiller number. In reference to rice, Arber (1) said that primary tillers arise out of one or two lower subterranean leaf axils of the mother culm. A secondary tiller arises from the lower-most leaf axil of the primary tiller.

Sharman (25) and Bonnett (5) agreed that tiller buds or axillary buds* are initiated by periclinal cell division in the third cell layer in the internode, just above the axil of the last leaf. The first prophyll is initiated early in the development of the tiller.

III. RADIATION EFFECTS

Few references pertaining to histological observations of plants resulting from irradiated seeds are available. Mackie et al. (15) found that meristematic regions of plants grown in solutions containing P^{32} showed a drastic reduction in cell division and even plant death. Plants grown in solutions of comparatively low specific activity exhibited evidence of damage to shoots, but with no apparent injury to root tips.

Johnson (12) subjected dry wheat grains to 1,000, 5,000, and 10,000 roentgens of X-rays; she found the survival rate of the developing

*The terms "tiller buds" and "axillary buds" will be used interchangeably.

seedlings to be as high as that of the controls. Heavier doses caused death to seedlings within three weeks. Kernels soaked before irradiation were much more sensitive to injury than dry ones, and seedlings from grains treated with heavier doses than 50,000 roentgens all died within three weeks. Tillers on six-week-old seedlings from irradiated dry grains were more numerous in 1,000 and 5,000 roentgens groups than they were in the controls.

Saric (22) irradiated wheat kernels with doses ranging from 500 to 15,000 roentgens. He observed that some doses stimulated growth while others showed inhibitory effects. The percentages of germination decreased with dose, as also did height and weight. He also noticed that reactions of varieties toward the same dose were different.

CHAPTER III

MATERIALS AND METHODS

I. DORMANT EMBRYOS

Eight cultivars of Hordeum vulgare L. (Himalaya, Hudson, Unicula, Pennrad, Kenbar, Holston, Dayton, and Watauga) were utilized in the dormant embryo study. All embryos were excised, killed, and fixed (twenty-four hours) in Randolph's modified Craf solution (20). All tissues were dehydrated in a graded series of tertiary butyl alcohol and embedded in Paraplast. The embryos were sectioned serially at 10 microns in transverse and longitudinal planes, affixed to glass slides with egg albumen, stained with safranin, counterstained with fast green, and mounted in Permount.

II. DEVELOPING SEEDLINGS

Two cultivars--Himalaya, a spring variety, and Hudson, a winter variety--were selected for a study of developing seedlings following dormant embryo irradiation. Grains were equilibrated at 60 per cent relative humidity for two weeks in a glycerine-water system described by Osborne and Bacon (19). Following moisture equilibration, grains were exposed to 0, 15, or 30 kiloroentgens* of gamma radiation from a

*The term "kiloroentgen" will hereafter be abbreviated as kr.

cesium-137 source. Immediately after irradiation, kernels were sown in Perlite-peat growth medium and were placed in an environmental-controlled growth chamber under a sixteen-hour continuous light regime at 70° F. The medium was irrigated from one to two hours on alternate days with modified Hoagland's nutrient solution. Seedling collections were made twice daily at eight-hour intervals for ten days, beginning with the fourth day post-sowing, and then processed for histological observations. Developing seedlings were processed in the same manner as were the dormant embryos.

III. TILLER EMERGENCE

One hundred and twenty grains of the cultivar Himalaya were planted in a greenhouse, watered daily, and grown for five weeks. At the end of four and five weeks, observations were made to determine the number of tillers which had emerged and their sites of origin.

CHAPTER IV

RESULTS

I. VARIETY "HIMALAYA"

Dormant Embryos

Histological observations of eight cultivars revealed few differences (Table 1). Himalaya appeared to be more developed, the dormant embryo possessing four embryonic leaves with two axillary buds (Figure 2). Axillary buds were found in the axils of the coleoptile and the first developed leaf (L_1^*) in all varieties, with the largest tiller bud always observed in the axil of the coleoptile (Figure 3). The second axillary bud was observed in the L_1 axil (Figure 4); it generally exhibited no more development than the apex and showed no leaf initiation. No other bud primordia were recognized as such. It is of interest to note that the variety Unicula, which normally emits a single spike, had two axillary branches in the dormant embryo.

The dormant plumular regions of the remaining varieties were identical, with each containing three developed leaves and two axillary buds (Figure 5 and Table 1).

Locations and origins of axillary tillers are shown schematically in Figures 6 and 7; the first primary tiller will be designated as P_1 ;

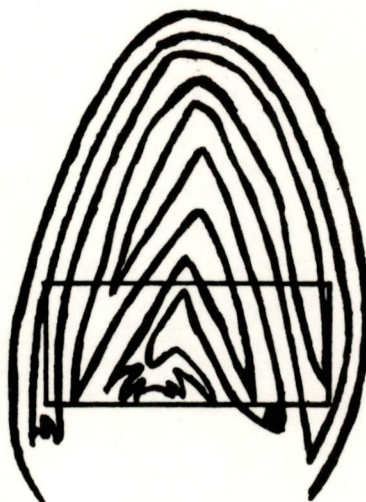
* L_1 is referred to as first developed leaf; L_2 , the second developed leaf, etc.

TABLE 1--Number of embryonic leaves and axillary buds in the dormant plumule in eight varieties of barley.

Varietal name	C. I. No.*	Embryonic leaves (No.)	Axillary buds (No.)
Dayton	9517	3	2
Himalaya	620	4	2
Holston	9571	3	2
Hudson	8067	3	2
Kenbar	7574	3	2
Pennrad	11170	3	2
Unicula	11530	3	2
Watauga	9172	3	2

*Crop identification number of U. S. Department of Agriculture.

A



B

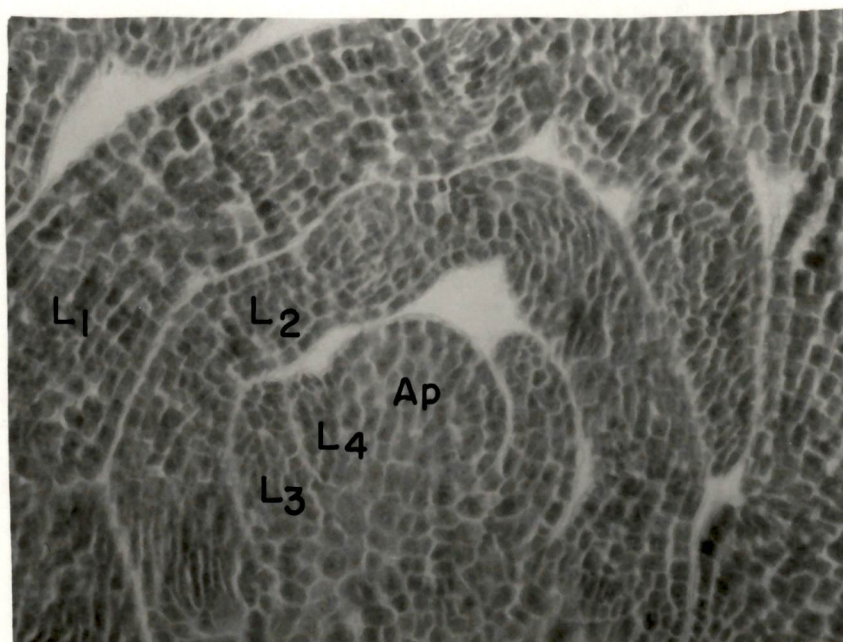


Figure 2. Dormant plumule of Himalaya barley. A. The area in rectangle is shown enlarged in B. B. Longisection of Himalaya barley dormant plumule showing four embryonic leaves and the apex (300x). Ap = apex, L₁ = leaf 1, etc.

A



B

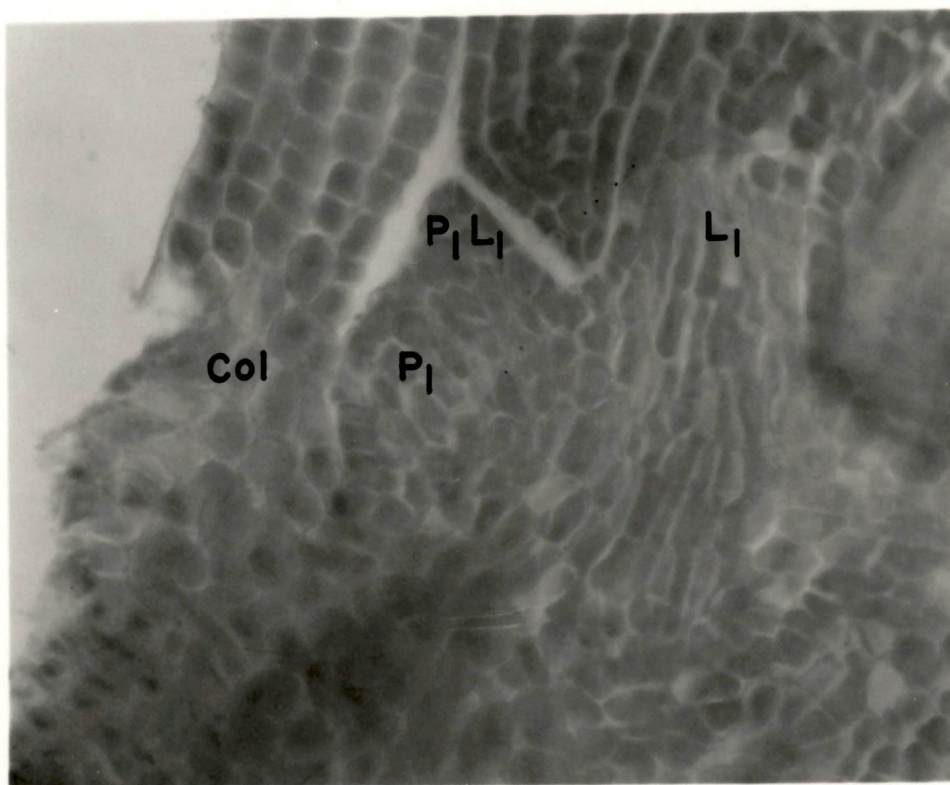
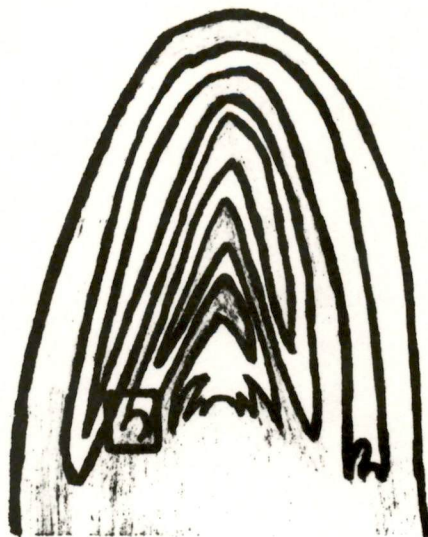


Figure 3. Dormant P_1 tiller bud of Himalaya barley. A. The P_1 tiller bud (rectangle) is shown enlarged in B. B. Dormant coleoptylar bud (P_1) and its first leaf (400x). Col = coleoptile, L_1 = first developed leaf in dormant embryo, P_1 = first tiller bud in dormant embryo, P_1L_1 = first leaf initiated by P_2 .

A



B

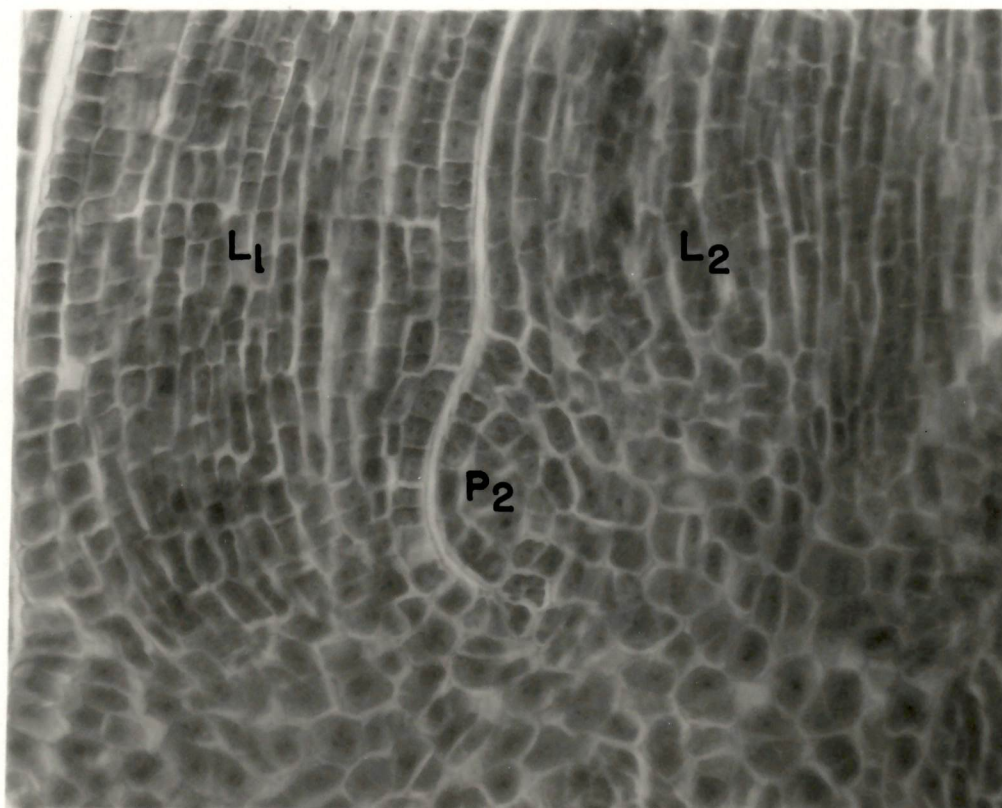


Figure 4. Dormant P_2 tiller bud of Himalaya barley. A. The P_2 primordium (rectangle) is enlarged in B. B. Second primary bud primordium of barley embryo, in axil of the first leaf (400x). L_1 = first developed leaf in dormant embryo, L_2 = second developed leaf in dormant embryo, P_2 = second primary tiller bud primordium.

A



B

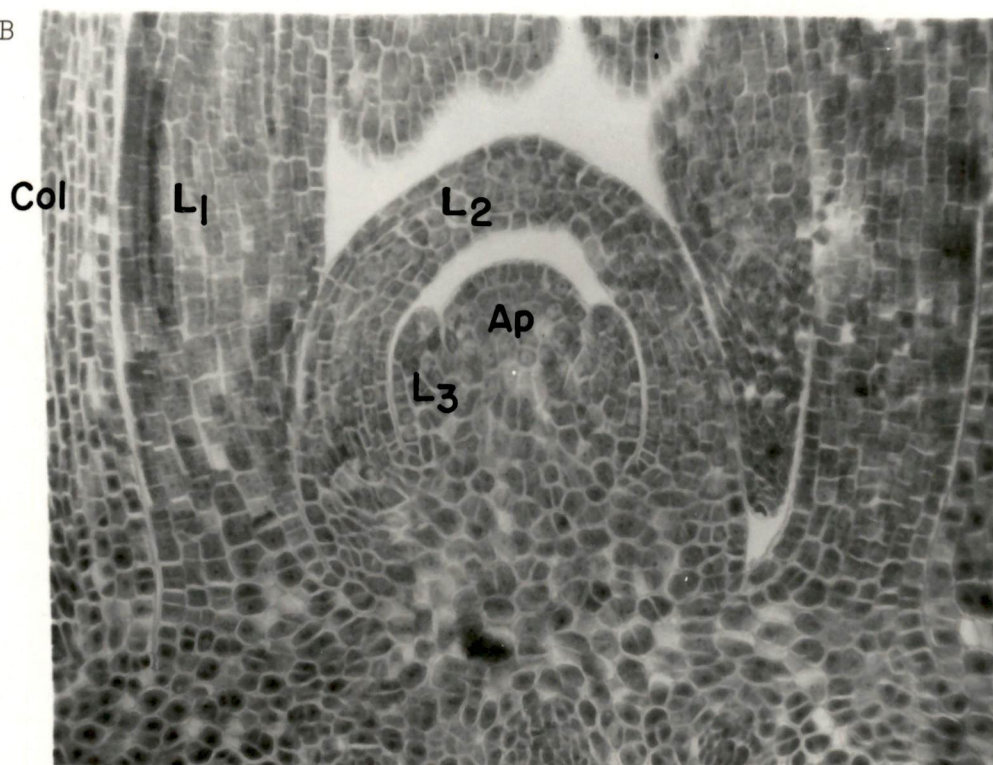


Figure 5. Dormant plumule of Hudson barley. A. Area in rectangle is shown enlarged in B. B. Longisection of Hudson barley dormant plumule showing three embryonic leaves, typical of all cultivars studied except Himalaya (300x). Ap = apex, Col = coleoptile, L_1 = leaf 1, etc.

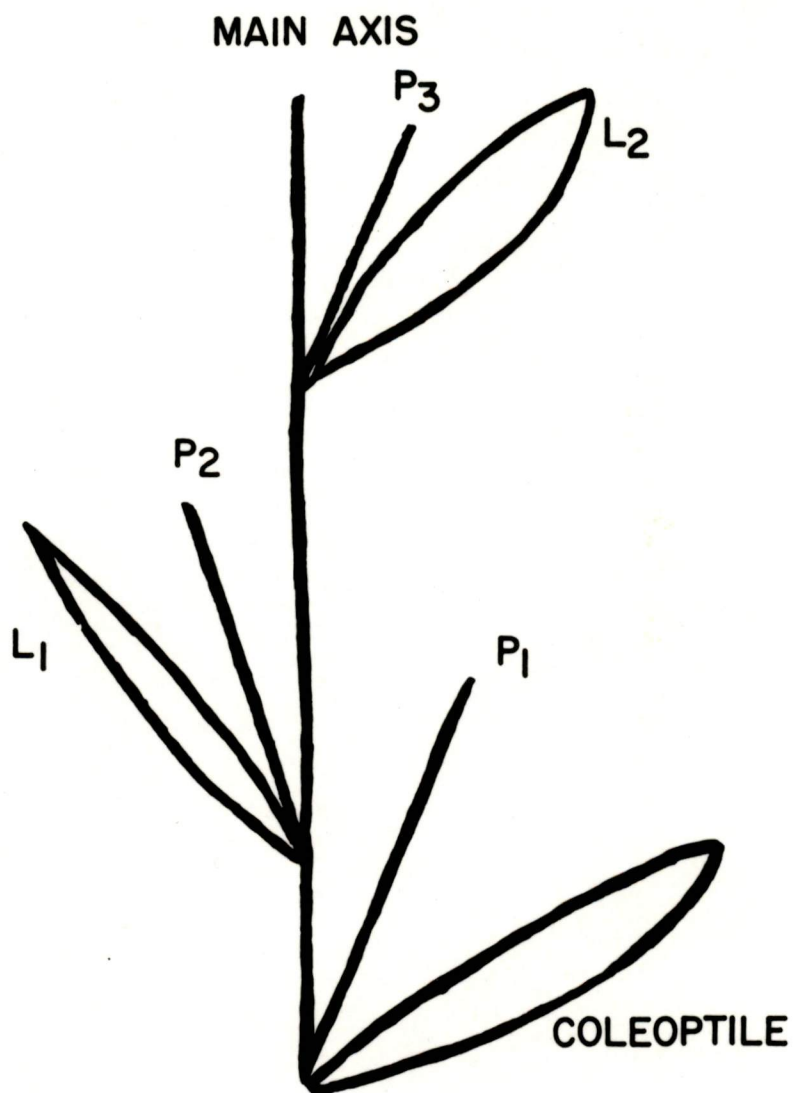


Figure 6. Schematic and proposed nomenclature for primary tillers. (See text.)

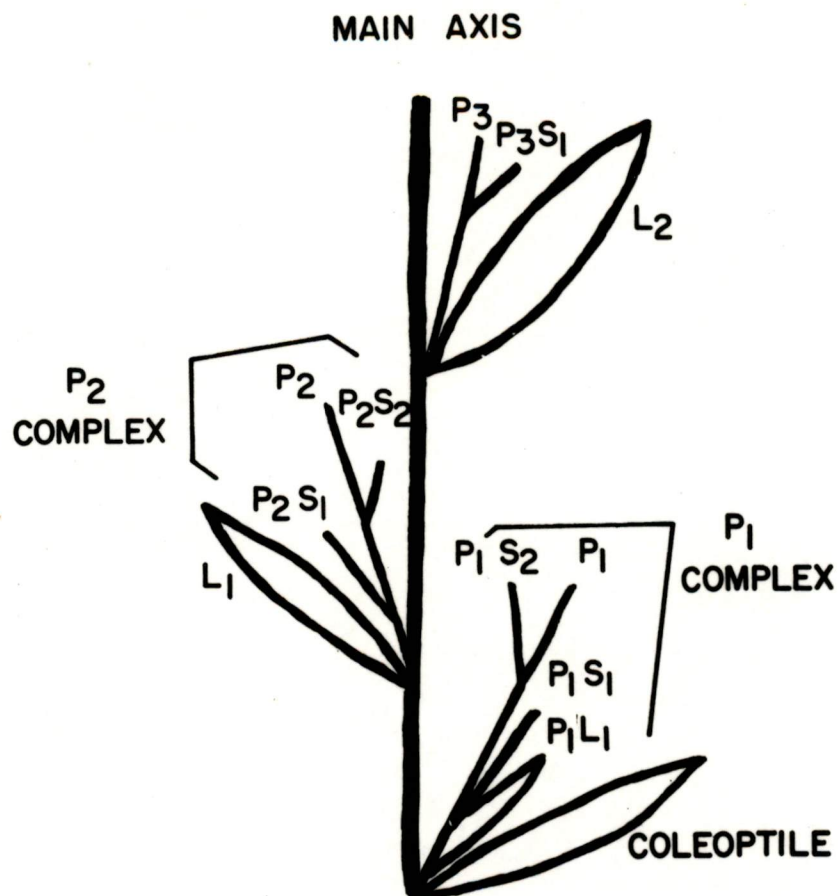


Figure 7. Schematic and proposed nomenclature for primary and higher order tillers. (See text.)

the second, P_2 ; etc. (Figure 6, page 16). Secondary tillers will be identified according to their location. For example, the first secondary tiller initiated by P_1 will be named P_1S_1 ; the second secondary tiller as P_1S_2 , etc. (Figure 7, page 17). The first leaf developing on P_1 will be identified as P_1L_1 . In the event a tertiary tiller should develop on P_1S_1 it would be identified as $P_1S_1T_1$. Leaves on the main axis are denoted simply as L_1 , L_2 , etc. The term " P_1 complex" is used to include all structures (tillers, leaves, and their primordia) that are derived from the first primary (P_1) tiller.

Developing Seedlings

Four days post-planting. (Refer to Tables 2, 3, and 4.) The control primary shoot apices always had five foliage leaves and often the sixth leaf primordium. "Leaf primordium" will be used to designate a protrusion of the shoot apex which has not elongated to be recognizable as a leaf (Figure 8). All developing seedlings from treated kernels possessed five foliage leaves on the main plumule. Tiller P_1 in the nonirradiated plants exhibited four leaves whereas in the seedlings from irradiated seeds, tiller P_1 exhibited only three leaves. In the 15 kr. group all tillers located in the coleoptylar axil had three leaves, and those of the 30 kr. group had either three leaves or a primordium of a third leaf. All seedlings from the control group had three leaves on the P_2 tiller, while the same tiller in both irradiated groups had two leaves and a primordium of a third. The majority of the control plants had one developed leaf on the P_3 tiller. The occurrence of a leaf primordium on the P_3 tiller was rare

TABLE 2--Chronological development of structures in seedlings of the Himalaya control group.

Days	Main plumule	Tiller complex				
		P ₁	P ₂	P ₃	P ₄	P ₅
Dormant	4 leaves	P ₁ -1 leaf	initiated			
4	L ₅ primordium	P ₁ -4 leaves P ₁ S ₁ -initiated	P ₂ -3 leaves	P ₃ -initiated		
5	6 leaves and 7th primordium	P ₁ -4 leaves and 5th primordium P ₁ S ₁ -1 leaf	P ₂ -3 leaves and 4th primordium	P ₃ -2 leaves	P ₄ -initiated	
6	7 leaves and 8th primordium	P ₁ -4 leaves and 5th primordium P ₁ S ₁ -1 leaf	P ₂ -4 leaves and an occasional 5th P ₂ S ₁ -2 leaves	P ₃ -2 leaves	P ₄ -An occasional 1st leaf primordium	
7	8 leaves and 9th primordium	P ₁ -4 leaves and 5th primordium P ₁ S ₁ -1 leaf	P ₂ -4 leaves 5th primordium P ₂ S ₁ -2 leaves	P ₃ -3 leaves	P ₄ -1 leaf	
8	9 leaves	P ₁ -5 leaves P ₁ S ₁ -2 leaves P ₁ S ₂ -initiated	P ₂ -6 leaves 7th primordium P ₂ S ₁ -2 leaves P ₂ S ₂ -initiated	P ₃ -4 leaves	P ₄ -2 leaves	
9	9 leaves	P ₁ -6 leaves P ₁ S ₁ -2 and 3 leaves P ₁ S ₂ -1 leaf	P ₂ -7 and 8 leaves P ₂ S ₁ -2 leaves and an occasional 3rd P ₂ S ₂ -1 leaf	P ₃ -5 and 6 leaves	P ₄ -2 leaves and 3rd primordium	
10	9 leaves	P ₁ -6 or 7 leaves P ₁ S ₁ -3 leaves P ₁ S ₂ -1 leaf	P ₂ -7 or 8 leaves P ₂ S ₁ -3 leaves P ₂ S ₂ -1 leaf	P ₃ -6 leaves P ₃ S ₁ -1 leaf	P ₄ -3 leaves	

TABLE 3--Chronological development of structures in seedlings of the Himalaya 15 kr. group.

Days	Main plumule	Tiller complex				
		P ₁	P ₂	P ₃	P ₄	P ₅
Dormant	4 leaves	P ₁ -1 leaf	initiated			
4	5 leaves	P ₁ -3 leaves and 4th primordium P ₁ S ₁ -1st leaf primordium	P ₂ -2 leaves and an occasional 3rd leaf primordium	P ₃ -initiated		
5	6 leaves and 7th primordium	P ₁ -3 leaves and 4th primordium P ₁ S ₁ -1st leaf primordium	P ₂ -3 leaves with 4th primordium P ₁ S ₁	P ₃ -1 leaf		
6	7 leaves and 8th primordium	P ₁ -4 leaves P ₁ S ₁ -1 leaf	P ₂ -4 leaves P ₂ S ₁ -initiated	P ₃ -2 leaves		
7	8 leaves and 9th primordium	P ₁ -4 leaves P ₁ S ₁ -2 leaves	P ₂ -4 and 5 leaves P ₂ S ₁ -1 or 2 leaves	P ₃ -3 leaves	P ₄ -initiated and an occasional 1st leaf	
8	8 leaves and 9th primordium	P ₁ -5 leaves P ₁ S ₁ -2 leaves	P ₂ -5 leaves and 6th primordium P ₂ S ₁ -2 leaves P ₂ S ₂ -initiated	P ₃ -4 leaves	P ₄ -1 and 2 leaves	
9	9 leaves	P ₁ -5 leaves P ₁ S ₁ -2 leaves P ₁ S ₂ -initiated	P ₂ -5 and 6 leaves P ₂ S ₁ -2 leaves P ₂ S ₂ -initiated	P ₃ -5 leaves P ₃ S ₁ -initiated	P ₄ -2 leaves	P ₅ -initiated
10	9 leaves	P ₁ -5 leaves P ₁ S ₁ -2 leaves P ₁ S ₂ -initiated	P ₂ -6 and 7 leaves P ₂ S ₁ -2 leaves P ₂ S ₂ -no leaves	P ₃ -5 leaves P ₃ S ₁ -no leaves	P ₄ -3 leaves	P ₅ -1 leaf primordium

TABLE 4--Chronological development of structures in seedlings of the Himalaya 30 kr. group.

Days	Main plumule	Tiller complex				
		P ₁	P ₂	P ₃	P ₄	P ₅
Dormant	4 leaves	P ₁ -1 leaf	P ₂ -initiated			
4	5 leaves	P ₁ -3 leaves	P ₂ -2 leaves and an occasional L ₃ primordium	P ₃ -initiated and often L ₁ primordium	P ₄ -initiated*	
5	L ₅ and often L ₆ primordium	P ₁ -3 leaves P ₁ S ₁ -initiated	P ₂ -2 leaves and L ₃ primordium	P ₃ -L ₁ primordium		
6	L ₆ and L ₇ primordium	P ₁ -3 leaves P ₁ S ₁ -initiated	P ₂ -3 leaves and L ₄ primordium	P ₃ -2 leaves	P ₄ -initiated and often 1 or 2 leaves	
7	varied from L ₆ with L ₇ primordium to L ₇ with L ₈ primordium	P ₁ -4 leaves P ₁ S ₁ -with L ₁ and often L ₂	P ₂ -L ₃ and primordium of L ₄ P ₂ S ₁ -initiated	P ₃ -2 leaves	P ₄ -2 leaves	
8	8 leaves	P ₁ -4 leaves P ₁ S ₁ -2 leaves	P ₂ -5 and often 6 leaves P ₂ S ₁ -1 leaf P ₂ S ₂ -initiated	P ₃ -2 leaves	P ₄ -2 leaves	
9	8 leaves and L ₉ primordium	P ₁ -4 leaves P ₁ S ₁ -2 leaves	P ₂ -6 leaves P ₂ S ₁ -1 or 2 leaves P ₂ S ₂ -no leaves	P ₃ -4 leaves and often an L ₅ primordium P ₃ S ₁ -initiated with L ₁	P ₄ -2 leaves with L ₃ primordium	P ₅ -initiated
10	9 leaves	P ₁ -4 leaves and often L ₅ primordium P ₁ S ₁ -2 leaves P ₁ S ₂ -initiated with L ₁	P ₂ -4 and 5 leaves P ₂ S ₁ -2 leaves P ₂ S ₂ -no leaves	P ₃ -varied from 4 to 6 leaves P ₃ S ₁ -L ₁	P ₄ -3 leaves	P ₅ -L ₁

*This did not seem to follow the usual development pattern, as the P₄ tiller was not seen in any other seedling until the 6th day.

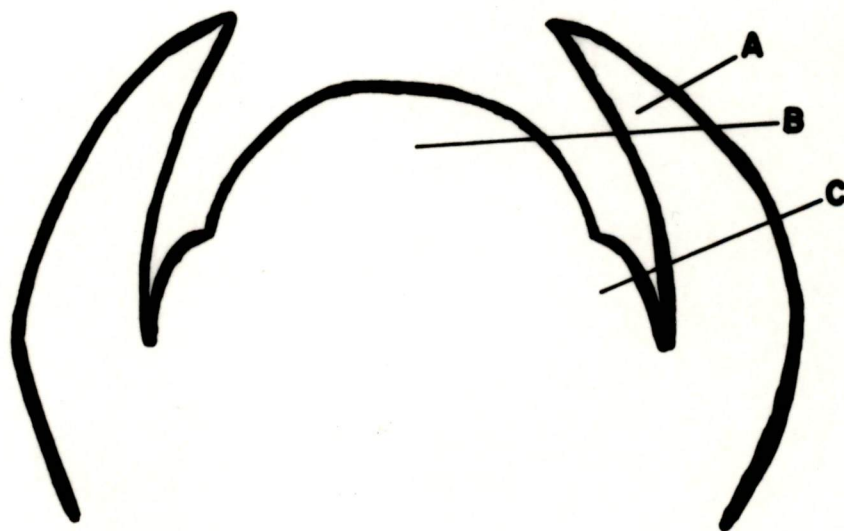


Figure 8. Part of germinating plumule (diagrammatic), showing (A) leaf, (B) apex, (C) leaf primordium (approximately 525x).

in plants which had developed from treated grains. The sole P_4 tiller observed was seen in the L_3 axil of a plant which had grown from a grain treated with 30 kr.

The earliest recognizable evidence of leaf initiation is usually the event of periclinal mitotic activity in the hypodermis (first corpus layer) and occasionally in the subhypodermis (second corpus layer) (Figure 9). Anticlinal divisions in the dermatogen (tunica) succeed the preceding events to allow leaf buttress expansion. Initiation of a new leaf occurs near the base of the apex and above the last differentiated leaf (4).

Generally, only one bud emerges from each coleoptylar or leaf axil, but on occasion two will arise at an axil. This phenomenon appears often in seedlings from both control and irradiated grains; it was reported by Sarvella et al. (23) and is shown in Figure 10.

Five days post-planting. Plants from both the control and the 15 kr. groups usually displayed six leaves and the primordium of the next leaf on the main plumule. Representatives of the 30 kr. group had five leaves and a sixth primordium visible (Figure 11).

In the control group the P_1 tiller had four developed leaves, whereas the 15 kr. group possessed three leaves, and a primordium of a fourth was usually visible. All seedlings of the 30 kr. group had three leaves, with no evidence of a fourth primordium. P_1S_1 was always present in the control seedlings and occasionally its first leaf was present. The P_1 complex in the 15 kr. group contained P_1S_1 , but the

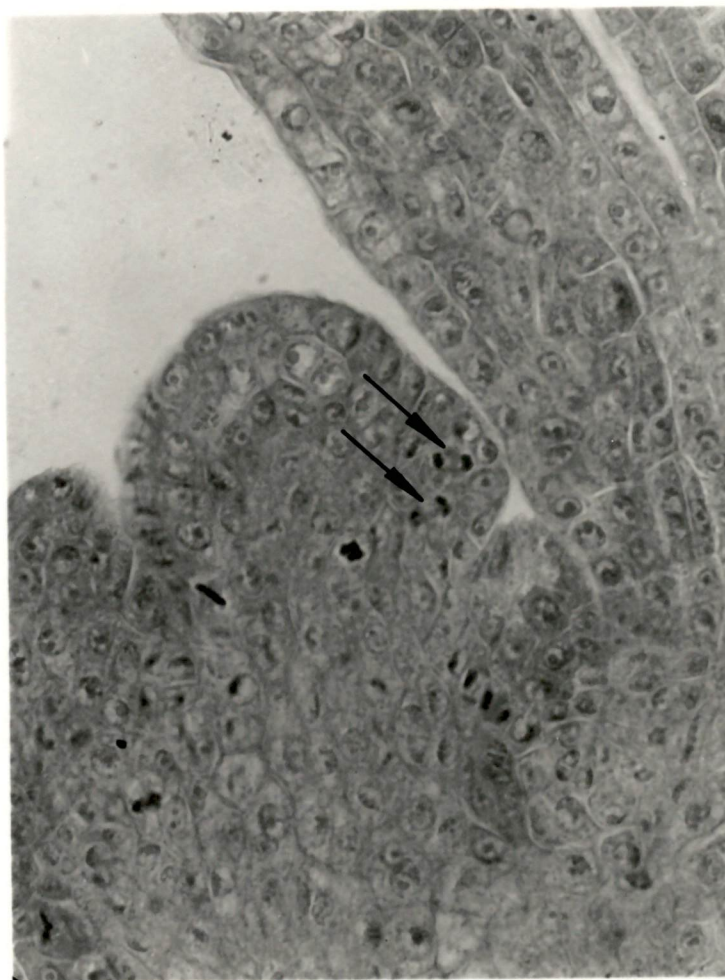


Figure 9. Longisection of five day post-planting shoot apex (500x) from the 30 kr Himalaya series. Note the periclinal divisions (arrows) indicating the initiation of the sixth leaf.

A



B

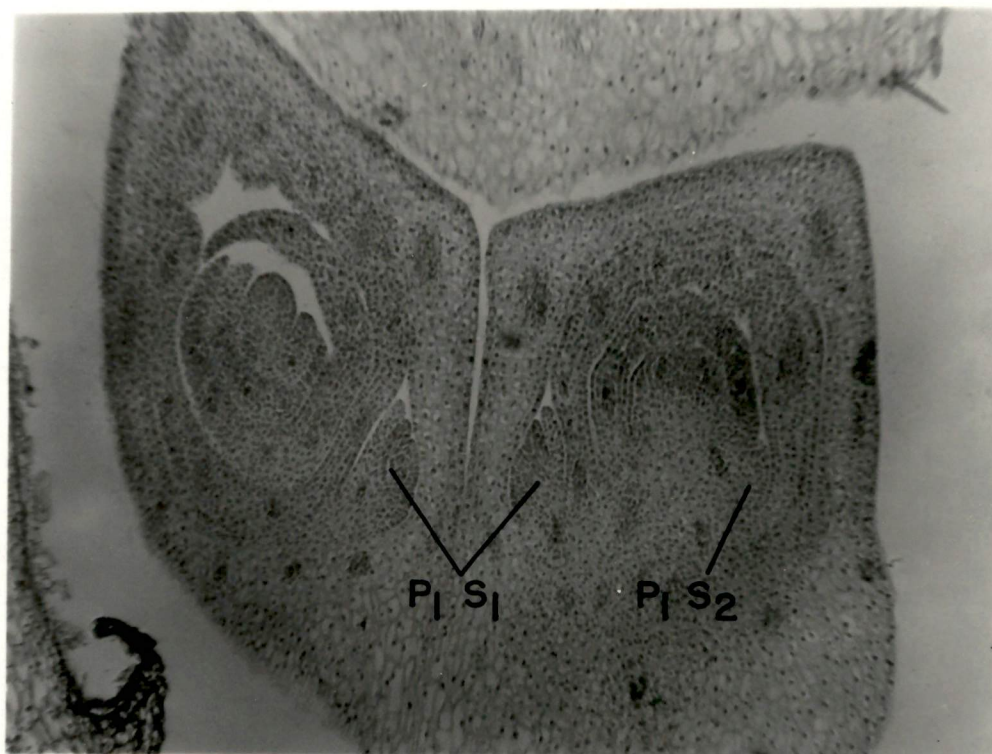


Figure 10. Twin primary tillers at eight days post-planting.
 A. The twin P_1 tillers (rectangle) are shown enlarged in B (diagrammatic).
 B. Longisection of twin P_1 tillers (72.5x) appearing in a control seedling at eight days post-planting. Secondary tillers P_1S_1 and P_1S_2 are also visible. P_1S_1 = first secondary tiller bud, P_1S_2 = second secondary tiller bud.

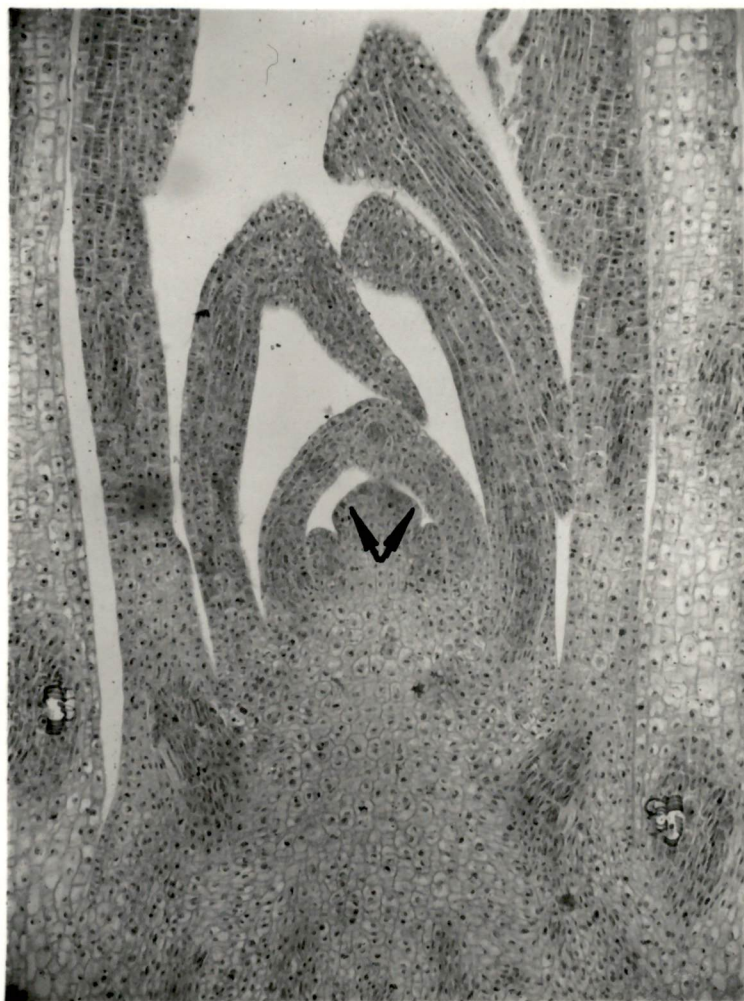


Figure 11. Five day post-planting seedling (100x) from 30 kr group showing coleoptile and five leaves. The protrusion (arrows) at the base of the apex is the L_6 primordium.

occurrence of prophyll initiation was rare. P_1S_1 was not always seen in the 30 kr. group, but when present exhibited less development than did the comparable structures of the 15 kr. group.

The P_2 tiller of the control group had three leaves and on occasion a fourth primordium was observed (Figure 12). Tiller P_2 development in the 15 kr. group ranged from those having two leaves and a third primordium to those showing three leaves and a fourth primordium. Seedlings developing from grains which received 30 kr. displayed either three leaves or a primordium of the third leaf. Several of the control seedlings showed P_2S_1 initiation. In the 15 kr. group only one P_2S_1 was observed, and it was non-existent in the 30 kr. group.

Tiller P_3 contained two leaves in the control seedlings, whereas only one was present in the 15 kr. group. In most seedlings the P_3 bud of the 30 kr. group was only a mass of cells at the base of L_2 , but two seedlings did show one prophyll.

Two of the control seedlings had initiated tiller P_4 , whereas none of the seedlings from irradiated groups showed any evidence of tiller P_4 .

Six days post-planting. The main shoots of the control and 15 kr. groups were similar in that both showed seven developed leaves and usually an eighth leaf primordium. Seedlings of the 30 kr. group had developed six leaves and a seventh leaf primordium.

In the control and 15 kr. groups no new structures were observed in the P_1 complex. In the 30 kr. group three leaves were seen on the P_1

A



B

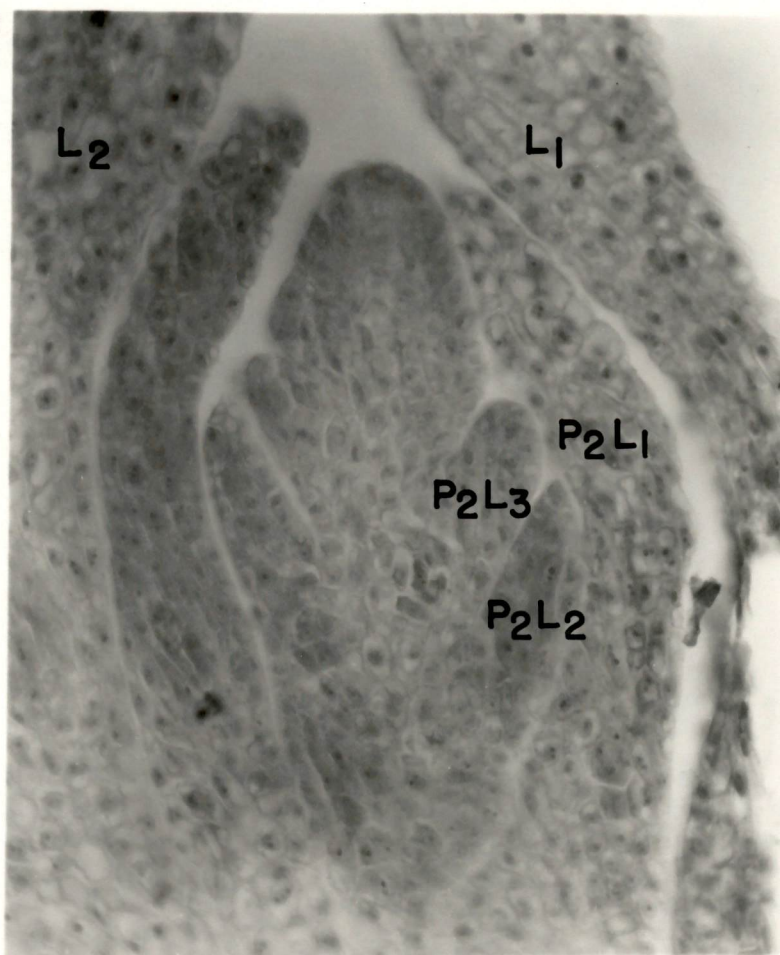


Figure 12. The second primary tiller at five days post-planting of a Himalaya control plant. A. The P_2 tiller (rectangle) is shown enlarged in B. B. Longisecton of a control P_2 tiller (300x) at five days post-planting. L_1 , first leaf of main culm; L_2 , second leaf of main culm; P_2L_1 , P_2L_2 , and P_2L_3 are leaves of the P_2 tiller.

bud and a fourth primordium was frequently present. In all three groups the P_2 tiller appeared to be growing at a more rapid rate than tiller P_1 , and by this time P_2 had attained the same number of leaves as P_1 .

Two leaves were present in the P_3 tiller in all control plants; in both irradiated groups tiller P_3 had one or two leaves. An occasional leaf primordium was seen on tiller P_4 in the control plants. Tiller P_4 was present in the irradiated groups but showed little or no leaf initiation.

Seven days post-planting. The main plumule of nonirradiated and 15 kr groups had eight leaves and a primordium of a ninth leaf, as contrasted with the 30 kr group which possessed seven leaves and a primordium of an eighth leaf. In all three groups the leaf number of tiller P_1 was four, while neither the control group nor the 15 kr showed an increase in leaf number on tiller P_1 over the previous day. The 30 kr group did show some advancement in that four leaves were apparent. P_1S_1 appeared in all seedlings but with various degrees of differentiation. The P_1S_1 tiller in the control group displayed one leaf, while two were present on the same structure in the 15 kr group. The 30 kr group displayed either one or two leaves on the P_1S_1 tiller. Tiller P_2 also appeared with various degrees of development, ranging from four leaves and a fifth leaf primordium in the control plants to four or five leaves in the 15 kr group. The 30 kr group possessed three leaves and a fourth leaf primordium on tiller P_2S_1 . Similarly, P_2S_1 varied from two leaves in the control group to one leaf in the 15 kr group to none in the

30 kr. group. Three leaves were seen on tiller P_3 in all control seedlings as well as in those of the 15 kr. group; the same tiller was somewhat retarded in the 30 kr. group, as it displayed only two leaves. The P_4 tiller from representatives of the control group usually possessed a single leaf while the same tiller was differentiated but rarely had a first leaf initiated in the 15 kr. plants. This same tiller (P_4) showed the most development in the 30 kr. group in that two leaves were commonly observed.

Eight days post-planting. The main plumules in the control and 15 kr. plants displayed either nine leaves or a ninth primordium; the main plumules of the 30 kr. group exhibited eight leaves or an eighth leaf primordium (Figure 13).

The P_1 tiller in the control groups showed five developed leaves, as did the P_1 tiller in the 15 kr. group. Four leaves were present on the same structure in plants from the 30 kr. group. Two leaves were characteristic of the P_1S_1 tillers representing all groups. A new structure, P_1S_2 , was differentiated in the control group in L_2 axil of primary tiller P_1 . This structure was not observed in either of the irradiated groups. Between the seventh and eighth day, tiller P_2 underwent rapid leaf initiation; six leaves and an occasional seventh primordium appeared on P_2 in the control group, while five leaves and a sixth primordium were typical of the 15 kr. and 30 kr. groups. The P_2S_1 tillers in the control group still displayed two leaves while the 15 kr. P_2S_1 tillers showed one or two leaves. The 30 kr. group revealed the P_2S_1 tiller to possess a single leaf.



Figure 13. Main culm of Himalaya seedling at eight days post-planting from the 30 kr series, showing eight leaves and developing spike (100x).

A new tiller, P_2S_2 , was seen in the L_2 axil of primary tiller P_2 . It was newly initiated and showed no evidence of leaf initiation. Tiller P_3 usually exhibited four leaves in both the control and 15 kr groups. Only two leaves were present, however, on P_3 in the 30 kr plants.

P_4 tiller in the control plants exhibited two leaves while one or two leaves were seen on P_4 in the 15 kr group. No additional leaves were observed in tiller P_4 in the 30 kr group.

Nine days post-planting. Nine leaves were either formed or a ninth primordium was obvious on the main plumule in all three groups. Nine leaves appear to be the full complement of leaves initiated by the shoot apex in this particular variety. Structures initiated by the apex after the ninth day were reproductive.

One leaf was added to tiller P_1 in those seedlings representing the control group while none of the P_1 tillers of the irradiated groups had initiated any new leaves. The P_1S_1 tiller was observed in all groups and all showed two leaves. P_1S_1 tiller had by this time two leaves in the control group, but was not differentiated in either of the irradiated groups.

The P_1 complex appeared retarded when compared to P_2 . Tiller P_2 in control seedlings had initiated an additional one or two leaves, bringing the total to seven or eight leaves. Six leaves and a seventh leaf primordium marked the development of the P_2 tiller in the 15 kr group, and six leaves were also characteristic of the P_2 tiller developing from grains receiving 30 kr of radiation. The P_2S_1 tiller in the

control seedlings usually possessed two leaves, and a third leaf primordium was frequently observed. Both irradiated groups had two leaves on the P_2S_1 tiller. In the control group tiller P_2S_1 had initiated one leaf, but no leaf initiations were evident on the P_2S_1 tiller in those plants from the treated groups.

Five or six leaves were prevalent on tiller P_3 in the control plants. Five and four leaves were seen on the P_3 tiller on seedlings of the 15 and 30 kr. plants, respectively. P_3 made its initial appearance in the L_1 axil of tiller P_3 . P_3S_1 was seen in plants of both irradiated groups but, interestingly, not in the controls. Tiller P_3S_1 was barely initiated in the 15 kr. plants but did show one leaf in the 30 kr. plants. All three groups showed tiller P_4 to possess two leaves and third primordium. Tiller P_5 , another new structure, was differentiated in all treated plants, but was not yet initiated in the control plants.

Ten days post-planting. The main shoot in all groups possessed nine leaves. The control groups were usually more advanced than the irradiated groups. Tiller P_1 displayed six or seven leaves on the control plants, whereas five and four were seen on P_1 in the 15 and 30 kr. groups, respectively. P_1S_1 was commonly seen in the control groups possessing three leaves, while the P_1S_1 tiller in the irradiated groups showed one leaf. The P_2 tiller examined in the control seedlings possessed six or seven leaves, and the observed P_2S_1 buds usually had three leaves and P_2S_2 was initiated. The 15 kr. group revealed tiller P_1 also to possess six or seven leaves; P_2S_1 was present and exhibited one

prophyll, but there was no evidence of P_2S_2 . Usually the control seedlings showed six leaves in tiller P_3 . P_3S_1 was present and often one leaf was initiated. Tiller P_3 in the 15 kn group showed four to six leaves; P_3S_1 was sometimes present, showing one leaf primordium. Those P_3 tillers representing the 30 kn group had from three to five leaves and in the more advanced plants P_3S_1 was present with one leaf. The P_4 tiller in all groups typically had three leaves. A new structure, tiller P_5 , located in the L_4 axil on the main shoot, appeared in both irradiated groups at ten days post-planting, but, strangely, was not seen in any of the control seedlings.

Tiller Emergence

Four weeks post-planting. Of the one hundred twenty seeds planted, there was 100 per cent germination, emergence, and survival. The observation after one month revealed that there were no tillers whatever emerging from the axil of the coleoptile and only seven arising from the axil of L_1 . The greatest number of tillers was seen emerging from the L_2 axils (see Table 5 and Figure 14a).

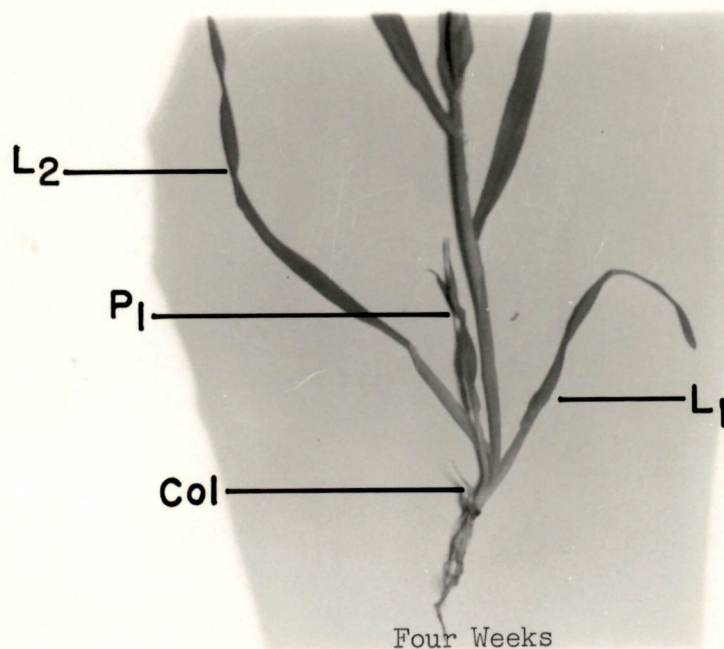
Five weeks post-planting. Observations one week later showed no tillers developing from the coleoptile. Forty-three tillers, however, were seen in the axil of L_2 , while thirty-seven were seen emerging from the L_3 axil (see Table 6 and Figure 14b).

Further investigations were made to determine the fate of the coleoptile bud. The plants were removed from the soil and the coleoptile, when present, removed; observations were made under a

TABLE 5--Number of tillers emerging in the axils of the coleoptile, L_1 , and L_2 of Himalaya barley after four weeks' growth.

	Coleoptile axil	L_1 axil	L_2 axil
No. of plants examined	120	120	120
No. of plants having tillers at:	0	7	19

A



B

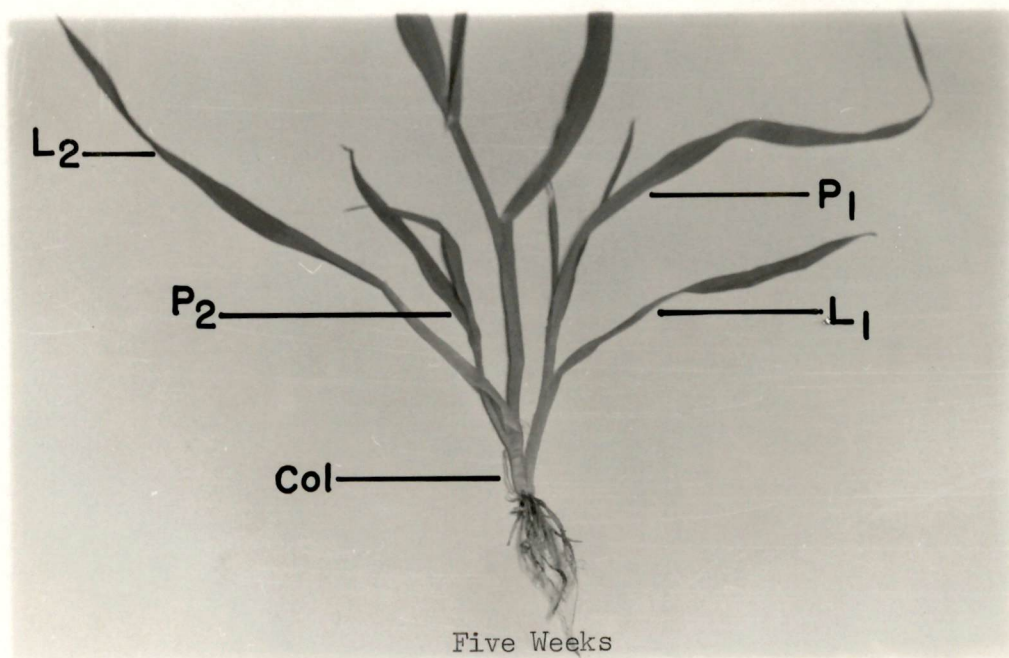


Figure 14. Tiller emergence at four and five weeks post-planting. A. The first tiller (P_1) arising from the axil of the L_2 at one month post-planting. B. Tillers P_1 and P_2 are emerging from axils of L_1 and L_2 , respectively. Col = coleoptile, P_1 = first primary tiller, P_2 = second primary tiller, L_1 = first leaf, L_2 = second leaf.

TABLE 6--Number of tillers emerging in the axils of the coleoptile, L_1 , L_2 , and L_3 of Himalaya barley after five weeks' growth.

	Coleoptile axil	L_1 axil	L_2 axil	L_3 axil
No. of plants examined	120	120	120	120
No. of plants having tillers at:	0	43	92	37

dissecting microscope. The coleoptile bud seemed to have deteriorated, as it was never observed on the plants at five weeks.

Summary of Variety "Himalaya"

The initiation of primary tillers, secondary tillers, and leaves occurred rapidly during ten days post-germination. By this time the control plants had differentiated forty-four plumular structures, excluding reproductive structures, which were not present in the dormant embryo. Thirty-four and thirty-eight new structures were added to the 15 and 30 kn groups, respectively. In all groups each of the main plumules produced nine leaves by ten days. The control plants developed the full complement of nine leaves about two days before the same structures were shown on the treated plants. The first primary tiller, P_1 , produced leaves rapidly through seven days; but by about the eighth or ninth day, tiller P_2 had produced more leaves and had become larger and more prominent than tiller P_1 . Tiller P_1 in the irradiated groups did not produce as many leaves as did tiller P_1 in the control plants. Tiller P_2 in the irradiated groups also displayed more growth than the P_1 tillers in the same groups.

Fewer new structures were observed on the irradiated groups, and these structures were primarily leaves produced by the tiller complexes. However, the irradiated groups did differentiate a new structure, tiller P_5 , which was not seen in the control plants. Figure 15 shows the number of structures initiated daily beginning with the fourth day through ten days post-planting.

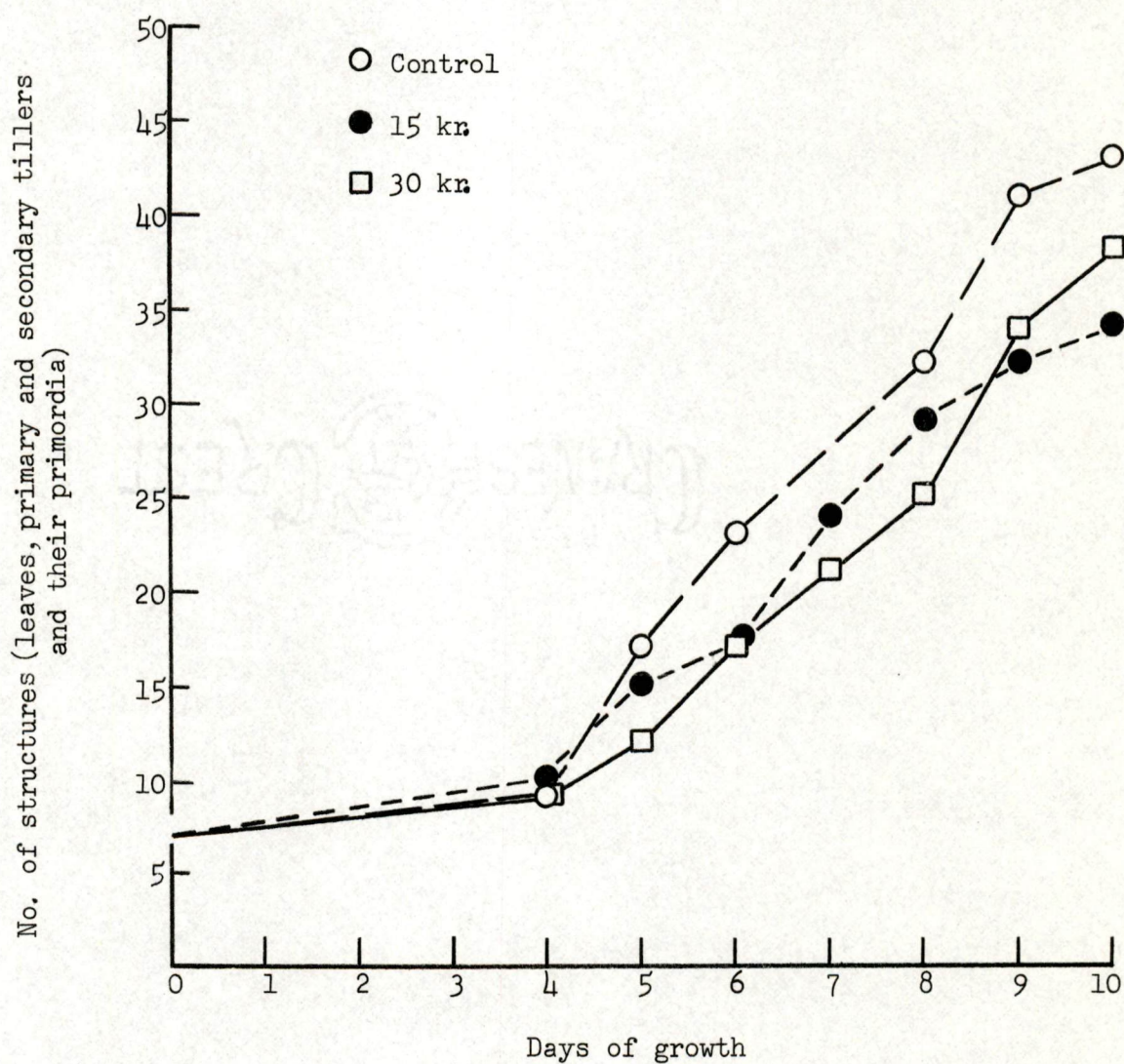


Figure 15. Daily addition of new structures beginning with four days post-planting through ten days post-planting in control and irradiated groups of Himalaya barley.

Macroscopic observations of one hundred twenty control plants showed that the P_1 tiller did not emerge even though it produced several leaves and even secondary tillers with leaves. Furthermore, many of the P_2 tillers did not emerge by five weeks. The highest percentage of emerging tillers occurred at the second leaf axil, which would indicate that higher numbers of P_3 tillers developed and emerged than did either P_1 or P_2 tiller.

II. VARIETY "HUDSON"

The second variety incorporated in this study was Hudson, which is a winter variety. Grains were not vernalized and were subjected to the same growing conditions as was the Himalaya variety.

Developing Seedlings

Four days post-planting. The four-day collections showed few differences between the control seedlings and those seedlings developed from irradiated grains (Tables 7, 8, and 9). In fact, there were no observed differences between the control and 15 kr. groups. The 30 kr. group did not exhibit a third leaf primordium on tiller P_1 nor did a fifth primordium appear on the main plumule; these were the only found differences between the control and the irradiated groups.

Five days post-planting. Five leaves were seen on the main plumules of both the control and 15 kr. groups. A fifth leaf primordium was observed, however, on the 30 kr. plumules. The P_1 tillers from the control and 15 kr. groups showed the same degree of development, both

TABLE 7--Chronological development of structures in seedlings of the Hudson control group.

Days	Main plumule	Tiller P ₁	Tiller P ₂	Tiller P ₃	Tiller P ₄
Dormant	3 leaves	1 leaf	initiated		
4	4 leaves and L ₅ primordium	2 leaves with L ₃ primordium	2 leaves	initiated	
5	5 leaves	3 leaves	L ₃ primordium	1 leaf	
6	5 leaves and L ₆ primordium	3 leaves	3 leaves	1 leaf	
7	6 leaves	3 leaves	3 leaves	2 leaves	
8	6 leaves with L ₇ primordium	3 leaves	3 leaves	2 leaves and often L ₃ primordium	initiated
9	7 leaves	3 leaves	3 leaves	2 leaves and L ₃ primordium	1 leaf
10	7 leaves and an 8th primordium	3 leaves	3 leaves	3 leaves	1 leaf

TABLE 8--Chronological development of structures in seedlings of the Hudson 15 kr group.

Days	Main plumule	Tiller P ₁	Tiller P ₂	Tiller P ₃	Tiller P ₄
Dormant	3 leaves	1 leaf	initiated		
4	4 leaves with L ₅ primordium	2 leaves and L ₃ primordium	2 leaves	initiated	
5	5 leaves	3 leaves	2 leaves	no leaves	
6	6 leaves	3 leaves	2 leaves often with L ₃ primordium	1 leaf	
7	6 leaves and L ₇ primordium	3 leaves	3 leaves	1 leaf with L ₂ primordium	initiated
8	6 leaves and L ₇ primordium	3 leaves	3 leaves	2 leaves and often L ₃ primordium	no leaves
9	6 leaves and L ₇ primordium	3 leaves	3 leaves	3 leaves	no leaves
10	7 leaves	3 leaves	3 leaves	3 leaves	1 leaf

TABLE 9--Chronological development of structures in seedlings of the Hudson 30 kz group.

Days	Main plumule	Tiller P ₁	Tiller P ₂	Tiller P ₃	Tiller P ₄
Dormant	3 leaves	1 leaf	initiated		
4	4 leaves	2 leaves	2 leaves	initiated	
5	L ₅ primordium	2 leaves and L ₃ primordium	2 leaves	initiated	
6	5 leaves	2 leaves and L ₃ primordium	2 leaves	initiated	
7	5 leaves with L ₆ primordium	2 leaves and L ₃ primordium; often 3 developed leaves	2 leaves and L ₃ primordium; often 3 developed leaves	1 leaf	initiated
8	L ₆ primordium	3 leaves	3 leaves	2 leaves	no leaves
9	6 leaves and L ₇ primordium	3 leaves	3 leaves	2 leaves	no leaves
10	7 leaves	3 leaves	3 leaves	2 leaves with L ₃ primordium	no leaves

having three leaves. The same tiller in the 30 kr group revealed but two leaves, and a third primordium was occasionally observed. The P_2 tiller from the control group displayed a third leaf primordium, while the same tiller in the irradiated groups was not as advanced. The control groups clearly displayed one leaf on the P_3 tiller, whereas a comparable structure was not seen in any of the representatives of the irradiated groups.

Six days post-planting. The main plumule of the 15 kr group showed more development at this time than did the control group. Six leaves were well developed, whereas only the sixth primordium was readily recognized in the control group. The main plumules of the 30 kr plants showed only five leaves. At this time, tiller P_1 in both the control and 15 kr group consistently showed three leaves. The same tiller in the 30 kr group usually revealed only a third leaf primordium. Three leaves were also observed on tiller P_2 in control plants. Tiller P_2 in the 15 kr group on occasion did possess three leaves, but most observations revealed only two leaves and a third primordium. Seedlings from the 30 kr group showed only two leaves on the P_2 tiller. At this time tiller P_3 in the control and 15 kr groups was seen to have a leaf primordium, while this structure was not observed in the 30 kr group.

Seven days post-planting. Six leaves were found on the main axis in the control group, but the sixth primordium, in most instances, was seen in the 15 kr group. The 30 kr group usually possessed only five leaves and a sixth primordium. No new structures were produced on the

P_1 tillers in either the control or irradiated groups. The P_2 tiller exhibited three leaves in the control group, while the irradiated groups generally showed only a third leaf primordium. The P_3 tiller in the control group displayed two leaves, whereas only a primordium of a second leaf was usually seen on the same structure in the 15 kr group. A single leaf was present on the P_3 tiller in the 30 kr group. A new tiller, P_4 , was first seen initiated seven days post-planting. This tiller (P_4) was not at all evident in the control group but was restricted to the irradiated groups.

Eight days post-planting. A seventh leaf primordium was present on the main axil of all plants studied in both the control and 15 kr groups, while the 30 kr group usually displayed only six developed leaves. The addition of new structures to the P_1 and P_2 tillers seemed to have ceased, both in the control and in the irradiated groups. In all three groups tiller P_3 usually displayed three leaves. The P_4 tiller, which appeared on the seventh day post-planting in both irradiated groups, was present in every control seedling observed. Neither the 15 kr nor the 30 kr group showed any evidence of leaf initiation on tiller P_4 .

Nine days post-planting. The main plumules from the control group exhibited seven well developed leaves, while the 15 and 30 kr groups displayed the seventh leaf primordium. Representative P_1 tillers of all three groups still displayed three leaves. Tiller P_2 had not progressed any further than the three leaf stage in any of the

three groups. Tiller P_3 , in all groups, displayed two leaves and in almost every seedling a third leaf primordium was seen. An L_3 primordium was initiated on tiller P_4 in the control plants but was not observed in either of the treated groups.

Ten days post-planting. Plants from the two irradiated groups showed the main plumule to possess seven leaves, while the control group had also an eighth leaf primordium (Figure 16). No reproductive structures were observed. Tiller P_1 and P_2 in all three groups had three leaves. No new leaves were seen being initiated in the control and 15 kr groups on tiller P_1 since the fifth day's observation. The third leaf was well developed at seven days post-planting but new leaf initiation had ceased, at least through the ten-day observation period. Tiller P_2 , in the control group, had initiated three leaves by the sixth day post-planting and no new leaves were developed by the tenth day. The 15 and 30 kr groups showed their third leaf on tiller P_2 at seven and eight days post-planting, respectively, and no evidence of leaf formation was seen thereafter.

Each control tiller P_3 examined displayed three leaves, while the same tiller in the irradiated groups usually showed two leaves and a third primordium. Each P_4 tiller examined in the control group had one leaf. Several seedlings from the 15 kr group possessed a P_4 tiller showing one leaf being initiated, while the 30 kr group representatives simply revealed the P_4 tiller (see Figure 17).

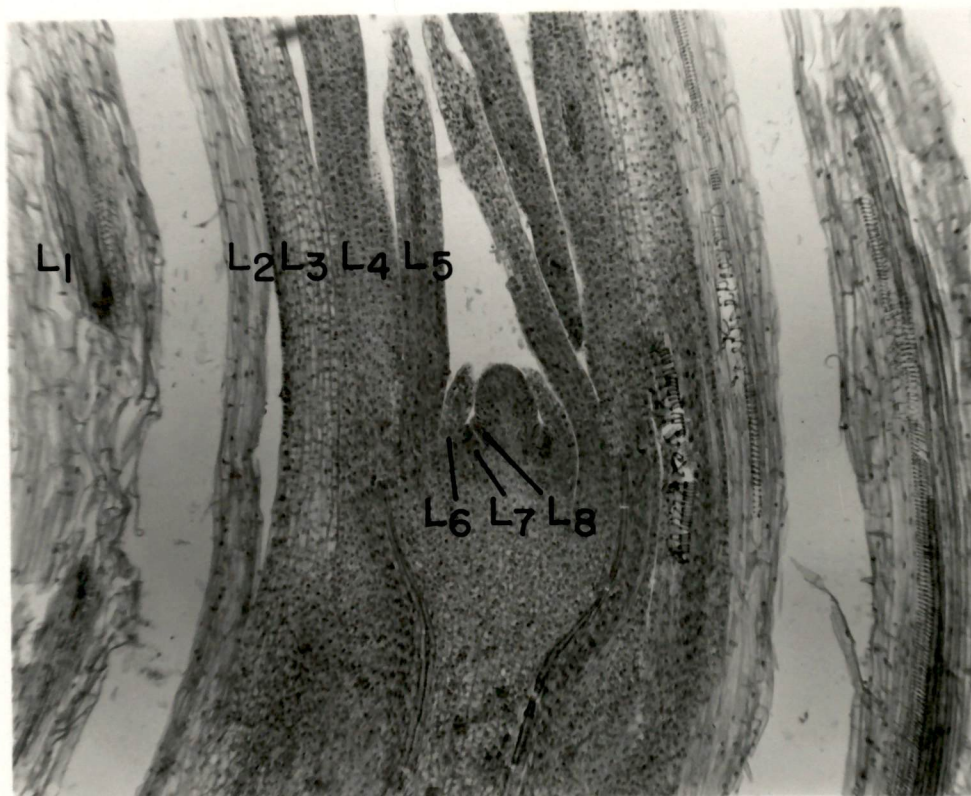


Figure 16. A control Hudson seedling at ten days post-planting showing seven leaves and an eighth leaf primordium (100x). Ap = apex, L₁ = leaf 1, L₂ = leaf 2, etc.

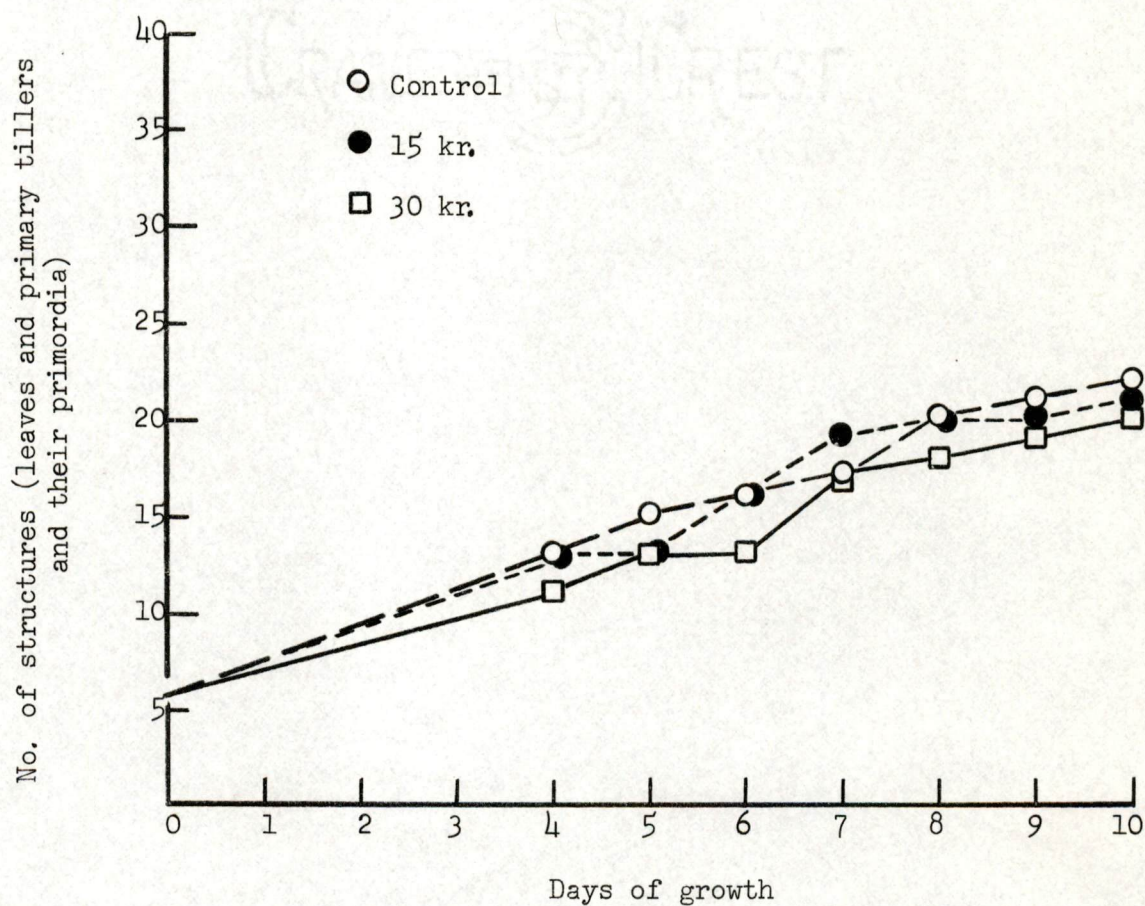


Figure 17. Daily addition of new structures beginning with four days post-planting through ten days post-planting in control and irradiated groups of Hudson barley.

Summary of Variety "Hudson"

This variety showed less initiation of structures than did the Himalaya in that fewer were developed. Sixteen, fifteen, and fourteen structures (leaves and buds or their primordia) which were not present in the dormant embryo were present in the control, 15, and 30 kr groups respectively at ten days post-planting. It appears there was little visible difference in relation to structures differentiated between control plants and those plants which had developed from irradiated kernels. Even though less development occurred in Hudson than in Himalaya, there was less visible evidence to show retardation of growth due to radiation.

CHAPTER V

DISCUSSION

Radiation apparently reduced the number of structures (leaves, tillers, and their primordia) initiated by seedlings developing from treated grains. This was true especially regarding the number of structures produced by the P_1 complex. The P_1 complex in the control groups produced as many as seven leaves and two secondary buds, while plants from the irradiated groups only initiated five leaves on the P_1 tiller. The secondary tillers (P_1S_1 and P_1S_2) in the treated groups were somewhat retarded in their initiation of leaves. In regard to production of other tiller buds and prophylls there were few differences by the tenth day. However, a tiller, P_5 , occurred in the axil of L_4 on the main shoot in the irradiated plants but was not observed in the control plants. No explanation can be offered for this phenomenon.

After four and five weeks of growth it was observed that the P_1 complex did not emerge. This phenomenon does not appear to be unusual: Sarvella et al. (23), using tetrazolium chloride, observed only 11.1 per cent of the control buds to be viable after one month's growth. Those plants to which 10 kr. was administered showed 11.9 per cent tiller P_1 emergence. This may or may not be typical, since plants in this study examined at four and five weeks post-planting under a dissecting microscope revealed no evidence of a coleoptylar bud.

The data of this study reveal that the P_1 tiller seldom, if ever, emerges even though several leaves and two secondary tillers, P_1S_1 and P_1S_2 , are developed during the first few days following germination. The data presented by Sarvella et al. also indicate that the majority of the time the P_1 complex does not remain viable. It should be mentioned again that the variety Uniculm has two tillers in the dormant embryo but neither emerges; the single spike arises from the main shoot apex. It is not known, however, at exactly what stage or how the P_1 tiller becomes nonfunctional or if a specific number of prophylls are differentiated before becoming inactive.

Macroscopic observations showed that the P_2 complex may not always develop, as more than twice the number of P_3 tillers than P_2 tillers had emerged after five weeks post-planting.

The Hudson variety data also indicated that the P_1 tiller does not develop. The control plants had three leaves on the P_1 tiller by five days post-planting and no others were initiated through ten days post-planting. No more than three leaves were observed on the P_1 tiller developing from the irradiated groups.

No reproductive structures, as expected, were seen on the Hudson variety as it is a winter variety; the grains were not vernalized and the plants were exposed to long-day growing conditions. This variety, except for the first developmental stages, seemed to have more resistance to radiation because by ten days post-planting there were only one or two differences between the number of plumular structures produced by the control and the irradiated groups.

CHAPTER IV

CONCLUSIONS

Based on microscopic and/or macroscopic observations, the following may be concluded:

1. The dormant plumules of eight cultivars of barley show only one observable difference: Himalaya possesses four leaves on the main plumule, while the other cultivars studied have three leaves. Two buds were seen in all cultivars.
2. Fifteen and 30 kr. of gamma radiation retards growth, but the extent of growth appears not to be severely affected. The spring variety, Himalaya, is more delayed in relation to initiation of structures than is the winter variety, Hudson.
3. The first tiller, which is the most highly developed in the dormant embryo, does not emerge in unirradiated Himalaya barley and by four or five weeks post-planting it has completely disappeared.

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