appeared from a quadrat in which it formed most of the cover in 1932. Whether the mosiac described in this paper can be attributed to the 7-year drought that preceded this study cannot yet be determined. But coverage data are being taken from the permanent plots to resolve this point.

Summary and Conclusion

Two communities, one dominated by *Andropogon scoparius* and the other by *Aristida longiseta* and forbs, form a mosaic on a Rendzina at Austin, Texas. Frequency data taken on 9 days at intervals varying from 4 to 8 weeks over a 1-year period show an average species correlation over the year of 0.24 between the two communities. Soil depth to limestone averages 7.6 decimeters in the *Aristida* community and more than 16 decimeters in the *Andropogon*. Soil moisture percentages taken at about bi-weekly intervals show that the *Aristida* is the more xeric of the two communities and that soil moisture in this community goes below the permanent wilting percentage during July and August. Phenological data taken at weekly intervals correlate well with soil moisture during a 1-year period. *A. scoparius* forms a dense stand in the *Andropogon* community and appears to prevent the invasion of species not tolerant of shade and crowding. The shallowness of the soil and the smaller amount of soil moisture available for plant growth in the *Aristida* community apparently prevent the establishment of *A. scoparius*.

References

Albertson, F. W., G. W. Tomanek, and Andrew Riegel. 1957. Ecology of drought cycles and grazing intensity on grasslands of the Central Great Plains. Ecol. Monographs **27**: 27-44.

Briggs, L. J., and J. W. McLane. 1907. The moisture equivalent of soils. U. S. Dept. Agr. Bur. Soils. Bull. 45, 23 p.

Dyksterhuis, E. J. 1946. The vegetation of the Fort Worth Prairie. Ecol. Monographs **16**: 1-29.

Hill, Robert T., and T. Wayland Vaughan. 1902. The Austin folio, in the Geologic Atlas of the United States. U. S. Geol. Survey.

Launchbaugh, J. L. 1955. Vegetational changes in the San Antonio Prairie associated with grazing, retirement from grazing, and abandonment from cultivation. Ecol. Monographs **25**: 39-57.

Templin, E. H., A. H. Bean, J. W. Huckabee, Jr., Leslie H. Smith, and M. H. Layton. 1938. Soil survey of Williamson County, Texas. U. S. Dept. Agr. Bur. Chem. and Soils, Series 1934, No. **10**, 55 p.

Tharp, B. C. 1926. Structure of Texas vegetation east of the 98th meridian. Univ. of Texas Bull. **2606**, 100 p.

U. S. Dept. of Commerce. 1960. Local climatological data, Austin, Texas.

Weaver, J. E., and R. W. Darland. 1944. Grassland patterns in 1940. Ecology **25**: 202-215.

ECOTYPIC VARIATION IN MEDUSAHEAD, AN INTRODUCED ANNUAL GRASS[1]

Cyrus M. McKell,[2] John P. Robison, and Jack Major[3]

Introduction

Many thousands of acres of grazing land in California, Oregon, Washington, and Idaho are now infested with the undesirable annual grass, medusahead (*Taeniatherum asperum* (Simonkai) Nevski) (*Elymus caput-medusae* L. of American authors). Medusahead was introduced into the United States from the Mediterranean region of Eurasia where it consists of three geographically and morphologically distinct taxa. Spain, Portugal, and southern France are occupied only by *Taeniatherum caput-medusae* (L.) Nevski (*Elymus caput-medusae* L. ssp. *bobartii* (Asch. & Graebn.) Maire). *Taeniatherum crinitum* (Schreb.) Nevski occupies the area from North Africa, Sicily, Sardinia, southern Greece, southern Crimea, Anatolia, the Tien Shan Mountains, Sinai, Israel, Syria, Iraq, northern Iran, and Afghanistan. Specifically, the plant in the western United States appears to have come only from the area from Hungary to Apulia in southern Italy east through northern Greece to the Bosporus region on the south and in the northeast through coastal Rumania, the Ukraine, the Crimea, the Caucasus, and to the Pamir-Alai region of Turkestan. Historically the Ukraine is the most probable source. The best name for our plant seems to be *Taeniatherum asperum* (Simonkai) Nevski (Major 1960).

Taeiniatherum asperum was first collected in the U. S. near Roseberg, Oregon, on June 24, 1887, by Howell (no. 1326). In 1901 it was recorded from Steptoe Butte in eastern Washington by Vasey (no. 3076), and in 1908 near Los Gatos, California, by Hitchcock. The disjunct occurrences were

[1] Cooperative investigations of Crops Research Division, ARS, USDA, and the University of California, Davis, California.

[2] Plant Physiologist, Crops Research Division, ARS, USDA. Presently Assistant Agronomist, University of California, Riverside, California.

[3] Graduate Student, and Assistant Professor of Botany, University of California, Davis, California.

390 miles (630 km) northwest and 450 miles (730 km) south of Roseburg, respectively. The Steptoe Butte infestation persists; that of Los Gatos does not. Other pre-1910 collections show equiformal concentric circles of migration from the original Roseburg introduction, with a tendency to elongate in the direction of California to the south.

It is assumed that all *Taeniatherum asperum* in the United States at the present time came from one original introduction which was first collected at Roseburg, Oregon, and later at Steptoe Butte, Washington. If it could be shown that the Steptoe Butte infestation was derived from a different introduction than the one at Roseburg, thus possibly bringing into the U. S. diversity of genotypes, the different genetic material would not greatly affect the results of the study reported here. Of the 13 seed sources used in the present study, one was actually from Steptoe Butte and it was by no means exceedingly different from the others. *Taeniatherum asperum* was the plant introduced at Steptoe Butte as determined from the original specimens of Vasey and the illustration in Hitchcock's manual (1950:250). The same kind of medusahead still occurs at Steptoe Butte. It is possible that the Steptoe Butte infestation yielded the present stands in Idaho. However, Vasey recorded it as an "isolated plant." The infestation has not spread widely since 1901, although Piper and Beattie (1914:40) recorded it as "spreading rapidly." Judging by medusahead's present limited occurrence in the immediate Steptoe Butte area, its rapid spread must have slowed down quickly. The first Idaho collection was by J. F. Pechanec in 1944 near Payette, about 180 miles (290 km) due south of Steptoe Butte. Medusahead was previously noted by Fred Renner (personal communication) at Mountain Home, Idaho, in 1930. Sharp and Tisdale (1952:1) recorded that "a rancher in Washington Co. claims to have noticed the plant in 1942." Washington County is about 6 miles (10 km) north of Payette, and infestations are very heavy in this area today. The Idaho infestation could have come from the one at Steptoe Butte, directly from western Oregon, or from plants spreading across Oregon from the original introduction. California plants clearly came from Oregon by continuous southward migration.

At present, medusahead is distributed widely over the semi-arid regions in southeastern Washington, northeastern Oregon and adjacent Idaho, north of the Snake River in southwestern Idaho, with a few small areas of infestation south of the river of the Cascades in summer-dry climates in Oregon. It also occurs in California down through the Coast Ranges to Monterey County, on either side of the Sacramento Valley, including the Sierra Nevada foothills, south to Madera and Fresno Counties and is disjunct in the potreros (valleys) of transmontane Santa Barbara County. The spread has been rapid but continuous, with few spectacular long-distance jumps.

There is no reason to believe medusahead has yet reached its ecological limits. It competes successfully and overlaps both in area and in local habitat ecology with two other exotic, annual range invaders, namely *Bromus mollis* L. in California and southern Oregon and *B. tectorum* L. elsewhere within the range of medusahead. If the requirements of medusahead completely overlap those of *B. tectorum,* it could spread widely in the Great Basin, where it now has a start on the northern, low-altitude fringe of this physiographic province.

The phenology of medusahead, combined with present patterns of livestock use, appears to be important in the plant's success as a western rangeland invader. Medusahead stays green after its associated plants have matured seed and dried. Since the early-maturing, annual vegetation in California at least does not fully utilize winter-stored soil moisture (McKell, Major, and Perrier 1959), medusahead is able to mature later than other species. If late spring rains occur, the situation is even more favorable. Medusahead, in any case, is not readily grazed at maturity (Lusk *et al.* 1961) and thus escapes drought and livestock use and increases in abundance.

Ecotypic variation in medusahead was studied with the above characteristics of the plant in mind. Attention was centered on variations in phenological development, seed germination, plant height, and rate of root elongation.

Knowledge of the present variability in New World *Taeniatherum asperum* is desirable both to answer problems in evolution and perhaps to help correlate and extend weed control measures, explain further geographical spread, and relate ecological observations on the plant. The object of this study was to determine what variability exists in medusahead and if possible to relate this variability to environment.

Review of Literature

Much of the investigation of medusahead has been directed toward the ecology, control, or management of rangelands infested with it. A future paper on the ecology of medusahead will review this literature. None of the previous studies have investigated variability within the taxon.

There are few studies of ecotypic differentiation in annual grasses. Knowles (1943) found that soft chess (*Bromus mollis* L.) could be divided into two ecotypes when comparisons were made of plants grown from seed collected from several locations in California and Oregon. Hulbert (1955) studied variability in plants of cheatgrass grown from seed collected in 10 states and two foreign countries. Differences observed among ecotypes were plant height, date of flowering, color, and pubescence of various plant parts.

Cheatgrass and soft chess are more widespread than medusahead and were introduced into the United States prior to 1860 (Robbins 1940). Probably both species were introduced several times, while medusahead appears to have been introduced once.

Most studies of ecotypic variation in grasses have considered perennials. McMillan (1959) studied clonal variations in 12 perennial grass species common throughout the Great Plains and Central Lowlands of North America. In a uniform garden at Lincoln, Nebraska, he demonstrated heredity and selected fitness to the clones' original environments as expressed in many phenological aspects. Plants from different geographical locations developed at different rates and at different times. McMillan reviewed his earlier work and other similar work on grasses of the mid-continental grassland. The work of Olmsted (1944) on daylength ecotypes in *Bouteloua curtipendula* (Michx.) Torr. is well known. With respect to flowering and vegetative responses, strains from southern latitudes are primarily short-day plants, whereas strains from northern latitudes are long-day plants. Cornelius (1947) studied growth and adaptation variations among 16 different seed sources of *Andropogon scoparius* Michx. (=*Schizachyrium scoparium* (Michx.) Nash), and also reviewed older work on hereditary variations of Great Plains grasses. Anderson and Aldous (1938) showed that the greatest variation among collections of *Andropogon scoparius* was between samples collected from regions great distances apart and subject to different environmental conditions. Similar variation correlated with geographical origin of the seed was shown for *Bouteloua curtipendula* by Hopkins (1941), for *B. gracilis* (H.B.K.) Lag. ex Steud. by Riegel (1940), and for *Andropogon hallii* Hack. by Kneebone (1958). Other data on variation in grasses outside the Great Plains includes a study of progenies of 800 collections of *Poa pratensia* L. from 27 states in which Smith, Nielsen, and Ahlgren (1946) observed ecotypic variation in relative vigor, disease resistance, uniformity, number and size of culms, plant height, and earliness of maturity. Progenies from seed collected in the western uplands had the highest frequency of ecotypes. Bohmont and Lang (1957) found palatability differences and morphological variation in *Oryzopsis hymenoides* (Roem. & Schult) Ricker. *Deschampsia caespitosa* (L.) Beauv. ecotypes were described by Lawrence (1945). The ecotypes within *Deschampsia caespitosa* could not be brought into any relationship with recognizable taxonomic entities (Lawrence 1945; Hulten 1950: 1706).

Selection of ecotypes in response to grazing is pertinent to the present study. Gregor and Sansome (1927) showed that several years of close grazing selected prostrate growth habits in a number of pasture plants. Stapledon (1928) demonstrated a similar selection in *Dactylis glomerata* L.

Numerous garden studies have been conducted to determine the variation existing within plant species. In a garden with uniform environment genetic differences between plants persist and can thus be separated from habitat modifications. DeCandolle appreciated this method; Jordan used it to study hereditary variation within many Linnaean species of the French flora as Heslop-Harrison (1953:46) pointed out. Kerner von Marilaun (1895:507-14) in 1875-80, before the beginning of modern ecology, found that differences between plants occupying very different habitats in the eastern Alps were hereditary at any of several sites (gardens). Kerner thus anticipated the conclusions later reached in Turesson's (1922a, b, 1925, 1926, 1931) experimental taxonomic investigations of ecotypic adaptations of plants to habitats. Clausen, Keck, and Hiesey (1940, 1948) extended, amplified, and strengthened the study of ecotypes with their work in western North America. Plant species found in a wide variety of habitats, particularly those species differentiated by regionally expressed and geographically conditioned differences in climate, frequently consist of numerous ecotypes. The ecotypes are genotypical responses and adaptations to a particular habitat.

Methods

Medusahead seed was collected from 13 locations in California, Oregon, Washington, and Idaho in August 1959. The locations extend north to south over 11° of latitude or 900 miles, and in altitude from 175 feet (50 m) in Solano County, California, to 4,365 feet (1,330 m) in Modoc County, California (Table I, Fig. 1). Soil samples were obtained and particle size distribution and textural classification was determined

TABLE I. Location, elevation, and climatological data[1] for each medusahead seed source

Ident. No.	Seed source (state and county)	Collection area	Elevation (feet)	Mean annual temperature (°C)	Mean annual precipitation (inches)
1.	California—Santa Barbara	Los Padres National Forest, Potrero Seco	2,100	12.5	25.0
2.	California—Stanislaus	Orvis Ranch, 9 miles east of Farmington	215	13.0	13.7
3.	California—Solano	Shellhammer Ranch, 4 miles northeast of Vacaville	175	16.5	22.3
4.	California—Mendocino	Potter Valley, Fritsche Bros. Ranch	1,014	16.0	43.7
5.	California—Modoc	Mackey Ranch, 15 miles south of Canby	4,365	8.5	12.8
6.	Oregon—Douglas	5 miles north of Roseburg	505	11.5	25.9
7.	Oregon—Benton	Corvallis, Oregon State College hill pasture	225	11.5	33.2
8.	Oregon—Jackson	Ireland Ranch, 2 miles northeast of Ashland	1,750	11.0	20.1
9.	Idaho—Gem 1	5 miles north of Emmett in association with *Artemisia tridentata* Nutt.	2,500	10.5	12.1
10.	Idaho—Gem 2	15 miles north of Emmett in association with *Artemisia arbuscula* Nutt.	3,000	9.5	15.0
11.	Idaho—Gem 3	20 miles north of Emmett, Crane Flat, on *Artemisia tridentata* site	2,800	10.0	14.0
12.	Idaho—Nez Perce	Breaks of Clearwater River	1,413	11.0	16.1
13.	Washington—Whitman	Steptoe Butte	1,955	9.0	21.1

[1] U. S. Department of Commerce. Climatological data. Annual Summary 1959.

TABLE II. Textural classification of soils from medusahead seed locations in California, Idaho, and Washington

Seed source (state and county)	SOIL DEPTH (inches)			
	0-6	9-12	12-24	24-36
California—Santa Barbara	—	Loam	Loam	Sandy clay loam
California—Stanislaus	—	Clay	Clay	—
California—Solano	—	Clay loam	Clay loam	Sandy clay loam
California—Mendocino	Clay loam	—	Clay	Clay
California—Modoc	—	Clay	Sandy clay loam	Clay loam
Oregon—Benton	Clay loam	Clay	Clay loam	Sandy clay loam
Oregon—Douglas	—	Clay	Clay	Clay loam
Oregon—Jackson	—	Clay	Clay	Clay
Idaho—Gem, site 1	Clay	Clay	Clay	—
Idaho—Gem, site 2	Loam	Clay	—	—
Idaho—Gem, site 3	Loam	Loam	Clay loam	—
Idaho—Nez Perce	—	Silty clay loam	Silty clay loam	Silty clay loam
Washington—Whitman	Silty clay loam	Silty clay loam	Silty clay loam	Silty clay loam

(Table II). All profiles had at least one horizon with a large proportion of clay.

Seed was removed from the heads by passing the plant material through a hammermill with ¼-inch screen. The seed was separated from the chaff and after each batch was cleaned, the seed cleaner was cleaned to avoid mixing seed from the different locations. Three replications of 50 seeds each from the 13 collections were placed in a germinator equipped with automatic temperature and light control. Germination temperature was 20° to 22° C. with alternating 12 hours light and 12 darkness. Seeds were placed on sterilized filter paper in three ¼-inch-diameter clear plastic Petri dishes and kept moist with tap water. Germination counts were made every 12 hours until germination was completed. Results are expressed in two ways: 1) percentage of seed germinated, and 2) percentage of live seed germinated in each 12-hour period. The latter measurement enabled a direct comparison of germination speed for each location since it was based on live seed only.

Rates of root elongation were studied in the greenhouse and growth chamber. Seed from locations with extremes of moisture and latitude were used. The collection locations used were Santa Barbara County, California; Whitman County, Washington; Modoc County, California; and Benton County, Oregon. These locations represent the southernmost, northernmost, driest,

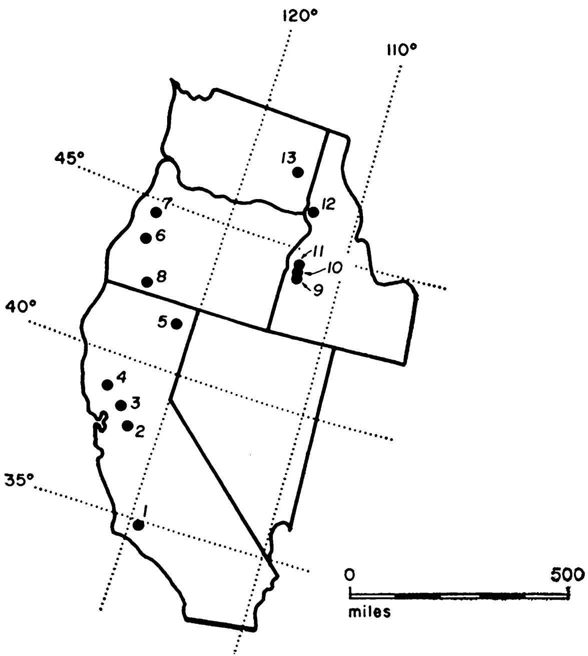

Fig. 1. Medusahead seed collection sites in the Western States. Each dot represents a location from which medusahead seed was collected in the summer of 1959. The numbers identify the seed source as shown in Table I.

and wettest collection areas of medusahead growth, respectively. Glass cylinders 2 inches (5 cm) in diameter and 12 inches (30 cm) long were filled with fine sandy loam screened through a ⅛-inch wire mesh. Compaction which might affect uniform root growth was avoided. Seeds from four locations, replicated four times with three seeds per replicate were placed ½ inch apart in the soil next to the side of the cylinders. The soil was wet to field capacity by adding a calculated volume of water prior to planting of seed, and no additional water was added. Black paper around each cylinder eliminated light. Cylinders were placed in a rack which tilted them at a 30° angle. The temperature in the greenhouse varied from a nighttime low of 20° C to a daytime high of 24° C, and relative humidity varied from 36 to 80%. The trial began on December 2, 1959, when daylength is nearly 10 hours at Davis, California. Root elongation was measured by marking the daily growth increment on the glass as the roots grew downward along the side of the cylinder.

Identical procedures were followed in the study of root elongation in a growth chamber. The temperature in the growth chamber was 11° C and the relative humidity varied from 38 to 75%. A photoperiod of 12 hours was supplied by fluorescent and incandescent lamps yielding 1,100 ft-c at plant height.

For the uniform garden study, seed was planted September 28, 1959, at a uniform rate with a funnel-type garden planter in 10-foot (3 m) rows 2 feet (0.6 m) apart on the agronomy farm of the University of California at Davis. The 13-seed collections were replicated five times in a randomized block design.

Three annual grasses, which are often associated with medusahead in many locations, were compared with medusahead in their phenology. They were soft chess, cheatgrass, and goatgrass (*Aegilops triuncialis* L.). The cheatgrass seed was collected near Boise, Idaho, the goatgrass seed on the Orvis Ranch, Stanislaus County, California, and the soft chess seed was from a commercial source in California. Seed of all three species was planted at the same time and by the same method as medusahead seed.

Seed from collections of medusahead (*Taeniatherum asperum* and *T. crinitum*) from Greece and Turkey were also planted near the western U. S. collections. Phenology was recorded for comparison with the United States medusahead plants. The habitats of the Eurasiatic plants are characterized in Table III.

Precipitation in 1959 at Davis, California, was 12.9 inches (328 mm) and the mean temperature was 16° C. The elevation at Davis is 51 feet (16 m) above sea level, and the soil of the uniform garden is a Yolo fine sandy loam, a fertile alluvial soil.

Field observations recorded for the U. S. medusahead plants were heading dates, plant heights, maturation dates, coloration of plant parts, morphological appearance, and seed shattering. A plant was considered to be headed when the inflorescence of one or more culms was completely emerged from the sheath. In addition, a row was recorded as headed when at least 10 culms for each foot of the 10-foot row were headed. These criteria allowed an estimate of heading variability within rows.

Plant height from each collection area was measured just before maturity was reached. The tallest culm (including the head) was measured at each intersecting foot of the 10-foot row, resulting in 50 measured heights for plants from each collection. Mean heights for each replicate were analyzed for variability.

The same procedures used in measuring heading dates were followed in establishing maturity dates. A plant was considered mature when the seeds were indurate and all other parts were brown and dry.

Plant weights were recorded to provide a basis for evaluation of vigor. Five feet of each row

TABLE III. Habitats of the medusahead of Eurasiatic origin grown at Davis, California

Species	Geographical source of seed	Associated plants	Soil description
Taeniatherum asperum	Turkey, coastal Anatolia, 34 miles west of Izmit in run-down vineyard	*Olea europaea* L. *Centaurea solstitialis* L. *Cichorium intybus* L. *Brachypodium distachyon* (L.) Beauv. *Dactylis glomerata* L. *Aegilops ovata* L. *Hordeum bulbosum* L.	Alluvial, red, loamy clay
T. asperum	Greece, 20 km west of Alexandropolis, 170 m elevation	*Brachypodium distachyon* (L.) Beauv. *Triticum villosum* (L.) M. Bieb. *Eryngium campestre* L. *Bromus squarrosus* L. *Hordeum bulbosum* L. *Medicago* cf. *hispida* Gaertn. *Cynodon dactylon* (L.) Pers. *Centaurea solstitialis* L.	Black, from basic igenous breccia, clayey
T. crinitum	Greece, just over the first pass north of Lamiz, 760 m elevation	*Quercus coccifera* L. *Prunus* cf. *webbii* Vierh. Bushes with annuals in openings including *T. crinitum* and *asperum* (also in bushes) *Aegilops ovata* L. *A. triuncialis* L. *Poa bulbosa* L. *Cynosurus echinatus* L.	Dark, purple-red, from olivine basalt, clayey
T. crinitum	Turkey, just west of Amasya, near river, 465 m elevation	*Bromus danthoniae* Trin. *Cynodon dactylon* (L.) Pers. *Paliurus aculeatus* Lam. = *Pispina-christi* Mill. *Onopordon* sp. *Althaea* sp.	Alluvium from igneous rock, loamy clay
T. crinitum	Turkey, Ankara reservoir, 18 km northwest of the city, 1000m elevation. Ungrazed.	*Eryngium campestre* L. *Thymus squarrosus* Fisch. & May. *Aegilops ovata* L. *Artemisia fragrans* Willd. *Bromus tectorum* L. *Phlomis herb-venti* L. *Festuca valesiaca Schleich.* ex Gaudin *Xeranthemum annuum* L. *Stipa lagascae* Roem. & Schult.	Residual from shales and sandstones, loamy clay

were clipped at ½-inch stubble height after maturity but before seeds dropped.

Data were subjected to analysis of variance and Duncan's multiple range test was applied to all data having a significant F-test (LeClerg 1957).

To determine whether medusahead is self-fertile, individual plants were transplanted to 12-inch pots prior to anthesis. The plants were isolated by placing the pots in two separate greenhouses and also outside the greenhouse.

RESULTS

Germination studies

Total germination percentages among the 13 seed collections varied from 97%, the highest, for seed from Nez Perce County, Idaho, to 52%, the lowest, for seed from Santa Barbara County, California (Table IV). Mendocino County, California seed had 91% germination while the remainder of the locations ranged from 55 to 76%. In previous work medusahead seed was found to have approximately a 3-month dormancy period; Laude (1956) also found a dormancy period. Such large differences in germination, however, cannot be explained by differences in dormancy since the seed used was mature by July, collected in August, and not germinated until November. Thus ample time was allowed for dormancy to be broken. Care was used in selecting only plump seed for germination. The seed which did not germinate became soft or moldy, indicating it was not viable. Environmental conditions at some of the collection areas may have been detrimental to production of a high percentage of viable seed in 1959. Physiological requirements met in each respective environment may not have been provided by the germination technique used. There is no evidence of any clinal relationship between

TABLE IV. Percentage of live seed germinating within 36 hours and total germination in 2 weeks

Seed source (state and county)	PERCENTAGE GERMINATION[1]	
	36 hours	Total
Idaho—Nez Perce	80	97 ± 2.4
California—Mendocino	62	91 ± 4.5
Idaho—Gem, site 2	10	76 ± 2.6
Oregon—Benton	49	75 ± 3.1
Washington—Whitman	27	75 ± 3.5
Idaho—Gem, site 3	12	65 ± 10.0
California—Solano	25	63 ± 14.6
Idaho—Gem, site 1	33	61 ± 6.1
California—Modoc	16	58 ± 10.0
Oregon—Jackson	8	57 ± 5.2
Oregon—Douglas	26	55 ± 5.5
California—Santa Barbara	41	52 ± 4.9

[1] Each value is a mean of three replications of 50 seeds each.

total germination and the environmental extremes of latitude or precipitation.

Large differences in rate of seed germination were found to exist (Figs. 2, 3, 4). High germination percentages within 36 hours in seed from Nez Perce County, Idaho; Benton County, Oregon; and Mendocino County, California, were

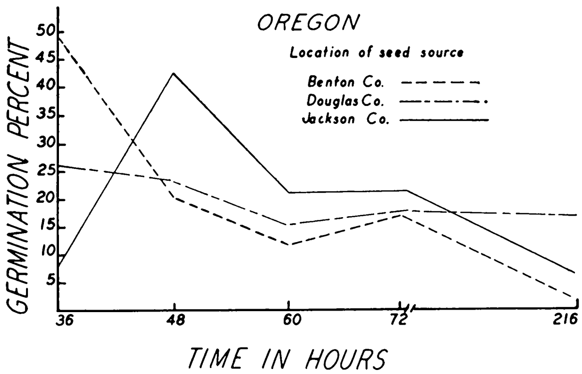

FIG. 2. Percentage germination at 12-hour intervals for seed collected from three locations in Oregon.

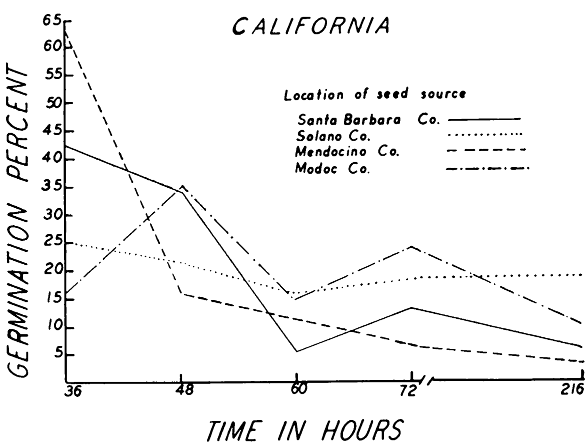

FIG. 3. Percentage germination at 12-hour intervals for seed collected from four locations in California.

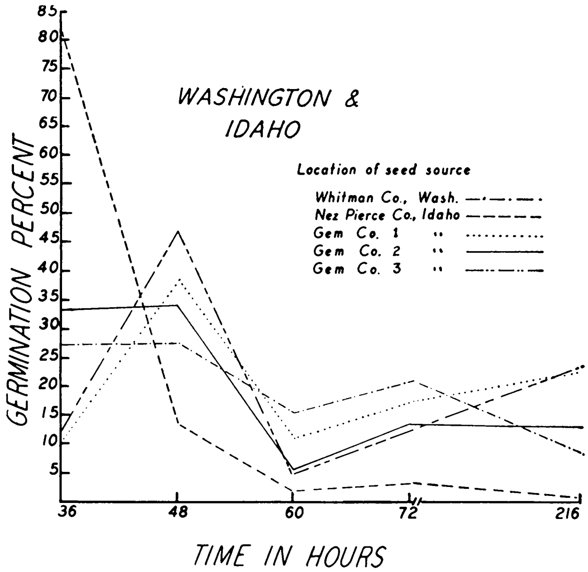

FIG. 4. Percentage germination at 12-hour intervals for seed collected from four locations in Idaho and one location in Washington.

significantly different (at the 5% level) from all other seed source locations within the same period. Seed from Jackson County, Oregon, and Gem County, Idaho, did not reach a germination peak until 48 hours. Seed from Solano County, California, and Douglas County, Oregon, had no clearly defined peaks of germination but proceeded at rather uniform rates. Reasons for the observed differences are not clear. Several seed sources with a high total percentage of germination also had a relatively high rate of germination within 36 hours (Table IV), but not all seed showed this relationship. For example, seed from Douglas County, Oregon, had a total germination of 55% and 36-hour rate of 26%, while Jackson County, Oregon, seed had 57% total germination and a 36-hour rate of 8%. High total germination and rate of germination do not necessarily coincide. There seems to be a relationship, however, between rate of germination and annual precipitation. For example, 36-hour rates of germination for seed from Benton, Douglas, and Jackson Counties, Oregon, were 49, 26, and 8%, respectively (Fig. 3), and in the same order these locations receive 33.2, 25.9, and 20.1 inches (840, 660, and 510 mm) of annual precipitation. The same general relationship is also seen in California seed locations. Seed from Mendocino County, California, had the highest 36-hour rate of germination followed by Santa Barbara, Solano, and Modoc Counties. Annual precipitation decreases in the same order as rate of seed germination. Similar relationships are shown by seed from Washington and Idaho locations. The two lowest rates of germination are shown in seed from locations 1 and 2 in Gem County, Idaho, which had 12.1 and 14.0 inches (310 and 355 mm) of precipitation, respectively. The relationship between relatively high germination rate and relatively high annual precipitation and vice versa, seems quite apparent. It is possible that a slow rate of germination has some adaptive value for locations with low or erratic precipitation. It is a general rule that low precipitation is also more erratic than high precipitation.

Root elongation

Root elongation in the greenhouse environment (20° C) was most rapid in plants from Whitman County, Washington, and slowest in plants from Benton County, Oregon. Differences in elongation rates were significant at the 5% level. Plants from the two California counties (Modoc and Santa Barbara) were intermediate in root elongation (Fig. 5). Plants from Whitman County, Washington, required 16 days for roots to reach a 26-cm depth as compared to 22 days for roots of plants from Benton County, Oregon. In the cool environment of the growth chamber (11° C) root elongation to a 26-cm depth required about 3 days more than in the greenhouse trials. Roots of plants from Santa Barbara County, California, and Whitman County, Washington, required significantly fewer days to elongate 26 cm (19 and 21 days, respectively) than roots of plants from Modoc County, California, and Benton County, Oregon (24 and 25 days, respectively) (Fig. 6).

Medusahead plants from Benton County, Oregon, the location with the greatest amount of precipitation where rapid root elongation would not be critical, were slowest in developing root systems. Plants from Whitman County, Washington, the northernmost seed collection location and an area also subject to cold winters, generally had the highest rate of root elongation.

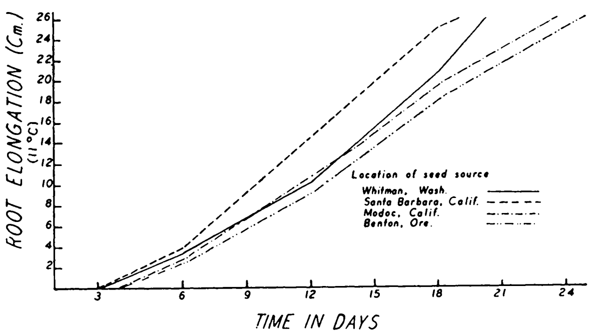

FIG. 5. Rate of root elongation recorded in the greenhouse (22° C).

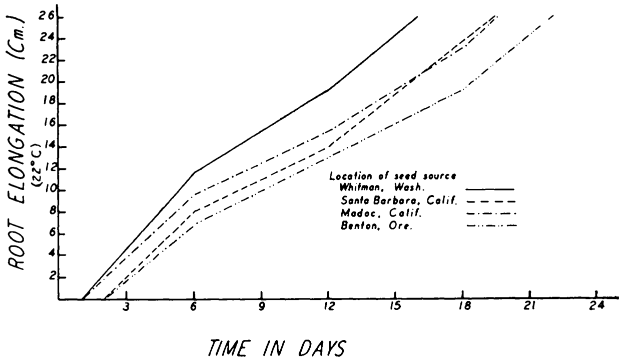

FIG. 6. Rate of root elongation recorded in the growth chamber (11° C).

Uniform garden study

A range of variability in heading dates of 38 days was quite noticeable in the field (Fig. 7). Plants from Stanislaus County, California, were headed by April 6, 1960, and plants from Benton County, Oregon, were not headed until May 13. However, there was a high degree of uniformity among plants from each collection. There is no orderly pattern of heading in relation to latitude, nor is there any trend in earliness of heading from west to east as found by McMillan (1956, 1959) in Nebraska. Although McMillan described neither the environments nor the plant communities where his plants were collected, it is probable that he had an environmental gradient from dry to moist going from west to east. Our stations, however, show no such simple environmental gradients. The climatic patterns, especially in the late winter and spring months, which prevail in each environment may have affected selection of plants which are better adapted to the seasonal rhythm of the various collection areas. For example, precipitation is relatively low and temperatures are relatively high during spring months in the Stanis-

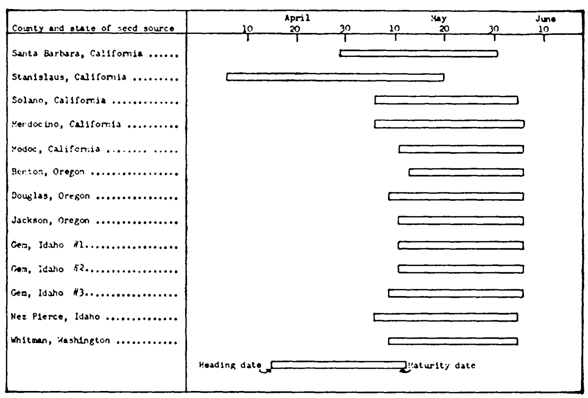

FIG. 7. Heading and maturity dates of plants grown in a uniform garden at Davis, California. Seeds were planted September 28, 1959.

laus County, California, area in comparison to the same climatic factors and season in the Benton County, Oregon, area.

Variability in date of maturation was negligible except for plants from Santa Barbara and Stanislaus Counties, California (Fig. 7). Unseasonally hot weather from June 1 to 7, 1960, with hot dry winds and temperatures at Davis from 37° to 42° C, probably helped to mask differences in maturity which were evident prior to these extreme weather conditions.

Cheatgrass was completely headed by March 14 and mature by May 14, 1960. Soft chess was not headed until March 22 and reached maturity by May 16, 1960. Goatgrass was headed by May 9 and mature by June 6, 1960, which is almost parallel in phenology to medusahead collected from Modoc County, California, Jackson County, Oregon, and Gem (sites 1 and 2) County, Idaho.

Taeniatherum asperum and *T. crinitum* from Greece and Turkey (Table III) headed by May 16 and matured by June 20, 1960, while *T. asperum* from near Izmit in Turkey failed to head. When medusahead plants from the U. S. are grown continuously in the warm greenhouse (17°-22° C), seeds fail to develop just as in *T. asperum* from near Izmit, Turkey, when it was grown in the field (Major 1958). Evidently temperatures at Davis, California, are not low enough to induce heading in medusahead from Izmit, Turkey. The variability in heading, shown by medusahead from the two foreign locations, indicates that *Taeniatherum* as a whole has an even wider range of environmental adaptability than do its representatives now in the U. S.

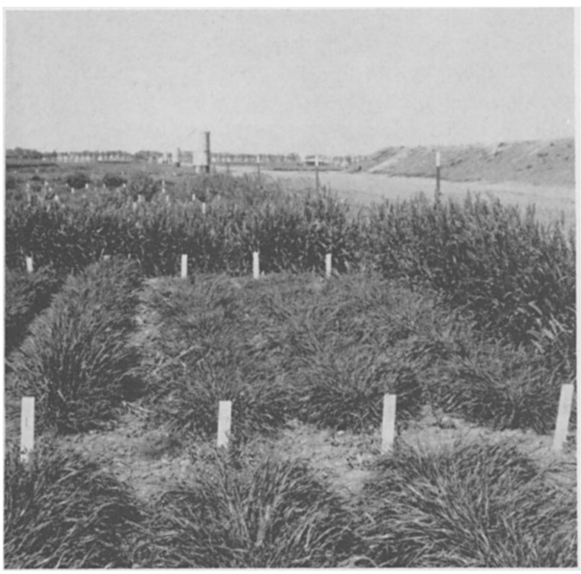

FIG. 8. Variability in height prior to heading as shown by plants from Santa Barbara County, California, at the extreme left, behind the stake marked 1, when grown at Davis, California.

FIG. 9. Plants from Santa Barbara County, California, are heading (stake 1) and are taller than plants from the other two locations when grown at Davis, California.

Variability in plant height was quite apparent before (Fig. 8) and after (Fig. 9) plants headed. Plants from Stanislaus County, California, (shortest) had a mean height of 20 inches (505 mm), while Santa Barbara County, California, plants (tallest) had a mean height of 26 inches (671 mm) (Table V). There is no apparent pattern of height expression relative to geographic location, environmental conditions, or phenology. Heights attained at the Agronomy Farm at Davis, California, are not necessarily similar to those of the parent plants in their respective environments.

Mean weights of plants did not differ signifi-

TABLE V. Mean heights of plants and significance of differences

Seed source (state and county)	Mean height (mm)	Significance[1]
California—Stanislaus	505	
Oregon—Benton	551	
Washington—Whitman	553	
Idaho—Gem 2	561	
California—Mendocino	563	
California—Modoc	566	
Oregon—Jackson	571	
Oregon—Douglas	602	
California—Solano	602	
Idaho—Gem 3	612	
Idaho—Nez Perce	614	
Idaho—Gem 1	635	
California—Santa Barbara	671	

[1] Any two means not included by the same line are significantly different at the 5% level.

cantly despite height differences. Possibly the shorter plants had more tillers than the taller plants, which tended to equalize plant weights. Tiller counts were not recorded since individual plants within the rows tillered profusely and could not be clearly separated from each other. Seeds were sown close together.

No measurable amount of variability was apparent in pubescence of plant parts or head and awn length among plants from the 13 locations. Leaf width and length was quite uniform throughout. Coloration was the most noticeable difference. A very evident reddish color was observed in plants from Santa Barbara County, California, in January after a week of temperatures ranging from —2° to 5° C. Plants from other locations did not change color. When temperatures became warmer, the reddish coloration disappeared. Plants from Modoc County, California, and Benton County, Oregon, exhibited a blue-green coloration in April which remained until maturity approached, and all other plants were darker green throughout the growing season. After maturity plants were light straw-colored in all instances except one. Plants from Stanislaus County, California, retained a definite purplish cast, particularly the heads.

In plants from two locations, extreme differences were seen in the amount and earliness of seed shattering from the heads. Plants from Santa Barbara County, California, which had matured by May 29, had more than 75% of the seed shattered from the head by June 5, 1960. On the other hand, plants from Stanislaus County, California, had matured by May 20, but had undergone very little shattering even as late as July 15, 1960. Differences in degree of shattering among plants of the same species have been reported by others. Baltensperger and Kalton (1959) reported considerable variation of shattering in 12 clonal selections of reed canarygrass (*Phalaris arundinacea* L.). The shattering pattern of medusahead seed heads was the same for plants from all locations. Seed loss began at the apex of the inflorescence and proceeded in an orderly fashion downward to the base.

Evidence that medusahead is self-fertile was the production of viable seeds from isolated plants grown in pots in and out of the isolation greenhouse. Seeds were well-filled at the time of maturity on July 15, 1960, and seed production was not materially reduced under isolation. Germination was near 90%.

Further evidence of ecotypic variation in medusahead might result from measurements of number of tillers per plant, weight and number of seeds per head, number of heads per plant, and other quantitative and/or qualitative measurements.

Discussion

From comparison of plant responses under uniform conditions it may be concluded that ecotypes exist in the medusahead population on western rangelands. These ecotypes were differentiated mostly on phenological grounds. Other physiological attributes which may determine the success of medusahead in its particular environments, such as frost hardiness, response to soil-moisture stress, palatability to livestock, soil-mineral nutrition, especially in relation to leached and unleached soils, were not investigated. The characteristics chosen for investigation were conservative ones. Therefore, if they show ecotypic differentiation, other characteristics may also be expected to do so.

Soils of the 13 seed-collection sites used in this study all had a high clay content in at least one horizon. Mallory (1960) observed a relation between the occurrence of medusahead and clay soils in the soil-vegetation survey of Tehama and Humboldt Counties of California. Soils high in clay will apparently be most subject to future medusahead invasion.

There seems to be a relation between rate of medusahead seed germination and mean annual precipitation. Other relationships between environmental conditions and ecotypic variations in medusahead were not observed. Medusahead in all its variability appears to be a better indicator of habitat characteristic than most environmental measurements made to date.

In most biosystematic studies it has been supposed that any plant population sampled for ecotypes is in equilibrium with its environment. Such equilibrium cannot be assumed for the American population of medusahead, for in many of the 13 locations sampled medusahead is a recent invader. Insufficient time has elapsed in some locations for true ecotypes, which reflect a genotypical response to a habitat, to be selected. Instead some of the genotypically different forms discovered by means of the uniform garden study can best be named geographic races. The early maturing Stanislaus County plants and the Santa Barbara County plants that developed a reddish color during a low-temperature period are good examples. We have no adequate ecological explanation for the two response patterns.

Four factors appear to have had importance in producing the present status of medusahead variation. We emphasize that seed sources have been shown to differ in several characteristics when plants were grown from these seeds all under uniform conditions. First, medusahead is an annual with a high reproductive capacity so evolution can proceed rapidly. Second, medusahead does not have to find a niche in an almost closed community as do the seedlings of many perennial plants. Communities of annual plants are extraordinarily open, as Went and his associates (Juhren, Went, and Phillips 1956) have shown for desert vegetation of southern California, and as Stewart and Hull (1949) have shown for stands of *Bromus tectorum*. Third, medusahead was introduced into a biological near-vacuum, a range vegetation which was depleted or was actively being destroyed. Medusahead had almost unlimited opportunities for increase and has therefore spread widely.

Fourth, it is assumed that American medusahead penetrated the migration barrier between the Old and the New World in very limited numbers. It thus came without many of its normal associates or competitors. Savile (1959) has recently emphasized the importance of such limited penetration of a migration barrier in evolution. Medusahead spread into a natural biological vacuum in the New World, and whatever biotic factors keep it in check in its homeland do not appear to operate on it in the western states. The biotic factors include not only diseases, insects, other animals, and other plants, but also other biotypes of medusahead itself. For example, only *Taeniatherum asperum* was introduced; *T. crinitum* was not. In Eurasia the distribution of these two species overlaps to some extent. There is some ecotypic specialization in the Eurasiatic *T. asperum* as compared to that introduced and evolved here.

Huffaker (1957) emphasized the importance of insects as part of the biocenose in controlling the abundance and competitive vigor of the plants. It is obvious that descriptions are needed of the biocenoses in which medusahead occurs not only naturally in its homeland but also as an introduced plant. Nowhere, from Morocco on the west to Anatolia on the east, was medusahead found by one of us (Major) in pure stands during 1959. Nearly pure stands do occur all too commonly in southern Idaho, in Oregon, and over many thousands of contiguous acres in California's foothills and Coast Ranges.

The great speed with which a probably single introduction of *Taeniatherum asperum* has evolved should be emphasized. In approximately 70 years genotypes have been produced differing in morphological and physiological characteristics. Some of the reasons for this rapid evolution have been outlined above.

The consequences of ecotypic and geographic variability in medusahead are considerable for range management, weed control, and study of the plant. In work on the biology of medusahead results can be expected to differ with seed source. Unfortunately, plant taxonomy as yet does not offer a means of identifying and naming such variations (Major 1961). The importance of such variations must be related to the scope and purpose of each study. Finally, management of medusahead-infested rangelands can differ according to the race of medusahead involved as well as with such commonly recognized factors as differences in associated species. Measures for control of the weed may also differ between seed sources.

Summary

An infestation of western rangelands by the aggressive weedy, annual grass, medusahead (*Taeniatherum asperum*) (*Elymus caput-medusae* L. of American authors), was first recorded in the U. S. in 1887 near Roseburg, Oregon, and now extends over parts of Oregon, California, Idaho, and Washington.

Medusahead seeds were collected from 13 locations in California, Oregon, Washington, and Idaho, and planted in a uniform garden at Davis, California. Detailed notes were taken on plant development, dates of floral emergence, plant height and weight, and seed maturity. In laboratory and greenhouse studies, seed germination, rate of germination, and rate of root elongation were observed. More limited studies were conducted on medusahead from Turkey and Greece. Soft chess, cheatgrass, and goatgrass were grown and compared to medusahead in phenology.

Significant differences in percentage germination, speed of germination, rate of root growth, plant height, and phenology appear in comparisons of the collections. No other measurable differences in morphology were encountered, although slight variations in plant color were observed. Plants from two locations exhibited differences in the amount and earliness of seed shattering.

Seeds collected from locations with relatively low precipitation had the lowest germination percentages within 36 hours, while seeds from locations with relatively high precipitation had the highest germination percentages within 36 hours. There were apparently no environmental factors which correlated with total germination.

In a greenhouse study (22° C) root elongation

of plants from seed collected from Whitman County, Washington, was most rapid and that of plants from seed from Benton County, Oregon, was slowest. Plants from seeds collected from Santa Barbara and Modoc Counties, California, were intermediate in root elongation. In the growth chamber (11° C) plants from seeds from both Santa Barbara County, California, and Whitman County, Washington, had the most rapid root elongation. Modoc County, California, plants were intermediate in root elongation and Benton County, Oregon, plants were again the slowest in root elongation.

The time interval of heading between plants from Stanislaus County, California (earliest), and plants from Benton County, Oregon (latest), was 38 days, while the seed-maturity interval between plants from these two locations was 15 days.

The general problem of ecotypes and their relation to plant ecology is discussed.

References

Anderson, K., and A. E. Aldous. 1938. Improvement of *Andropogon scoparius* Michx., by breeding and selection. J. Am. Soc. Agron. **30**: 862-869.

Baltensperger, A. A., and R. R. Kalton. 1939. Variability in reed canarygrass, *Phalaris arundinacea* L. II. Seed shattering. J. Am. Soc. Agron. **51**: 37-38.

Bohmont, B. L., and R. Lang. 1957. Some variations in morphological characteristics and palatability among geographic strains of Indian ricegrass. J. Range Mgmt. **10**: 127-131.

Clausen, J., D. D. Keck, and W. M. Hiesey. 1940. Experimental studies on the nature of species: I. Effects of varied environments on western North American plants. Carnegie Inst. Wash. Publ. **520**, 452 p.

———. 1948. Experimental studies on the nature of species: III. Environmental responses of climatic races of Achillea. Carnegie Inst. Wash. Publ. 581, 129 p.

Cornelius, D. R. 1947. The effect of source of little bluestem grass seed on growth, adaptation, and use in revegetation seedings. J. Agron. Res. **74**: 133-143.

Gregor, J. W., and F. W. Sansome. 1927. Experiments on the genetics of wild populations. I. Grasses. J. Genetics **17**: 349-364.

Harberd, D. J. 1958. A spurious significance in genecological trials. Nature **181**: 138.

Heslop-Harrison, J. 1953. New concepts in flowering-plant taxonomy. Heinemann, London.

Hitchcock, A. S. 1950. Manual of the grasses of the United States. 2nd ed., rev. by Agnes Chase. U. S. Dept. Agr. Misc. Publ. **200**, 1051 pp.

Hopkins, H. H. 1941. Variations in the growth of side-oats grama grass at Hays, Kansas from seed produced in various parts of the Great Plains region. Trans. Kansas Acad. Sci. **44**: 86-95.

Huffaker, C. B. 1957. Fundamentals of biological control of weeds. Hilgardia **27**: 101-157.

Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual Bromegrasses. Ecol. Monographs **25**: 181-213.

Hulten, E. 1950. Flora of Alaska and Yukon. X. Lunds Univ. Arsskrift. N. F. 2, **46**: 1485-1902.

Juhren, M., F. W. Went, and E. A. Phillips. 1956. Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. Ecology **37**: 318-330.

Kerner von Marilaun, A. J. 1895. The natural history of plants. [Transl. by F. W. Oliver.] Blackie, London. 2 vols.

Kneebone, W. R. 1958. Heritabilities in sand bluestem (*Andropogon hallii* Hack.) as estimated from parental clones and their open-pollinated progenies. J. Agron. **50**: 459-461.

Knowles, P. F. 1943. Improving an annual bromegrass, *Bromus mollis* L., for range purposes. J. Am. Soc. Agron. **35**: 384-594.

Laude, H. M. 1956. Germination of freshly harvested seed of some western range species. J. Range Mgmt. **9**: 126-129.

Lawrence, W. E. 1945. Some ecotypic relations of *Deschampsia caespitosa*. Am. J. Botany **32**: 298-314.

LeClerg, E. L. 1957. Mean separation by the functional analysis of variance and multiple comparisons. U. S. Dept. Agr., Agr. Res. Serv. ARS **20-3**, 33 p.

Lusk, W. C., M. B. Jones, D. T. Torell, and C. M. McKell. 1961. Medusahead palatability. J. Range Mgmt. **14**: 248-251.

Major, J. 1958. Responses of medusahead (*Elymus caput-medusae* L.) to different planting dates. Research Progr. Rept., Reg. Comm. Western Weed control conf. **1958**: 29.

———. 1960. Medusahead—origin and current status. Proc. Calif. Sect. Am. Soc. Range Mgmt. Annual Meeting, Nov. 1960, Fresno, Calif. pp. 35-39.

———. 1961. Use in plant ecology of causation, physiology and definition of vegetation. Ecology **42**: 167-169.

Mallory, J. 1960. Soil relationships with medusahead. Proc. California Sect. Am. Soc. Range Mgt. Annual Meeting, Nov. 1960, Fresno, Calif. pp. 39-41.

McKell, C. M., J. Major, and E. R. Perrier. 1959. Annual range fertilization in relation to soil moisture depletion. J. Range Mgmt. **12**: 189-193.

McMillan, C. I. 1956. Nature of the plant community. I. Uniform garden and light period studies of 5 grass taxa in Nebraska. Ecology **37**: 330-340.

———. 1959. The role of ecotypic variation in the distribution of the central grassland of North America. Ecol. Monographs **29**: 285-308.

Olmsted, C. E. 1944. Growth and development in range grasses. IV. Photoperiodic responses in twelve geographic strains of side-oats grama. Botan. Gaz. **106**: 46-74.

Piper, C. V., and R. K. Beattie. 1914. Flora of southeastern Washington and adjacent Idaho. New Era Printing Co., Lancaster, Pa. 296 p.

Riegel, D. A. 1940. A study on the variations in the growth of blue grama grass from seed produced in various sections of the Great Plains region. Trans. Kansas Acad. Sci. **43**: 155-171.

Robbins, W. W. 1940. Alien plants growing without cultivation in California. Calif. Agr. Expt. Sta. Bull. **637**, 128 p.

Savile, D. B. O. 1959. Limited penetration of barriers as a factor in evolution. Evolution **13**: 333-343.

Sharp, and E. W. Tisdale. 1952. Medusahead, a problem on some Idaho ranges, a preliminary study. Univ. of Idaho Forest, Wildlife and Range Expt. Sta. Res. Note 3, 9 p.

Smith, D. C., E. L. Nielsen, and H. L. Ahlgren. 1946. Variation in ecotypes of *Poa pratensis*. Botan. Gaz. **108**: 143-166.

Stapledon, R. C. 1928. Cocksfoot grass (*Dactylis glomerata* L.) ecotypes in relation to the biotic factor. J. Ecology **16**: 71-104.

Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.)—an ecological intruder in southern Idaho. Ecology **30**: 58-74.

Turesson, G. 1922a.. The species and the variety as ecological units. Hereditas **3**: 100-113.

———. 1922b. The genotypical response of the plant species to the habitat. Hereditas **3**: 211-350.

———. 1925. The plant species in relation to habitat and climate, contributions to the knowledge of genecological units. Hereditas **6**: 147-236.

———. 1926. Die Bedeutung der Rassenökologie für die Systematik and Geographie der Pflanzen. Repert. Spec. Nov. Regni Veg. Beih. (Fedde) **41**: 15-37.

———. 1931. Geographic distribution of alpine ecotypes of some Eurasiatic plants. Hereditas **15**: 329-346.

PLANT COMMUNITIES OF THE GRAND CANYON AREA, ARIZONA

JOHN MERKLE
Flint Community Junior College, Flint, Michigan

INTRODUCTION

During the summers of 1949-55 ecological studies were made of the vegetation of Grand Canyon National Park, including both the South Rim and the North Rim as well as portions of the Kaibab National Forest. Reports on two of the communities have been published: the pinyon pine-juniper (Merkle 1952) and the spruce-fir (Merkle 1954). This paper defines three principal communities: (1) that dominated by ponderosa pine on the South and North Rims; (2) that dominated by white fir and ponderosa pine on the North Rim; and (3) the meadows of the higher parts of the North Rim. These communities are all within the limits of the montane forest which occurs in the Rocky Mountain region and on the east side of the Cascade and Sierra Nevada ranges from 4,000 to 7,000 ft in the north and from 6,000 to 9,000 ft in the south (Rydberg 1915, Shantz and Zon 1924, Weaver and Clements 1938, Daubenmire 1943, 1952, Oosting 1948, and Billings 1951). On the Coconino Plateau (South Rim) and the Kaibab Plateau (North Rim) this forest ranges from about 7,000 to 8,700 ft in altitude. The pinyon-juniper community occurs below 7,000 ft and the spruce-fir community above 8,700 ft. The meadows studied occur in shallow valleys on the Kaibab Plateau.

I wish to express appreciation to Mr. Louis Schellbach, Park Naturalist, and to Mr. E. T. Christensen, Naturalist in charge on the North Rim, for encouragement and time to pursue the field studies. Dr. T. H. Kearney and Dr. John T. Howell of the California Academy of Sciences assisted in plant identification. The responsibility for plant names used is mine. A grant from the Resa Fund of Sigma Xi defrayed the expenses for the forest studies. Grant No. 1464 from the Penrose Fund of the American Philosophical Society defrayed the cost of the meadow studies. The Flint Community Junior College Research Institute provided clerical assistance. My wife, Cherrie, helped in the field work. Nomenclature follows Kearney and Peebles (1960). Plant specimens are in the herbaria of Grand Canyon National Park and the California Academy of Sciences.

Comparable vegetation studies in the Grand Canyon area are limited. Best known is Pearson's classic work on the environmental factors, reproduction, succession, and physiological responses of ponderosa pine in central Arizona and New Mexico, published from 1913 to 1950. Rasmussen (1941) described the biotic communities of the Kaibab Plateau. Cooper (1960) recently completed an exhaustive study of the ponderosa pine forest of east central Arizona. He stressed vegetational changes that have taken place in these forests in the past 75-100 years, mostly under the influence of the white man.

Daubenmire (1952) described several plant communities of northern Idaho and adjacent Washington including four in which ponderosa pine is the dominant tree. These are *Pinus ponderosa* with (1) *Agropyron spicatum*, (2) *Purshia tridentata*, (3) *Symphoricarpos rivularis*, and (4) *Physocarpus malvaceus*. Weaver (1961) described one area of ponderosa pine east of the Cascade Mountains in Washington in which the dominant understory plants are pinegrass (*Cal-*