AN ANALYSIS OF ECOLOGICAL FACTORS LIMITING THE DISTRIBUTION OF A GROUP OF STIPA PULCHRA ASSOCIATIONS WITHIN THE FOOTHILL WOODLAND OF CALIFORNIA

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PREFACE

Native Californians and visitors alike, almost without exception consider the green and golden hills to represent the native grassland. It is now clear that what seems so much a part of the State, has been here no longer than the white man himself. Perhaps because of their limited economic importance today, little is known about the original grassland associations or their ecology.

The purpose of this study is to establish some of the factors of the environmental complex limiting the distribution of the originally dominant Stipa pulchra association. Towards this end a detailed field and laboratory analysis of the species and its surroundings has been completed. It is hoped that this information will aid future investigators in understanding the floral history of the region, and in managing a potentially valuable natural resource.

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L. Williams of the Soil Conservation Service, and J. Readio of Monterey Peninsula College provided information important in soil analysis. Dr. J. Davis of Hastings Reservation was most helpful in permitting the use of facilities and cumulative weather records. For permission to take samples and establish plots and transects on closed land, special gratitude is extended to Dr. J. Davis, Mr. E. E. Lowery and the Commanding General at Fort Ord. The tolerance of the Monterey Peninsula College Board of Trustees and Administration in permitting the establishment of experimental gardens and the use of laboratory facilities is acknowledged. A number of students have been most helpful in one aspect or another of the research. Special gratitude is due Joe Branco, Norma Mason and Ben Littlejohn. Financial support of parts of the program was provided through a series of three National Science Foundation Summer Fellowships and a Society of Sigma Xi Grant-in-Aid of Research. Finally, the help of my wife, Naeda must be noted, for without her day to day encouragement, this study could not have been completed.

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CHAPTER I

INTRODUCTION

The Valley Grassland Community is unique in California and perhaps in the world, in being composed almost entirely of exotic species. Though it has long been assumed that prior to European colonization the community was dominated by the endemic bunch grass *Stipa pulchra* Hitch., it is not a matter of historical record. Ecologists and agronomists alike have been intrigued by the processes that might bring about such a catastrophic change. Such being the case it is amazing to find no reports in the literature of serious attempts to analyze ecological factors which limit the distribution of the widely scattered relicts of this once more extensive perennial grassland. The problem has been interpreted, albeit somewhat subjectively, from at least four viewpoints. Though ranchers were well aware of the desirability of *Stipa pulchra* forage, and had watched its decline on their own ranges, Clements (1920) was the first to formally suggest that the bunchgrass relicts were remnants of climatically determined climax prairie, which had been almost entirely replaced by Mediterranean annuals as a result of overgrazing. Cooper (1922) in his analysis of the broad-sclerophyll vegetation, came to the conclusion that woody vegetation was climax in the coastal valleys and foothills, but had been locally replaced by grassland as a result of human disturbance. Shreve (1927) studied the Santa Lucia Range and came to the conclusion that grassland reflected either unusually deep soils or exposure to wind. Wells (1962) seems to have been the first to establish some sort of experimental basis for his conclusions. In his attempt to relate vegetation to geological substrata and fire he demonstrated that the problem was not so easily solved as his predecessors had supposed, and that grassland within the Central Coast Ranges is largely a result of disturbance by man through fire, overgrazing and wood cutting. All of these approaches are inadequate, for if change in the composition of the Valley Grassland does constitute an unsolved ecological problem, the solution can only lie in an understanding of the total environmental complex.

An understanding of the floral changes that have occured during the past 150 years demands an appreciation of the history of the California Floral Province (Howell, 1957). As it exists today it is botanically, physiographically, and climatically a distinct area, with the bulk of its species totally isolated by the Pacific Ocean, the mountains of southern Oregon, the montane axis from the

Sierra Nevada to the Sierra San Pedro Martir, and the desert of Baja California. Genetic and paleobotanical evidence suggests that the endemic species of the Valley Grassland are largely northern, and ultimately palearctic, in their affinities (Stebbins and Major, 1965). Stipa pulchra is presumed to have evolved from isolated steppe progenitors as the Mediterranean type climate slowly developed over the past million years or so. This adaptation did not include the tolerance to grazing pressure characteristic of steppes and prairies in other parts of the world, for through the present epoch at least, such animals have not been an important part of the California grassland ecosystem.

The impact of man has been only recently felt in this community. Though Indians have been present for at least 10,000 years, a great wealth of evidence indicates that their influence upon established communities was minimal (Sampson, 1944). With the colonization of Alta California by the Spanish during the latter part of the 18th century, profound changes took place (Burcham, 1961). The coastal and interior valleys provided such abundant grass and water that within 50 years much of the Valley Grassland was intensively grazed. The native bunchgrass, not being adapted to grazing, and at the same time being much preferred, was overutilized and declined rapidly. The Spanish, perhaps quite inadvertently, introduced a variety of Mediterranean annual forbs and grasses along with their livestock. These annuals, being preadapted to the California climate, and probably carrying the reservoir of heterozygosity and phenotypic plasticity characteristic of weedy species and crop-weed complexes (Harlan and de Wet, 1965) quickly replaced the declining endemics over most of their range, and today constitute what is known as the California Annual Type. In the hills near Monterey relicts of the *Stipa pulchra* association of the Valley Grassland survive and flourish. It has been the intent of this research to establish some of the factors in the environmental complex which control the present distribution of *Stipa pulchra*, and insofar as possible to relate these to the history of the whole community. While the results and conclusions must of necessity reflect the limited geographic scope of the investigation, they doubtless have relevance throughout the range of the species.

CHAPTER II

DESCRIPTION OF THE AREA

That limited portion of the central coast section of California chosen for this study is shown in Figure 1. Though Monterey was one of the first communities settled in California, and was the capitol under the Spanish and Mexicans and in the early days of U. S. occupancy, the rather rugged hills to the east and south were but little exploited until recent times. The "better" land was early awarded as land grants and almost immediately placed under intensive grazing pressure. Descriptions of the primeval vegetation are nonexistant, however it seems reasonable that *Stipa pulchra* and other palatable native perennial and annual grasses were quickly replaced by the Mediterranean annuals dominant today (Burcham, 1961). Because of this locally rugged topography, islands of native grasses which were not readily accessible to domestic grazing animals remain and can be approached over modern roads with no great difficulty. The data incorporated here were gathered at three such sites, and at the laboratories and experimental gardens of Monterey Peninsula College.

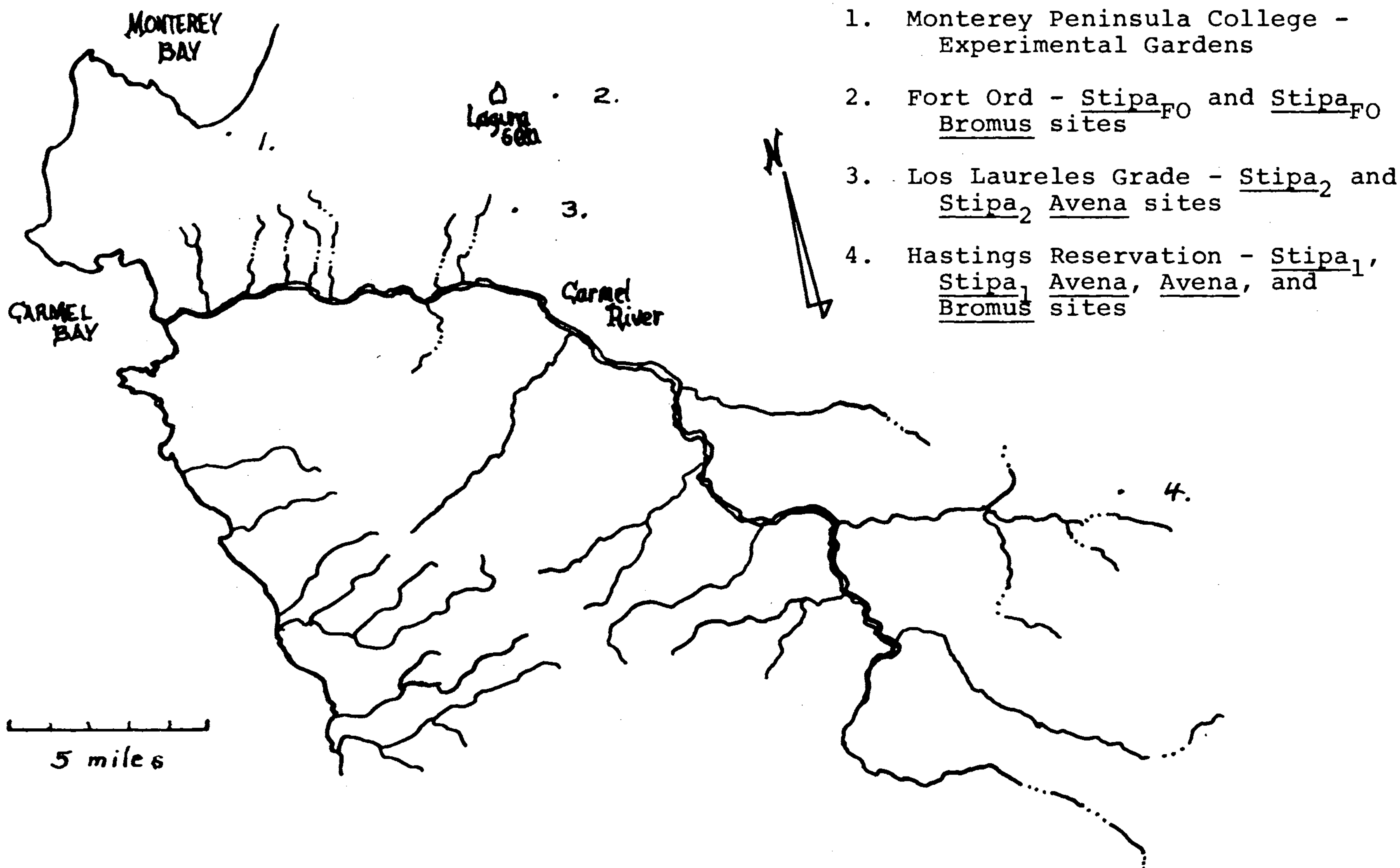

Figure 1. Location of Experimental Sites

Geology

Through most of recorded geologic history, the Coast Ranges and the intermontane valleys have been beneath the sea, or present only as an island archipelago (Taliaferro, 1943). The formations constituting the geologic column are Jurassic or younger. Those typical of the study area include: Jurassic Franciscan Sandstone, pre-Cretaceous Sur Series Metamorphics, the intruding Cretaceous Santa Lucia Granodiorite, and the Miocene Monterey Shale. Because this geologic province owes its origin to geosynclinal accumulation with its resultant compressive forces and elevation above the sea, the topography is dominated by folding and faulting. Though the initial elevation occured during the Cretaceous, periodic subsidence and re-elevation took place, culminating in the rapid mid-Pleistocene uplift which produced the present day relief. Along the coast and in the valleys are many well preserved marine and river terraces which are even more recent, and give evidence of continuing deformation. The great geologic complexity resulting from such a history has been clearly described in Fiedler's study of the Jamesburg Quadrangle (1944). It is thus not surprising that in walking through the countryside one passes quickly from one geologic formation to another.

Soil may be either transported or formed in place and is therefore even more variable than the rock upon which it rests. Though the soils are well known (Carpenter and Cosby, 1925) and are in the process of being resurveyed, published classifications are of limited utility in an area as diverse as the one here outlined.

Climate

The Central Coast Ranges exemplify a well-known climate (Dale, 1959), unique in the United States to the Pacific Southwest. The summer drought characteristic of this Mediterranean type climate results from the expansion of the Pacific High accompanied by the weakening and northward movement of the low, while the winter precipitation results from the retreat of the high far to the south of its summer position, allowing an influx of migratory storms from the Aleutian Low. While latitude, through fixing the amount of solar insolation, is the major climatic control over most of the surface of the earth, in California the Pacific Ocean and rugged topography exert equally important controls upon the large scale circulation, such that isotherms run mostly north-south instead of the expected east-west. Under general westerly to northwesterly air flow most of the year, the coastal regions have a maritime climate with relatively small diurnal and seasonal temperature ranges, mild winters, cool summers, and high relative humidities. The constancy of the summer high with its northwesterly winds together with the Coriolis force, causes the surface water along the coast to move toward the southwest. This in turn results in

TABLE I

MEAN RAINFALL AND TEMPERATURE DATA FROM TWO STATIONS IN THE STUDY AREA

	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June
HASTINGS - 28 years (mean yearly total - 20.23 inches precip.)												
Mean - °F	68.3	67.7	66.4	60.7	53.6	49.7	46.8	48.4	49.3	52.7	56.0	62.0
Mean Max.	87.4	86.4	84.0	77.6	68.3	61.9	59.7	60.5	62.3	66.9	71.3	79.4
Mean Min.	49.3	48.9	48.1	43.9	38.9	36.6	34.0	35.3	36.3	39.1	41.1	44.6
Maximum	111	109	110	105	94	94	84	85	85	91	99	109
Minimum	31	29	29	22	22	15	10	17	21	22	28	28
Precip. - inches	0	.10	.28	.79	1.93	3.78	3.91	3.72	3.18	1.88	.54	.12
MONTEREY - 42 years (mean yearly total - 16.38 inches precip.)												
Mean - °F	61.0	61.1	61.9	59.9	53.9	50.2	49.2	51.3	53.3	55.3	57.4	59.6
Mean Max.	69.4	69.4	71.8	69.2	65.3	60.7	59.0	60.9	63.1	64.6	66.1	68.4
Mean Min.	52.6	52.8	51.9	50.5	42.5	40.3	39.3	41.6	43.5	45.9	48.7	50.9
Maximum	98	89	101	94	95	89	80	87	86	92	93	94
Minimum	40	43	40	34	25	24	20	24	28	30	36	39
Precip. - inches 89 yrs.	.02	.02	.23	.61	1.46	3.13	3.53	2.84	2.71	1.22	.50	.11

POTENTIAL EVAPOTRANSPIRATION - mean

Hastings - 26.73 inches

Monterey - 27.09 inches

upwelling of deeper and colder water, and the formation of fog as the moist Pacific air masses drift over it and condense. This sea fog is carried inland by prevailing winds and has a profound effect on temperature and humidity throughout the study area.

With rainfall and natural plant growth occuring during the winter and spring, it is quite appropriate to think in terms of rain years rather than the calendar years which are the usual frame of reference for climatologists and botanists alike. Cumulative records provided by Hastings Reservation and extracted from U. S. Weather Bureau Climatic Summaries (1930, 1952, 1953-60) are compared in Table I. Though at first glance moisture stress through the growing season might seem quite different at the two stations, graphical determination of potential evapotranspiration by the Thornthwaite method (Palmer and Havens, 1958), indicates a remarkable similarity, with stress slightly higher at the cool summer station of Monterey. As illustrative of the pattern and variability of precipitation, data for Monterey are presented graphically in Figure 2.

Vegetation

The geologic and climatic diversity of the Central Coast Ranges is reflected in the many plant communities found there. Because of the unique character of the California Floral Province, systems of community classification devised for other parts of the country are of little

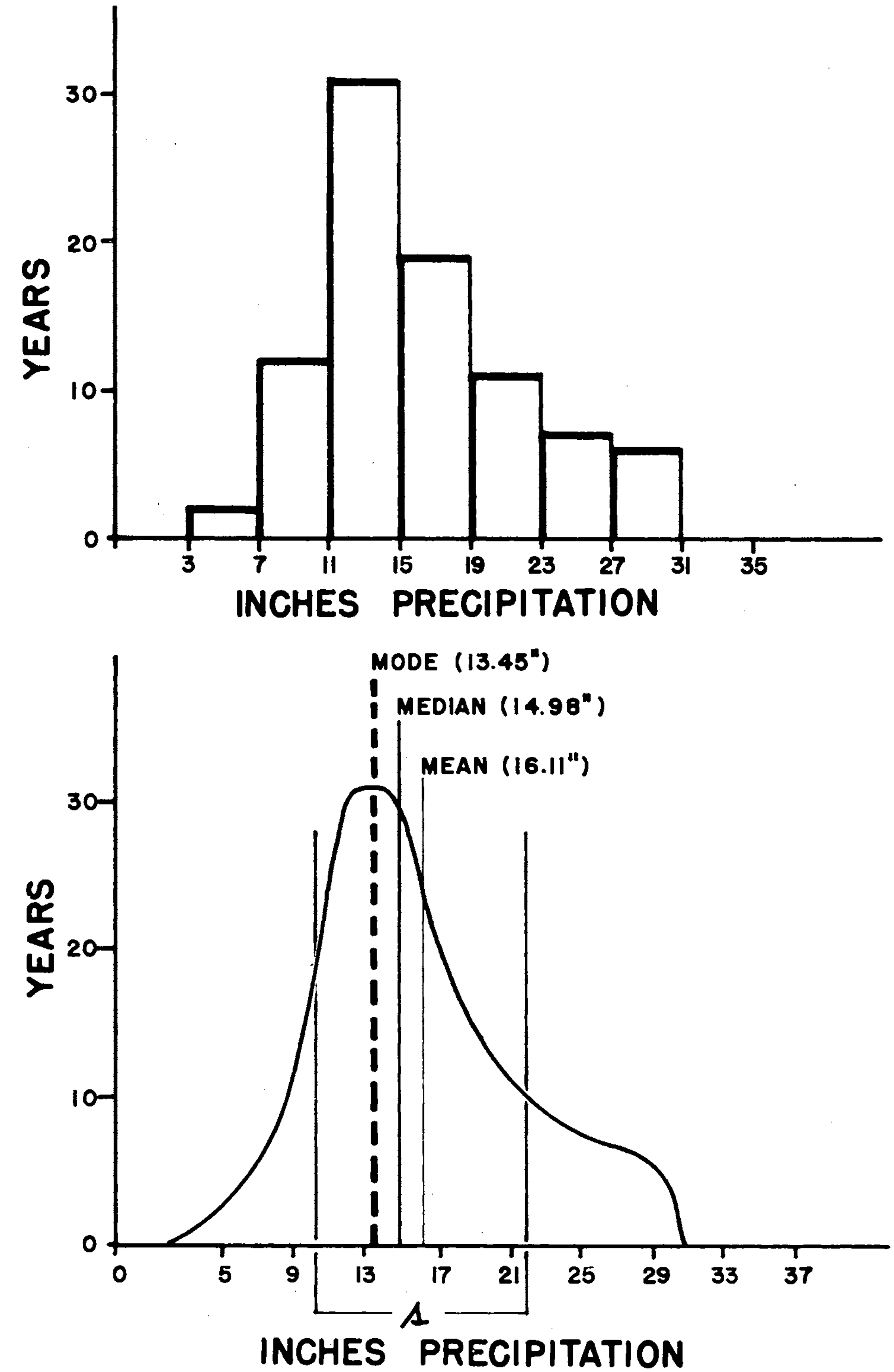

Figure 2. Precipitation at Monterey for 89 Years of Record

utility. Munz and Keck (1949) described the major vegetation types and plant communities of California with such clarity that their system has general acceptance and is the one employed in this study. Of the 29 communities they list, Valley Grassland, Foothill Woodland, and Chaparral are found in the immediate environs of the field sites. They describe them, in part, as follows:

Valley Grassland:
Average rainfall 6 to 20 inches, growing season 7 to 11 months, with 205 to 325 frost-free days; mean maximum summer temperatures 88° - 102°, mean winter minima 32° - 38° F. Subtropical type of open treeless grassland, with winter rain and hot dry summers; rich display of flowers in wet springs.

Foothill Woodland:
Average rainfall 15 to 40 inches, little or no fog; growing season 6 to 10 months, with 175 to 310 frost-free days; hot dry summers, with mean maximum temperatures 75° - 96°, and mean winter minima 29° - 42° F. Trees 15 to 70 feet tall, in dense or open woodland, with scattered brush and grassland between the trees. This composite community contains both the oak parklands of the valley floors and the digger pine woodland of the surrounding slopes.

Chaparral:
Average rainfall 14 to 25 inches; hot dry summers and cool winters; growing season 8 to 12 months, with 250 to 360 frost-free days; mean summer maximum temperatures 82° - 94°, mean winter minima 29° - 45° F.
A broad-leaved sclerophyll type vegetation, 3 to 6 or 10 feet high, and dense, often nearly impenetrable. Subject to fire following which many of the shrubs tend to stump-sprout.

Since these communities have a climatic rather than a purely edaphic basis, the great variations in microclimate characteristic of the topography lead to highly fragmented local populations.

This study is concerned with a mesic portion of the Valley Grassland as it comes in contact and mingles with the

Foothill Woodland. In a state where 37 per cent of the total surface area is producing grazing land (Sampson, Chase and Hendrick, 1951), it is no small wonder that there has been a long, sustained interest in range management. Because the assumed indigenous perennial grasses have been almost entirely replaced by Mediterranean annuals, research has been almost solely concerned with the latter. For further information concerning the California Annual Type, the reader is referred to publications by Bentley and Talbot (1948), Biswell (1956), Heady (1958) and Naveh (1960). Perhaps because of this emphasis upon management, there is no published account of the _Stipa pulchra_ facies of the Valley Grassland. Such _Stipa_ associations may best be characterized by the dominance of that species. Indeed, at the three sites studied cursory examination through most of the year would lead the uninitiated to the conclusion that nothing else survives (Figure 4). As the rain year progresses a great abundance and variety of annual and rhizomatous or bulbous plants make their appearance, so that by March the earliest Spring flowers are in full display. Through the rest of the growing season species follow species in rapid succession until the latter part of June, when once again the only apparent green plants are _Stipa pulchra_.

Figure 3. Islands of Grassland in the Foothill Woodland at Hastings Reservation

Figure 4. A Stipa pulchra Association and the Point Frame Used in Sampling

CHAPTER III

METHODS AND RESULTS

The ecology of individuals and populations must of necessity include a study of plants and their surroundings. The two years research recounted here covers those aspects of environmental and vegetational analysis that seemed relevant, and includes an attempt to establish correlations between the two.

In trying to understand the ecology of the typically small and inconspicuous members of the *Stipa* association, it was felt that both laboratory and field methods should be employed. While in the laboratory it is possible to more precisely identify and control variables in the study of individual plants, there is an inherent possibility that growth responses, while indicative of tendencies, are not necessarily those that would occur in the field. Conversely, work in the field enables one to measure the environment and to some extent the plants resident therein, but its very complexity makes much work with individuals impossible. Because of the large number of methods employed in this study, and the necessity for relating them directly with results, they are described in detail in the appropriate sections. As a frame of reference in consideration of the research, in toto, they are outlined in the following paragraphs.

Laboratory methods included: determination of relative photosynthetic and respiratory rates under different conditions of light and temperature, employing Warburg manometers; analysis of soil structure and composition through sieve, hydrometer and volumetric techniques, and chemical analysis for mineral nutrients; osmotic determination of the field capacity and permanent wilting point, and calculation of per cent water in field samples; germination studies with various temperature regimes; and the measurement of relative growth in planters with various soils and conditions of competition.

Field methods included: a systematic collection of the Stipa association; determination of community composition through the use of point frame quadrats; the collection of soil samples from various sites, at various depths, with Veihmeyer tubes; electronic measurement of soil temperature and moisture at various sites and depths with Coleman soil cells; the location and study of permanent transects through established associations, for germination-growth analysis; the locations and study of field plots for germination and growth studies without interspecific competition; the determination of herbage production through the use of clipped quadrats;

and the measurement of air temperature, relative humidity and light intensity under various conditions.

Community Composition

The flora of the *Stipa pulchra* facies of the Valley Grassland has never been described in the literature. In order to have some idea of the total floral complement, collections were made over a period of one calendar year. A total of 36 species were identified and mounted (Table II), and a voucher set is on file with the Department of Botany and Plant Pathology at Oklahoma State University. Terminology is that of Munz and Keck (1963).

Spatial Distribution

Until this study was undertaken in 1963, no attempt to analyze the composition of the *Stipa pulchra* associations had been published. K. L. White (1966) has since established the species present in *Stipa*-containing annual grass associations at Hastings Reservation through the use of 0.1 meter and larger quadrate, while the writer, employing a special frame modified after that of Heady and Rader (1958), has used point sampling to establish cover, basal area, and other sociological parameters in isolated "climax" *Stipa* associations and across their ecotones. No attempt will be made here to champion the validity of one sampling technique over another. The

TABLE II

FLOWERING PLANTS COLLECTED IN THE STIPA ASSOCIATION

Grasses:

*Avena fatua L.
*Avena barbata Brotera.
*Bromus mollis L.
*Bromus rigidus Roth.
*Bromus rubens L.
Festuca reflexa Buckley.
Festuca megalura Nutts.
Sitantion jubatum J.G. Smith.
Stipa pulchra Hitch.

Forbs:

Athsanus pusillus (Hook.) Greene.
Bloomeria crocea (Torrey) Coville.
Brodiaea pulchella (Salisb.) Greene.
Brodiaea lutea (lindl.) Mort.
Calochortus luteus Dougl. ex Lindl.
Caucalis microcarpa H. & A.
Chlorogalum pomeridianum (DC.) Kunth.
Clarkia purpurea quadrivulnera (Dougl.) Lewis & Lewis.
Dodecatheon clevelandii Greene.
*Erodium Botrys (Cav.) Bertol.
*Hypochoeris glabra L.
Linanthus bicolor (Nutt.) Greene.
Lomatium utriculatum (Nutt.) C. & R.
Lotus subpinnatus Lagasca.
Lupinus nanus Dougl. in Benth.
Madia gracilis (Smith) Keck.
Navarretia mitracarpa Jaredii (Eastw.) Mason.
Orthocarpus attenuatus Gray.
Plantago Hookeriana Californica (Greene) Poe.
Ranunculus californicus Benth.
Sanicula bipinnatifida Dougl. ex Hook.
Sidalcea malvaeflora (DC.) Gray ex Benth.
*Silene gallica L.
Sisyrinchium bellum Wats.
Trifolium gracilentum T. & G.
Verbena lasiostachys Link.
Viola penduncülata T. & G.

*exotic

problems involved have been more than adequately reviewed by Brown (1954), Cain and Castro (1959), Grieg-Smith (1964) and others.

In its potential for demonstrating the three dimensional relationships which seem so important in describing competition between annual and perennial grasses, the point frame is doubtless one of the most useful tools devised. First described by Levy and Madden (1933), it has since come to be used in a majority of grassland studies reported in the literature. At least theoretically, true points randomly selected, give an unbiased sample of the infinitely large number of possible points, and thus a measure of distribution the accuracy of which can be increased to any desired degree by simply increasing the sample size. With pins organized in a frame, point sampling is relatively quick, provides little opportunity for subjective evaluation, and is reasonably valid, though as Grieg-Smith (1964) points out, is open to some theoretical objections because of the lack of statistical independence of the observations in each set. The total number of sets necessary to adequately sample different communities can only be established through experience. Since the Stipa pulchra associations analyzed here are extremely homogeneous, only 2160 point contacts were recorded. Because of the very dense nature of the cover and the multitudes of very small annual plants in the understory, sampling was found to be demanding and extremely time consuming, with a single set requiring approximately 15 minutes to complete.

The frame used in these studies was fabricated from extruded aluminum channel so as to be easily portable over rugged terrain (Figure 4). The welding rod pins were carefully ground to a needle point with intent to reduce to a minimum the errors inherent in large size (Goodall, 1952), and installed in a leather braking device so that the pin was held at whatever position it was placed. In practice, most samples were taken at three step intervals across areas judged to be typical, the frame being placed down at a right angle to the line of travel with the right corner of the frame at the toe of the leading foot. Each pin was lowered to contact with vegetation (or recorded as a miss), with height in millimeters and species recorded, then lowered to soil level where the species, litter, or soil was recorded as appropriate.

The importance of height has not been emphasized by most grassland ecologists, perhaps because it has seemed such an illusive concept. Heady (1957) has summarized man's concern with the problem and suggests the point frame as a tool for an accurate, more clearly definable measure, of particular value in comparative studies. The inclusion of both aerial and basal contacts has been valuable in these analyses because of the dense vegetative cover and the relatively lower basal areas.

TABLE III

POINT QUADRAT ANALYSIS OF THE STIPA ASSOCIATION - 2160 points recorded

SPECIES	BASAL MEASUREMENTS BASAL AREA	REL. COMP.	FREQ.	REL. FREQ.	AERIAL MEASUREMENTS AERIAL COVER	REL. COMP.	FREQ.	REL. FREQ.	MEAN HT. AT ANTHESIS,MM.
STIPA$_1$ site - Hastings Reservation:									
Stipa pulchra	8.6	32.6	63.9	36.5	49.7	64.6	100.0	36.0	262
Festuca megalura	0.8	3.2	8.3	4.7	1.7	2.2	13.9	5.0	234
Bromus mollis	11.1	42.1	61.1	34.9	12.8	16.6	72.2	26.0	73
Avena fatua					1.9	2.5	13.9	5.0	369
Sisyrinchium bellum	0.3	1.1	2.8	1.6	1.9	2.5	11.1	4.0	91
Madia gracilis	0.3	1.1	2.8	1.6	3.6	4.7	22.2	8.0	181
Navarretia mitracarpa					1.7	2.2	11.1	4.0	56
Erodium Botrys	0.6	2.1	5.6	3.2	1.9	2.2	13.9	5.0	64
Clarkia purpurea	0.3	1.1	2.8	1.6	0.6	0.7	5.6	2.0	
Bromus rigida					0.3	0.4	2.8	1.0	
Bromus rubra					0.3	0.4	2.8	1.0	
Brodiaea pulchella					0.3	0.4	2.8	1.0	
Moss	3.3	12.6	22.2	12.7					
Grass Seedling	1.1	4.2	5.6	3.2					
Grass Litter	42.2								
Bare Ground	31.5								
Unidentified					0.6	0.7	5.6	2.0	
VEGETATION TOTALS	26.4%	100%	175.1%	100%	77.3%	100%	277.9%	100%	

TABLE III (Continued)

SPECIES	BASAL MEASUREMENTS: BASAL AREA	REL. COMP.	FREQ.	REL. FREQ.	AERIAL MEASUREMENTS: AERIAL COVER	REL. COMP.	FREQ.	REL. FREQ.	MEAN HT. AT ANTHESIS,MM.
STIPA$_2$ site - Los Laureles Grade:									
Stipa pulchra	12.8	54.1	77.8	51.8	65.3	74.8	100.0	46.1	153
Festuca megalura	7.5	31.8	50.0	33.3	16.4	18.8	75.0	34.6	132
Bromus mollis	0.6	2.4	5.6	3.7	2.2	2.6	13.9	6.4	162
Avena fatua					0.8	1.0	8.3	3.8	256
Sisyrinchium bellum					0.6	0.6	5.6	2.6	189
Bromus rigidus					0.8	1.0	5.6	2.6	248
Bromus rubra					0.3	0.3	2.8	1.3	
Sitanion jubatum	0.3	1.2	2.8	1.9	0.6	0.6	2.8	1.3	111
Chlorogalum pomeridianum					0.3	0.3	2.8	1.3	
Grass Litter	30.0								
Bare Ground	47.8								
Unidentified	2.5	10.6	13.9	9.3					
VEGETATION TOTALS	23.7%	100%	150.1%	100%	87.3%	100%	216.8%	100%	

Either alone would most certainly give one a grossly distorted view of the character of the Stipa pulchra association and its ecotones. The data are recorded in Table III. Basal area and aerial cover represent the total number of contacts for each species divided by the number of points. For the other parameters: relative composition is the number of contacts for all species; frequency is the number of quadrats in which a species occurs divided by the total number of quadrats; and relative frequency is the frequency for each species divided by the total frequency. The heights of aerial contacts are recorded in millimeters. A series of point frame transects across a very sharp ecotone between a Stipa association and a typical annual grass type, is analyzed in Table IV. A staked baseline was established in the Stipa association and transects were run across the ecotone at six foot intervals with a distance of three feet measured between successive samples in each transect.

The most striking revelation in these tables is the dominance of the Stipa pulchra association by that species. Its basal area and aerial cover are large, and the many hits on bare ground or litter would seem to reflect the inability of other plants to compete with these vigorous, well-established old perennials. Conversely, across the ecotone a matter of only three feet at most, the community has no dominant species, but is

TABLE IV

AN ANALYSIS OF TRANSECTS BY POINT QUADRATS ACROSS AN ECOTONE BETWEEN STIPA AND ANNUAL GRASS ASSOCIATIONS AT HASTINGS RESERVATION

	SP	FM	BR	AF	HG	EB	PE	BM	All Others
<u>Base Line</u>:									
basal area	8.6	18.6	2.9	1.4	2.9	0	0	1.4	7.1
aerial cover	37.1	37.1	2.9	0	0	0	0	0	1.4
relative aerial comp	47.3	47.3	3.6	0	0	0	0	0	1.8
<u>3 Ft. Interval</u>:									
basal area	8.6	15.7	1.4	1.4	8.6	2.9	0	0	0
aerial cover	44.3	27.1	1.4	4.3	4.3	2.9	0	0	0
relative aerial comp	52.5	32.2	1.7	5.1	5.1	3.4	0	0	0
<u>6 Ft. Interval</u>:									
basal area	2.9	8.6	0	0	8.6	1.4	0	0	0
aerial cover	41.4	28.6	2.9	2.9	1.4	2.9	0	0	0
relative aerial comp	51.8	35.7	3.6	3.6	1.8	3.6	0	0	0
<u>9 Ft. Interval</u>:									
basal area	0	2.9	1.4	0	25.7	2.9	0	0	1.4
aerial cover	1.4	14.3	14.3	15.7	8.6	2.9	1.4	2.9	4.3
relative aerial comp	2.2	21.7	21.7	23.9	14.0	4.3	2.2	4.3	6.5
<u>12 Ft. Interval</u>:									
basal area	0	10.0	5.7	0	14.3	0	1.4	0	5.7
aerial cover	0	17.1	7.1	18.6	21.4	0	2.9	5.7	8.6
relative aerial comp	0	21.0	8.8	22.8	26.3	0	3.5	7.0	10.5

KEY:

SP = <u>Stipa pulchra</u>
FM = <u>Festuca megalura</u>
BR = <u>Bromus rubra</u>
AF = <u>Avena fatua</u>
HG = <u>Hypochoeris glabra</u>
EB = <u>Erodium Botrys</u>
PE = <u>Plantago Hookeriana californica</u>
BM = <u>Bromus mollis</u>

characterized by a variety of annual grasses and forbs. The increasing basal area found as one crosses the ecotone is in large part a reflection of the prodigous quantity of seed (Kay, 1966). Germination in the California Annual Type has been reported by Heady (1958) to produce as many as 13,000 seedlings per square foot.

Temperature and Moisture in the Environment

The most striking feature of the study area is its great physical diversity. Since a preliminary survey and discussions with people in the field had indicated that *Stipa pulchra* associations were sharply defined and narrowly limited, it was logical to assume that this diversity was significant in defining distribution. On this premise, a whole series of techniques were adapted or devised to provide a quantitative basis for comparison of physical factors, and thereby of the associations with which they might be correlated. Beginning in the Fall of 1965 data were collected from a widely scattered selection of *Stipa*, *Avena*, and *Bromus* sites (Figure 1). Since to visit all required over 100 miles of difficult driving and many hours of arduous toil, no precise schedule was maintained, though on the average, each active site was visited every other week. Visits were more frequent during periods of rapid change, and less so during midsummer when the soil was at or below the permanent wilting point and most perennials were dormant.

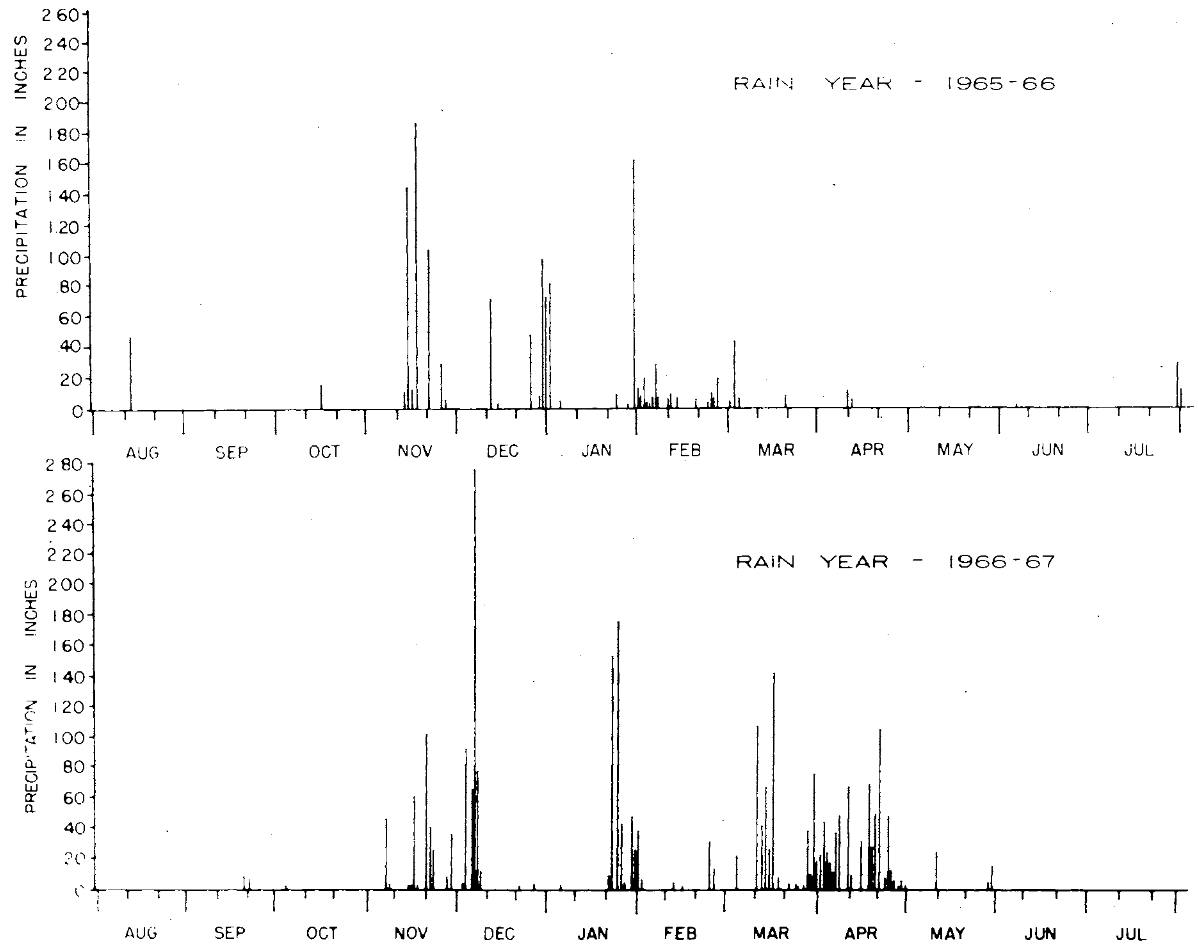

Figure 5. Daily Precipitation at Hastings Reservation

This being a semi-arid region, with a mean annual precipitation range of between 16.38 and 20.23 at the extreme sites (Table I), the total and distribution during any one rain year may be the crucial factor in determining the vigor of the grassland species. The daily precipitation recorded at Hastings Reservation (Figure 5) shows that the total for the 1965-66 season was below the mean, and came almost entirely in the late Fall and early Winter. By the period of Spring growth, soil moisture was nearly depleted, and most of the annual grasses never reached anthesis. Conversely, during the 1966-67 season, precipitation was above the mean and distributed more evenly and far into the Spring, in such a way that grasses and forbs alike flourished at all sites. This sort of variability has doubtless been important in community competition and is subjectively evaluated in this regard in subsequent sections.

Precipitation is important to grassland species only insofar as it becomes available in the soil. In recent years, agronomists and range managers have devised a number of techniques for soil moisture determination, (Richards and Wadleigh, 1952), only two of which were employed in this study. Random field sampling of soils, followed by laboratory analysis, gives the most reliable data, but also involves a great expenditure of time and effort. The data given in Table V were derived from samples taken with Veihmeyer tubes. Because of the dense nature of these virgin soils two tubes were used, one having a bulge point for shallow clay sampling and the other a constricted point for deeper sampling of light soils. A puller jack proved essential in extracting the tubes. Two replicates were taken at 1 foot, 2 feet, 3 feet, where practical, and occasionally at 4 feet. Promptly sealed in soil cans, they were returned to the laboratory, weighed, dried at 110°C for 24 hours, weighed again, and saved for further study. Percentage moisture determined on a dry weight basis was calculated for a total of 750 samples. The most interesting revelations of these data (Table V and Figure 6) are the greater percentage of soil moisture at the $\underline{Stipa}_1$ site, and the seasonal fluctuations at all sites. With the hope that soil moisture might be more quickly determined, a Soiltest MC-300A moisture meter with MC-310A soil cells, as described by Coleman and Hendrix (1949), was also employed (Figure 7). Though a total of 466 separate readings were made, the moisture cells proved inadequate in measuring the changes that occured under high moisture tension, and because of the deep cracking characteristic of clay soils, were often highly erratic.

Determination of the quantity of water in the soil is not necessarily an indication of the amount which may be available to plants. If one accepts 1/3 atmosphere of pressure as the field capacity of a soil, and 15 atmospheres as the permanent wilting point, it is possible

TABLE V

SOIL MOISTURE AT FIELD SITES AND UNDER LABORATORY CONDITIONS

MEAN SOIL MOIST. % Dry Wt. Basis:		1965 O	N	D	1966 J	F	M	A	M	J	J	A	S	O	N	D	1967 J	F	M	A	M
Stipa$_1$	1'		*19		23	23	23	22	18	17	15	-	10	14	24	24	23	23	24		22
	2'		15		23	28	26	25	23	21	23	-	15	16	25	23	20	20	27		24
	3'		16	22	21	22	26	25	25	24	25	-	18	20	28	22	17	20	14		16
	4'					23	24	24	25	24	24	-	20	20		15					
Stipa$_1$-Avena	1'							*8	5	10	4	-	-	3	-	16	12	17	25		11
	2'							12	9	7	5	-	-	6	-	9	13	14	16		19
	3'							10	11	7	6	-	-	5	-	R	10	11	14		18
	4'																				
Avena	1'			*14	13	14	12	9	5	5	6	-	2	-	10	12	12	15	15		16
	2'			16	16	16	16	15	15	12	14	-	7	-	14	15	14	16	17		16
	3'			22	13	15	13	14	13	12	11	-	R	-	13	13	13	13	12		14
	4'														12						
Bromus	1'		*13		15	16	12	10	4	5	5	-	2	-	10	13	9	16	23		12
	2'		16		14	19	16	15	13	10	9	-	7	-	10	13	13	15	22		16
	3'		11		14	14	12	12	12	7	10	-	6	-	10	10	12	12	13		11
	4'								11		0										
Stipa$_2$	1'			*16	18	17	11	15	9	-	-	-	-	6	-	14	11	17	11	19	
	2'			16	15	17	17	12	13	-	-	-	-	12	-	15	17	20	13	18	
	3'			10	15	15	12	13	13	-	-	-	-	8	-	R	7	13	18	R	
	4'													10							

SOIL MOISTURE AT EXPERIMENTAL D.P.D's (% dry wt. basis):

		0.3 atm.	6 atm.	11 atm.	15 atm.
Stipa$_1$	- 45°C	27	19	16	
	- 70°C			16	14
Stipa$_1$-Avena	- 45°C	17	12	8	
	- 70°C			8	7

* start of series
\- summer dormant period
R rock

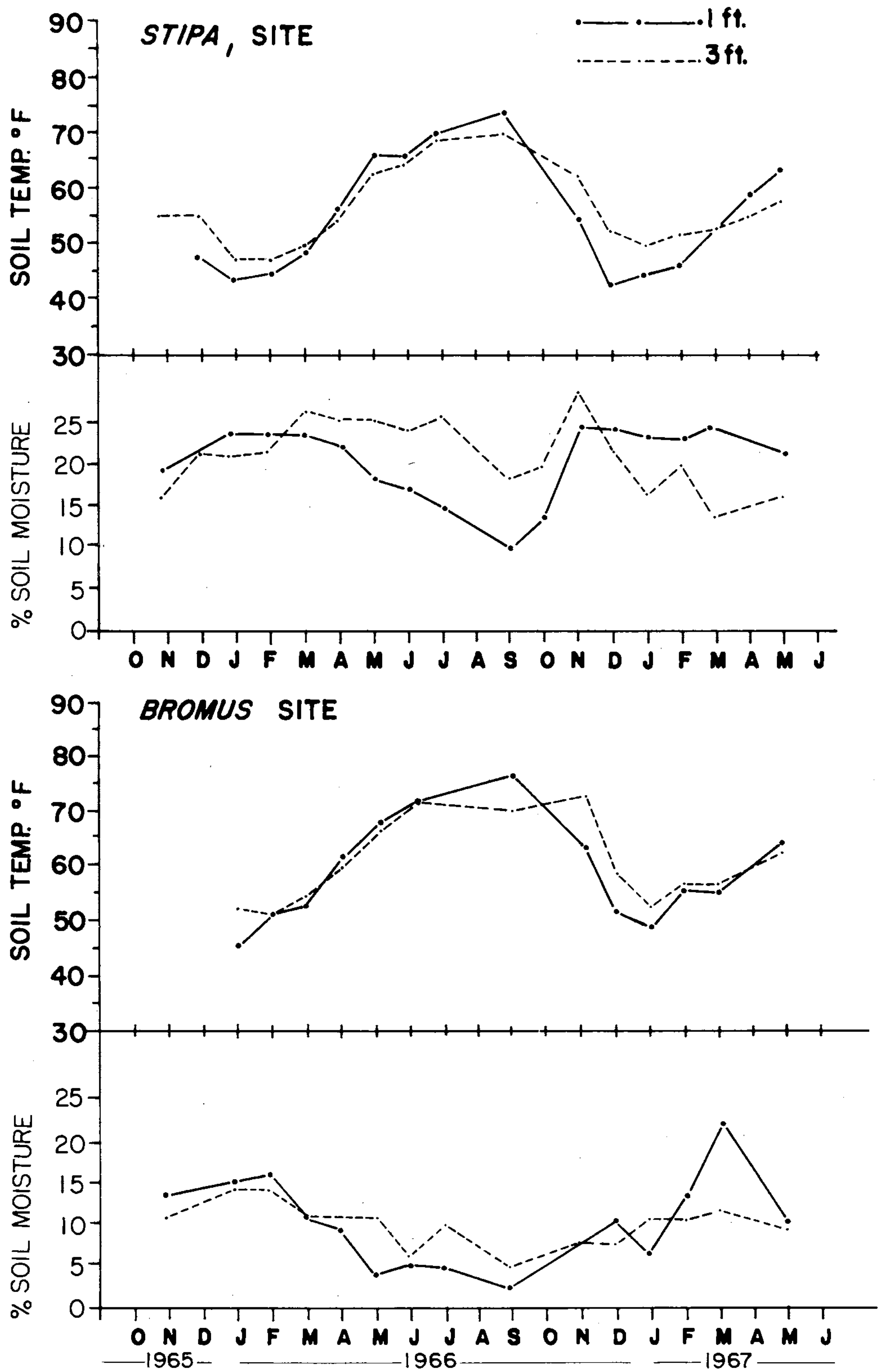

Figure 6. Soil Measurements at Stipa[1] and Bromus Sites Compared

to establish the volume of water available between these limits. Where the requisite equipment is available, the pressure-membrane technique will enable rapid determinations of these values. For the purposes of this study, the water was removed from soil samples by osmosis through a membrane of dialyzing cellophane into an aqueous solution of polyethylene glycol, as described by Vomocil, Waldron and Chancellor (1961). Air dry soil crushed to pass a #30 sieve was packed in 3-inch lengths of 3/4 inch tubing, placed in distilled water for 24 hours to insure saturation, and then allowed to reach equilibrium with solutions that produced diffusion pressure deficits of 1/3, 6 and 11 atmospheres. From these, a moisture characteristic curve was plotted and values at 15 atmospheres were interpolated (Table V). Since temperature is considered to have a marked influence on the cohesion of water and hence the quantity of water retained (Baver, 1956), temperatures were used which corresponded to those recorded in the field at the start of the growing season and the end of the summer. $\underline{\text{Stipa}}_1$ clay can be seen to have a consistently high moisture content, and about 25 per cent more available water than $\underline{\text{Stipa}}_1$ Avena. In addition there seems little doubt but that summer-cormant leafy plants like Stipa pulchra can continue to extract adsorbed water far below the content at the permanent wilting point. Though it may in fact occur over the course of a summer, release of water

TABLE VI

SOIL TEMPERATURE AT FIELD SITES

			1965		1966												1967				
MEAN SOIL TEMP. °F:		O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M
$Stipa_1$	1/2"				47	54	65	77	88	95	95	-	94	-	88	55	56	62	68	80	82
	1'			*47	43	44	48	57	67	67	70	-	74	-	53	42	44	46	51	58	63
	2'			51	45	46	49	56	64	67	70	-	70	-	59	47	43	46	50	56	59
	3'			55	47	47	49	54	62	65	69	-	70	-	62	51	48	50	51	53	57
	4'				50	49	49	56	62	67	68	-	71	-	67	57	53	53	54	55	55
$Stipa_1$-Avena	1/2"																*56	70	74	80	88
	1'																		52		65
	2'																		57		65
	3'																		58		61
Avena	1/2"				*52	60	65	83	100	88	-	-		-	94	59	74	71	72	88	
	1'				48	49	54	63	70	71	-	-	80	-	71	46	52	52	56	59	66
	2'				50	50	54	62	68	70	-	-	78	-	73	52	54	54	56	57	65
	3'				52	50	52	59	65	68	-	-	74	-	71	55	56	56	57	58	62
Bromus	1/2"				*54	68	67	74	91	92	-	-	98	-		59	68	66	79		89
	1'				47	51	53	62	68	71	-	-	77	-	64	51	49	56	56		65
	2'				51	52	56	62	69	71	-	-	78	-	70	53	51	50	57		64
	3'				52	51	54	60	67	71	-	-	70	-	73	59	52	57	57		63
$Stipa_2$	1/2"				59	58	70	83		-	-	-		-	-	-		58		72	
	1'			*50	52	50	57	64	71	-	-	-	77	-	-	-	55	47	49	49	
	2'			54	54	53	57	65	71	-	-	-	75	-	-	-	57	48	52	54	
	3'			57	57	57	57	66	70	-	-	-	76	-	-	-	60	54	54	55	

* start of series
\- summer dormant period

held in clay micelles was not apparent from the data procured with the two temperature regimes utilized.

Soil temperature was recorded because of its presumed importance in water relations, seed germination, and plant growth. The MC-310A moisture cells include thermistors which provide an accurate measure of temperature at depths of one foot or more (Figure 7). A total of 466 readings are summarized in Table VI and graphically illustrated for Stipa$_1$ and Bromus in Figure 6. The yearly march is well shown, but especially interesting are the consistently lower values at the Stipa$_1$ site. The mild winters are reflected in high temperature values, while the cool nights of the long, hot summers are doubtless a factor in the fairly low summer values. Whenever possible, meter readings were taken at 1 p.m. plus or minus one hour. With this degree of constancy, meaningful values at a depth of one-half inch were obtained with a "Novatherm" Transister Thermometer. Means of a total of 182 readings are shown.

Air temperature (Table VII) was derived from the charts of a recording hygrothermograph, located in a standard Weather Bureau shelter at Hastings Reservation. Seasonal variation in the mean is clearcut, but perhaps equally important is the fact that on any day of the year, temperatures in a 30° to 70° range may be registered. Though the midwinter means of 40 to 50°F. might seem high when compared with midwestern grassland environments, they are sufficiently low to interfere with active assimilation.

Figure 7. Measuring Soil Moisture and Temperature as Current Flow Through Coleman Soil Cells

Figure 8. Measuring Soil Volume With a Soiltest "Volumeasure"

Instantial temperatures at six inches above the soil were recorded with the "Novatherm", but are not included in the table.

Relative humidity is higher in this coastal region than in most of the rest of the state. Mean values for two rain years, as extracted from the charts of the recording hygrothermograph, are shown in Table VII. Again, we find great fluctuation with both high and low values to be expected any day of the year. A high monthly mean, remaining close to 50 per cent, is undoubtedly important in the survival of many plants. Because some investigators have suggested that the high relative humidity in the microclimate of the grass itself might be important in reducing transpirational loss, this difference was measured with a self-powered Bendix "Psychron" psychrometer. Three replicates each at two Stipa sites, indicated a mean increase in relative humidity of no more than 10 per cent during the May peak of growth to anthesis.

Because light plays a vital role in photosynthesis, assimilation and growth, intensity was measured with a Gossen "Trilux" foot-candle meter during the period of peak assimilation just prior to anthesis. At 12 noon on the 20th of May, under an open sky, a reading of 7400 f.c. was obtained. Immediately thereafter a series of 10 readings were taken under typical, well-formed Stipa pulchra mounds, the mean of which was 934 f.c. In a mature Stipa association, with its closely spaced mounds, there seems

TABLE VII

WEATHER AT HASTINGS RESERVATION

	1965			1966												1967				
	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M
AIR TEMPERATURE AT 4 FT. IN °F:																				
Mean	62	53	47	46	46	50	57	57	63	65	72	65	62	54	50	50	51	48	45	57
Max.	93	85	79	71	73	85	90	91	103	98	101	99	93	94	78	78	79	71	68	93
Mean Max.	80	55	61	60	58	65	75	75	81	84	91	82	80	66	63	64	67	60	53	71
Min.	32	31	23	22	22	23	28	33	30	36	38	37	32	30	23	22	27	26	30	31
Mean Min.	45	40	33	31	33	36	39	42	45	47	53	47	45	41	36	36	36	36	36	43
PRECIPITATION IN INCHES:	.24	6.82	3.82	1.92	1.48	.62	.16	0	.02	.39	0	.19	.01	3.23	5.32	5.16	.57	5.34	7.46	.44
REL. HUMIDITY %																				
Mean	51	63	64	62	62	60	57	58	49	54	*	*	41	62	60	58	50	66	69	60
Mean Max.	83	97	95	93	92	92	92	94	82	89	*	*	72	94	91	90	90	99	99	94
Mean Min.	18	28	33	30	29	27	22	22	16	19	*	*	10	30	30	27	19	33	40	25

* no record

little likelihood of seedlings becoming established with light at that level.

Soil Structure and Chemical Properties

The physical properties of a soil have much to do with determining the particular flora which it may sustain. It was assumed that the mosaic distribution of *Stipa* associations was at least partly a result of their competitive success on certain soil types. A field survey of a variety of neighboring grassland soils showed them to be quite different in texture from one another, with clayey soils seeming to characterize *Stipa* sites. This same relationship has recently been reported from other areas of Monterey County[1] and from San Luis Obispo County just to the south (Wells, 1962). On this basis a detailed laboratory analysis was undertaken. In establishing textural classification the larger soil separates were isolated by wet washing through U.S. Standard brass sieves in a mechanical shaker, while silt, clay, and colloidal clay fractions were determined by use of a 152h Bouyoucos hydrometer, following A.S. T.M. Standards. It is interesting that the data (Table VIII) support our field evaluations. Indeed, the best *Stipa* site (*Stipa*$_1$) was found to have over 70 per cent silt and clay, while across its ecotone, the *Stipa*$_1$ *Avena* site had only 19 per cent. A secondary *Stipa* site (*Stipa*$_2$) had

[1] L. Williams, Soil Conservation Service, Salinas, California, personal communication. (1967)

TABLE VIII

STRUCTURAL ANALYSIS OF SOILS

PHYSICAL CHARACTERISTICS	STIPA$_1$		STIPA$_1$-AVENA		STIPA$_{2B}$		BROMUS		AVENA	
Specific Gravity	2.5		2.5		2.5		2.6		2.5	
Volume Voids	322ml/1000ml		471 ml/1000ml		367ml/1000ml		405ml/1000ml		358ml/1000ml	
Sieve Analysis:	gms	%	gms	%	gms	%	gms	%	gms	%
#8 retained	5.47	2.7	4.72	2.5	16.14	8.4	11.81	6.0		
#16 retained	8.05	3.9	4.77	2.5	26.42	13.9	16.56	8.4		
#30 retained	8.54	4.1	5.05	2.7	31.04	16.3	27.24	13.8		
#50 retained	9.58	4.7	8.93	4.7	30.19	15.8	51.93	26.1		
#100 retained	10.91	5.3	85.46	44.8	24.63	12.9	44.97	22.9		
#200 retained	13.10	6.0	57.23	30.0	18.83	9.9	18.72	9.5		
Passed #200 sieve	149.8	72.9	24.62	12.8	42.75	22.5	24.80	12.6		
Hydrometer Analysis of Soil Passing #30 sieve:	%		%		%		%		%	
Silt	20		7		16		9		14	
Total Clay	52		12		20		12		18	
Colloidal Fraction	40		7		14		10		16	
U.S.D.A. Textural Classification	Clay		Loamy Clay		Sandy Clay Loan		Sandy Loam		Sandy Loam	

36 per cent silt and clay, while Bromus and Avena sites were intermediate. Since a large part of the water and mineral nutrients in the soil is held as a film on the surface of clay micelles, it appears that Stipa profits more from this type of structure than do the Mediterranean annuals.

Another important characteristic which must be established is pore space. While the distribution of separates gives some indication of this, the volume of voids can be precisely calculated. A Soiltest "Volumeasure" CN-980 (Figure 8) was used to obtain field volume measurements and therby soil density, while a Le Chatalier volumetric flask was used to calculate the specific gravity of soil solids. On these bases voids were calculated as follows:

given - field density = 1940 gm/1000 cc
per cent water + 15.2

then - weight solids = wet weight - weight of water

W_s = 1940 gm - 295 gm

W_s = 1645 gms

volume solids = weight solids/sp. gr. solids

V_s = 1645 gm/2.5

V_s = 633 cc

volume voids = total volume - volume solids

V_v = 1000 cc - 633 cc

V_v = 367 cc

The poorly graded *Stipa*$_1$ *Avena* soil is shown to be over 70 per cent fine sand and thus has by far the greatest pore space, and the greatest water holding capacity at saturation. It should not be surprising to find that it drains rapidly in response to gravity to a low value at field capacity (Table V). The *Stipa*$_1$ soil is also poorly graded, but being over 50 per cent clay with the remainder well graded, the total pore space is much smaller. Even so, because of adsorption of water in the clay micelles and its high tension in the capillary spaces, field capacity is comparatively high. It can thus be seen that soil texture, structure, and porosity can be expected to influence such moisture characteristics as percolation, infiltration, water-holding capacity, and capillary rise at the experimental sites. The expression of this influence in the community composition can be seen clearly across the ecotone at *Stipa*$_1$ (Table IV), and has been reported in other grassland contexts (Biswell, 1956 and Partch, 1962).

In relating vegetation types to soils one must always consider that chemical factors may play a hidden role. With this in mind, a complete analysis was made with a Hellige-Truog No. 697-18 Combination Soil Tester. A total of 167 tests were made on eight soils at depths of one and three feet, the relevant ones of which are summarized in Table IX. Though this particular test set is valid only for gross determination, it offers the only practical approach to a broad survey. The pH was found to be remarkably uniform in

TABLE IX

CHEMICAL ANALYSIS OF SOILS

	$STIPA_1$	$STIPA_1$-AVENA	$STIPA_2$	AVENA	BROMUS
pH - Surface	5.6	5.6	5.8	6.2	6.4
1'	5.7	6.0	6.0	6.5	6.0
2'	6.5	5.8	6.5	6.3	5.8
3'	6.5	6.0	7.0	6.0	6.0
Plant Nutrients (lbs/acre available):					
Phosphorus					
1'	200	25	< 25	< 25	25
3'	200	25	200	25	50
Potassium					
1'	> 320	320	120	240	80
3'	> 320	120	80	120	120
Calcium					
1'	6000	6000	500	6000	6000
3'	6000	1500	1000	6000	6000
Magnesium					
1'	1000	1000	1500	1500	1000
3'	750	2500	1500	1500	750
Nitrogen-Nitrate					
1'	< 5	< 5	< 5	< 5	< 5
Nitrogen-Ammonia					
1'	5	5	5	-	-
Chloride					
1'	750	750	500	900	1500
3'	1000	500	500	250	500
Sulfate					
1'	< 250	< 250	< 250	< 250	< 250
3'	< 250	< 250	< 250	< 250	< 250

both fresh and dry soils, being just slightly on the acid side of neutral. It was hoped that differences in available elemental totals might shed some light on distribution. Unfortunately, no consistent pattern is apparent except in the case of phosphorus, which is approximately eight times more plentiful at the *Stipa* sites. This may indicate a high phosphorus requirement, which coupled with the low nitrogen content of the soil might function in inducing early maturation, to the advantage of the species.

Germination and Growth

The place of any plant in a community is largely determined by its patterns of germination and growth. In recent years the physiology of seed germination has become an important part of that broad interdisciplinary area known as physiological ecology (Billings, 1957), and has been thoroughly reviewed by Mayer and Poljakoff-Mayber (1963). Unfortunately, for most species in most environments, the possible variables influencing germination simply are not known. In this study, per cent germination of fresh, hand sorted, *Stipa pulchra* seed was established for a wide range of laboratory and field conditions. (Table X), with the hope that the data would shed some light on community dynamics. The single outstanding characteristic of this seed was found to be its ability to germinate almost equally well under all conditions to which it was exposed. In no trial did less than 60 per cent germinate, and in some cases the percentage

TABLE X

STIPA PULCHRA GERMINATION UNDER LABORATORY AND FIELD CONDITIONS

Germination Medium and Number of Seeds	Per Cent Germination - Different Temp. Regimes				
	Field Temps	10°C	30°C	30°C with 1 hr pretreatment at -10°C	at 40°C
Germination disks - water, 800 seeds			82		
Germination disks - *Erodium Botrys* extract, 600 seeds			81		
Germination disks - water, 400 seeds		88			
Germination disks - *Erodium Botrys* extract, 400 seeds		76			
Germination disks - water, 200 seeds				75	
Germination disks - water, 200 seeds					76
Stipa$_2$ soil en situ, 174 seeds	71				
Stipa$_2$-*Avena* soil en situ, 77 seeds	64				
Stipa$_{FO}$ soil en situ, 77 seeds	61				
Stipa$_{FO}$-*Bromus* soil en situ, 99 seeds	61				
Avena soil en situ, 82 seeds	87				
Bromus soil en situ, 89 seeds	80				

approached 100. On this basis one must conclude that the abundant supply of seed germinates well. The fact that few if any natural seedlings are seen in the field must, therefore, be an indication of a very low survival rate during the first year of growth.

Two fundamentally different techniques were used in an attempt to verify this conclusion. Germination was initially established on germination disks in sterile Petri dishes. The highest percentage was obtained in water at 10°C. Higher temperatures, pretreatments at -10°C. or 40°., and germination in an extract of a possible inhibitor, Erodium Botrys, all had little effect. Since germination in an incubator is not necessarily an indication of natural germination, and since there seemed some real possibility of inhibition by various species including Stipa pulchra itself, a series of field germination trials were set up. At the start of the 1965-66 rain year a total of eight one meter strips of 100 seed each were staked and planted at the $Stipa_1$ and Avena sites. No germination was detected, and no seedlings were present at the end of the season. Since the rainfall during that growing season was far below the mean (Figure 5), this was not surprising. It was apparent, however, that a technique for identifying individual seedlings had to be devised if field trials were to yield significant results. The system finally adopted employed one inch lengths of plastic straws, slit on one side, filled with moist soil and a seed, and individually planted along a

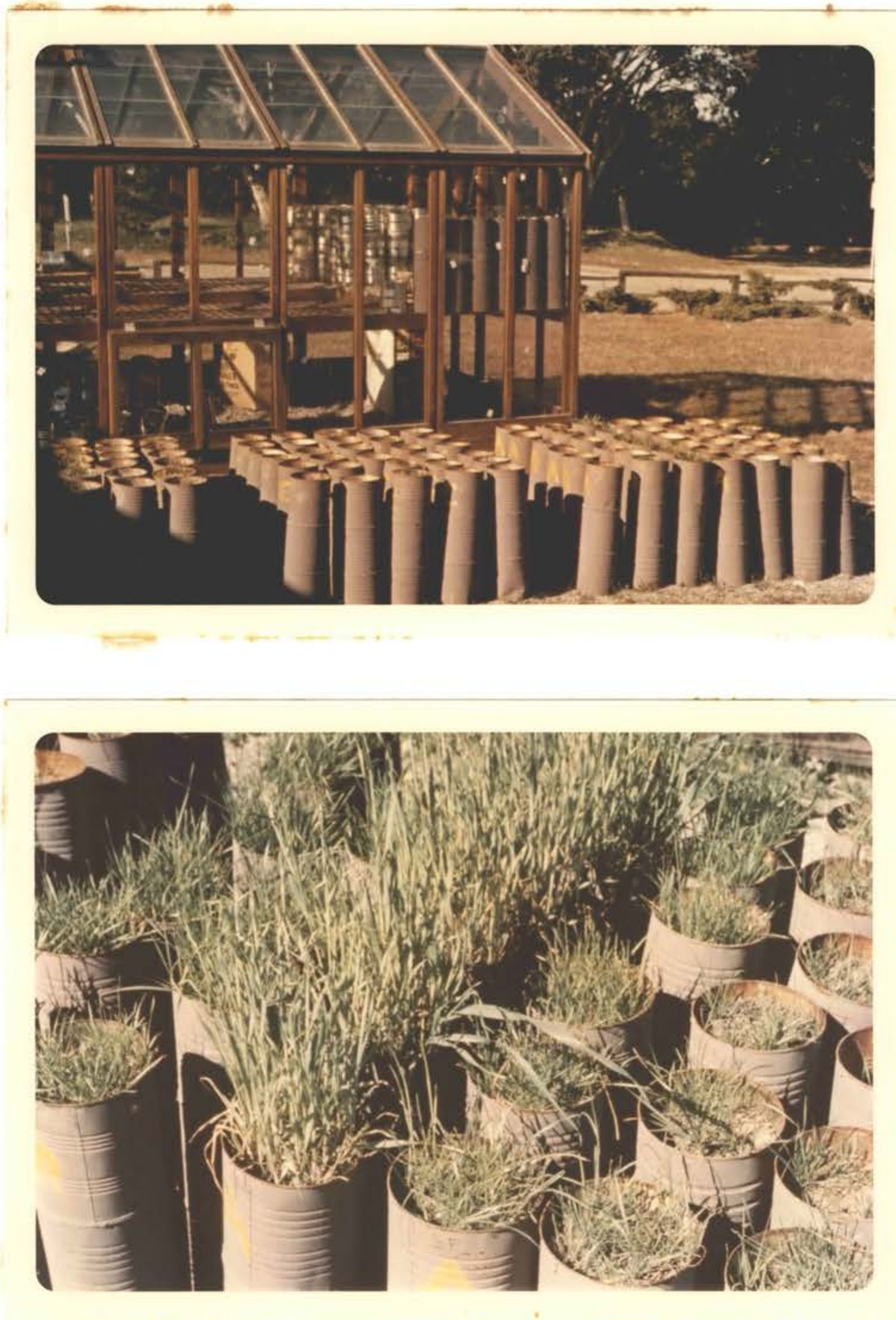

Figure 9. Experimental Gardens at Monterey Peninsula College

Avena fatua and *Stipa pulchra* on *Stipa*$_1$ Soil | *Stipa pulchra* on *Bromus* Soil | *Stipa pulchra* on *Stipa*$_1$ Soil

Figure 10. Relative Growth in Planters at the End of the 1965 Rain Year

TABLE XI

GROWTH IN EXPERIMENTAL GARDENS

GROWTH CONDITIONS AND DATE OF SOWING	MEANS OF OVERALL HEIGHT IN MM. Feb	Mar	Apr	May	Jun	PER CENT SEEDS PLANTED GROWING AT CONCLUSION
Experimental garden planters - 20 Nov 65						
SP in *Stipa*$_1$ soil, 450 seeds	47	80	129	262	631	
SP in *Bromus* soil, 300 seeds	52	56	85	101	234	
SP in *Stipa*$_1$ soil with AF, 300 seeds	47	53	63	73	87	
AF in *Stipa*$_1$ soil with SP, 300 seeds	107	201	223	591	892	
Experimental garden planters - 26 Nov 66						
SP in *Stipa*$_1$-*Avena* soil, 150 seeds		78	148		365	50
SP in *Stipa*$_1$-*Avena* soil with AF, 50 seeds		56	60	61	65	46
AF in *Stipa*$_1$-*Avena* soil with SP, 150 seeds		130	200	427	513	78

KEY: SP is *Stipa pulchra*
AF is *Avena fatua*
BM is *Bromus mollis*

staked transect in the otherwise undistrubed community (Figure 12). Associations of Stipa pulchra, Avena fatua, and Bromus mollis (with Erodium Botrys), were used with somewhat variable results. Again, all percentages were high, but were highest on the well-drained Avena and Bromus soils, and lowest on Stipa soils and those with an abundance of Erodium. This may well be evidence of inhibition, but if so, the level is sufficiently low to be of little importance in the maintenance or establishment of local species populations.

If Stipa pulchra seed germinates well under both laboratory and field conditions, the next logical step in understanding community dynamics is to measure seedling growth and vigor. This was accomplished through the use of planters in experimental gardens at Monterey Peninsula College, and in field plots and transects at a variety of sites. Through the late summer and early fall of 1965, over 600 Number 10 cans were collected and soldered end to end in groups of threes or fives (Figure 9). Immediately following the first rain of the 1965-66 growing season, 66 three can planters were sown, the 25 seeds in each being placed approximately one-half inch below the surface, and watered weekly to anthesis. Stipa, Bromus and Avena soils were used, although careful records were kept only for the first two (Table XI). As a quantitative measure of growth, overall height, leaf length, leaf width, and basal culm diameter were recorded each time a trial series was checked. Stipa

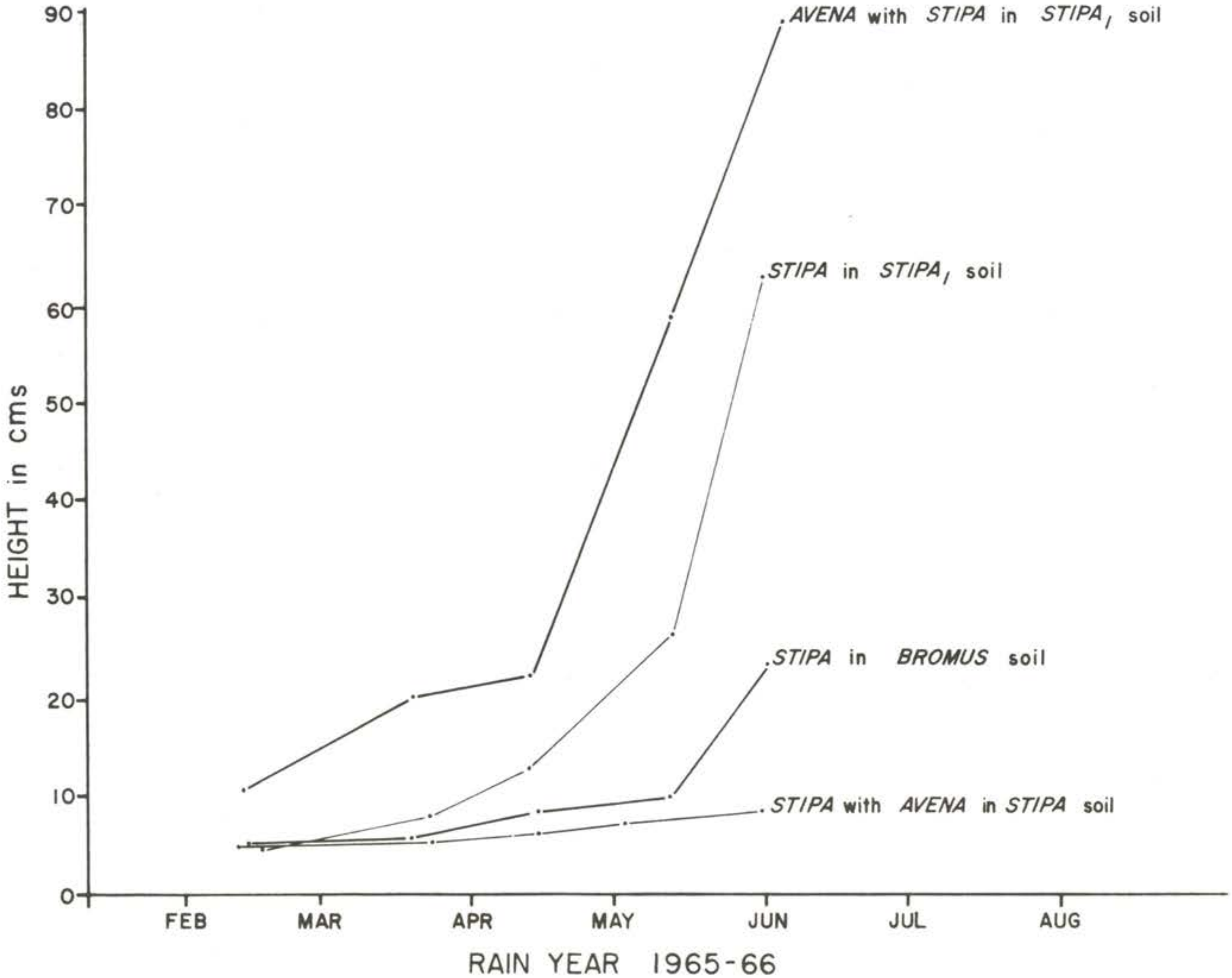

Figure 11. Relative Growth of Stipa pulchra and Avena fatua at Experimental Gardens

TABLE XII

GROWTH IN FIELD PLOTS AND STRIPS

GROWTH CONDITIONS AND DATE OF SOWING	MEANS OF OVERALL HEIGHT IN MM.					PER CENT SEEDS PLANTED GROWING AT CONCLUSION
	Feb	Mar	Apr	May	Jun	
Field plots, 1 M^2 cleared of other vegetation, 19-25 Nov 66						
SP on *Stipa*$_1$ soil, 200 seeds		43		77	188	36
SP on *Stipa*$_1$-*Avena* soil, 200 seeds		45		72	82	54
SP on *Stipa*$_{2B}$ soil, 200 seeds		52	68		113	52
SP on *Stipa*$_{2B}$-*Avena* soil, 200 seeds		51	69		118	66
SP on *Avena* soil, 200 seeds		62		104	235	56
AF on *Avena* soil, 10 plants by plot					816	
BM on *Avena* soil, 10 plants by plot					462	
Field strips in established grassland 19-25 Nov 66						
SP on *Stipa*$_2$ soil, 174 seeds		48	58		68	48
SP on *Stipa*$_2$-*Avena* soil, 77 seeds		43	49		56	36
SP on *Avena* soil, 82 seeds		58		60	67	65
SP on *Bromus* soil, 89 seeds		53		61	78	53
SP on *Stipa*$_{FO}$ soil, 77 seeds		40	53		63	26
SP on *Stipa*$_{FO}$-*Bromus* soil, 99 seeds		43	55		70	49

KEY: SP is *Stipa pulchra* BM is *Bromus mollis*
AF is *Avena fatua*

seedlings in *Stipa*$_1$ soil grew vigorously to a June anthesis (Figure 10, 11) following the typical growth curve described by Sampson and McCarty (1930) for mature bunches. In *Bromus* soil, the plants reached only a little more than one third that mean height, with only an occasional plant flowering. in *Avena* soil, the height of *Stipa* plants was intermediate between those in *Stipa*$_1$ soil and in *Bromus* soil. In competition with *Avena fatua* in *Stipa*$_1$ soil, the *Stipa* seedlings scarcely grew at all, and none reached anthesis. The *Avena* in these same cans grew almost 10 times faster and reached anthesis in May. It was quite obvious that both the soil in which it grows, and the plants with which it is associated, may function as limiting factors in the dynamics of *Stipa pulchra* in the communities in which it is found. Additional cans were prepared for the 1966-67 growing season, filled with *Stipa*$_1$ *Avena* soil, and sown in a similar manner. Overall growth of *Stipa* alone was intermediate between that recorded for *Stipa*$_1$ and Bromus soils, while *Stipa* and *Avena* in competition grew about one-third less than they had in the *Stipa*$_1$ soil.

Because experimental gardens cannot duplicate field conditions, it was decided to grow *Stipa pulchra* seedlings in the field, with and without competition, on soils similar to those used in the planters. Plots of one square meter were cleared at six sites, and 200 *Stipa* seeds were planted one-half inch below the surface at each (Figure 13). Because of the complete elimination of mulch, the sown surface

Figure 12. Controls Used to Determine Growth in Field Planting Straws

Figure 13. Field Plot for Determining Germination and Growth at *Avena* Site

was covered with pulverized sphagnum, and carefully hand watered each week through the first month. Growth was similar to that recorded in the planters except on *Stipa* soils, where *Stipa pulchra* survived well, but grew less (Table XII). The reason was not apparent, though it may reflect both better aeration for the same soil in planters and competition in the plots with the extensive feeder root systems of nearby bunches.

Seedlings grown along transects, through established associations, were also measured. The straw planters previously mentioned (Figure 12), made it possible to find the seedlings and, judging from the growth of controls in the experimental gardens, did not interfere with growth. In direct competition with *Stipa pulchra*, *Avena fatua*, *Bromus mollis*, and *Erodium Botrys*, *Stipa* seedlings did not do so well. Overall growth was approximately one-half of that in field plots and survival was somewhat lower. Because of the dense aerial cover of a mature *Stipa pulchra* association, and the relatively more vigorous growth of Mediterranean annuals, it appears that the poor growth of *Stipa pulchra* along these transects reflects reduced light intensities and/or a deficient water supply in the surface layers of soil. On the basis of the total failure of the 1965-66 planting, an even lower seedling survival was anticipated. This once again emphasized the great importance of growing season weather patterns. The 1966-67 season was one of the wettest on record, with a fairly even distribution of precipitation through the period of most active growth (Figure 5).

Photosynthetic Efficiency

The apparent inability of Stipa pulchra to compete with the more vigorous mesomorphic Mediterranean annuals such as Avena fatua has been assumed to be a factor in the disappearance of the association over much of its potential range, and in limiting its present distribution. Indeed, G. L. Stebbins[2] came to this conclusion during his genetic study of the species (Stebbins and Love, 1941) some 25 years ago. This investigator, quite independently arriving at a similar interpretation, sought to establish its validity through comparison of relative photosynthetic efficiencies.

Since natural grasslands are among the most important resources of this and many other countries around the world, it is only logical to assume that they have been intensively studied, if not from interest, at least from an economic point of view. The available literature indicates that while much is known about the phylogeny, productivity, and climatic and edaphic control of temperate grasses, very little is known about the much more basic aspects of physiological ecology. A knowledge of photosynthesis, and thus concomitantly water relations and gas diffusion, would seem to be essential to a more effective utilization of grasslands

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[2]Personal communication (1966)

everywhere. It was hoped that published researches would give some insight into the relationship between assimilatory metabolisms in annual and perennial grasses, but apparently nothing has been done with this end in mind. There has been a great deal of interest, particularly in the U.S.S.R. and South Africa, in the relative photosynthetic activity of xerophytes and mesophytes, and the adaptive mechanisms involved. Since Stipa pulchra and the closely related Stipa cernua are characterized by xeromorphic adaptations reducing water loss through leaf rolling and thickened epidermi (Dedecca, 1954) and remain green throughout the year, some of these findings are relevant to this study. Malkina-Krupnikova (1951) found that, with the requisite water and light, xerophytic grasses have much higher photosynthetic rates per unit surface area than do mesophytic ones. In light of findings presented in the section on soils, it is interesting that Iljin (1957) found that on dry sites mesophytes transpire much more per ml CO_2 assimilated than xerophytes. From a different point of view, Todd and Webster (1965) have shown that a more xeric species continues to photosynthesize at a higher rate under increasing moisture stress. Under such conditions the stomata close, yet because of the greatly thickened and structurally porous external epidermal walls demonstrated for Stipa and other grasses (Miroslavov, 1962), it seems probable that photosynthesis continues without great water loss. As might be expected, Malkina-Krupnikova (1951) also found that the

TABLE XIII

PHOTOSYNTHESIS AND RESPIRATION IN STIPA PULCHRA AND AVENA FATUA

	Apparent photosynthesis as $\mu l O_2$ evolved per gm. fresh wt. per hr.*		Repiration as $\mu l O_2$ consumed per gm. fresh wt. per hr.*	True photosynthesis as $\mu l O_2$ evolved per gm. fresh wt. per hr.	
	2000 f.c.	4000 f.c.		2000 f.c.	4000 f.c.
Stipa					
15°C	300	616	290	590	906
25°C	629	632	727	1357	1360
35°C	624	690	2546	3171	3236
Avena					
15°C	316	555	160	476	715
25°C	711	675	553	1265	1229
35°C	1033	1111	1900	2934	3012

* See Appendices A and B for experimental data

respiratory rates of xeric species are more intense, such that the production of organic material per unit time is markedly low.

In this study, relative photosynthesis was determined with various light and temperature regimes, employing turgid tissues and a CO_2 concentration of approximately 0.3%. A number of techniques have been used for measuring total gas exchange. No one is necessarily better in every respect than the others. A Precision Warburg apparatus was employed here simply because it was available. The determinations given in Table XIII and Appendices A and B were made during the height of the growing season. Each flask contained 0.10 gm of 1 cm sections of vigorous young leaves cut from plants in well-watered planters filled with native soil and exposed to full sunlight. In the photosynthetic series constant CO_2 concentration was obtained by using 1.5 ml of 0.5% $NaHCO_3$ in the center well and sidearm of standard ±15 ml flasks. Light was direct insolation. Respiration was determined at night in two series, one measuring total gas exchange and the other O_2 uptake with CO_2 absorbed by 0.3 ml of 20% KOH in the center well. When photosynthesis and respiration, as μl O_2 consumed or evolved per gram fresh weight are plotted against temperature and light intensity (Figure 14), it is apparent that though true photosynthesis in <u>Stipa pulchra</u> is higher under every regime, apparent photosynthesis in <u>Avena fatua</u> is superior at all temperatures at 2000 foot candles and most temperatures at 4000 foot candles.

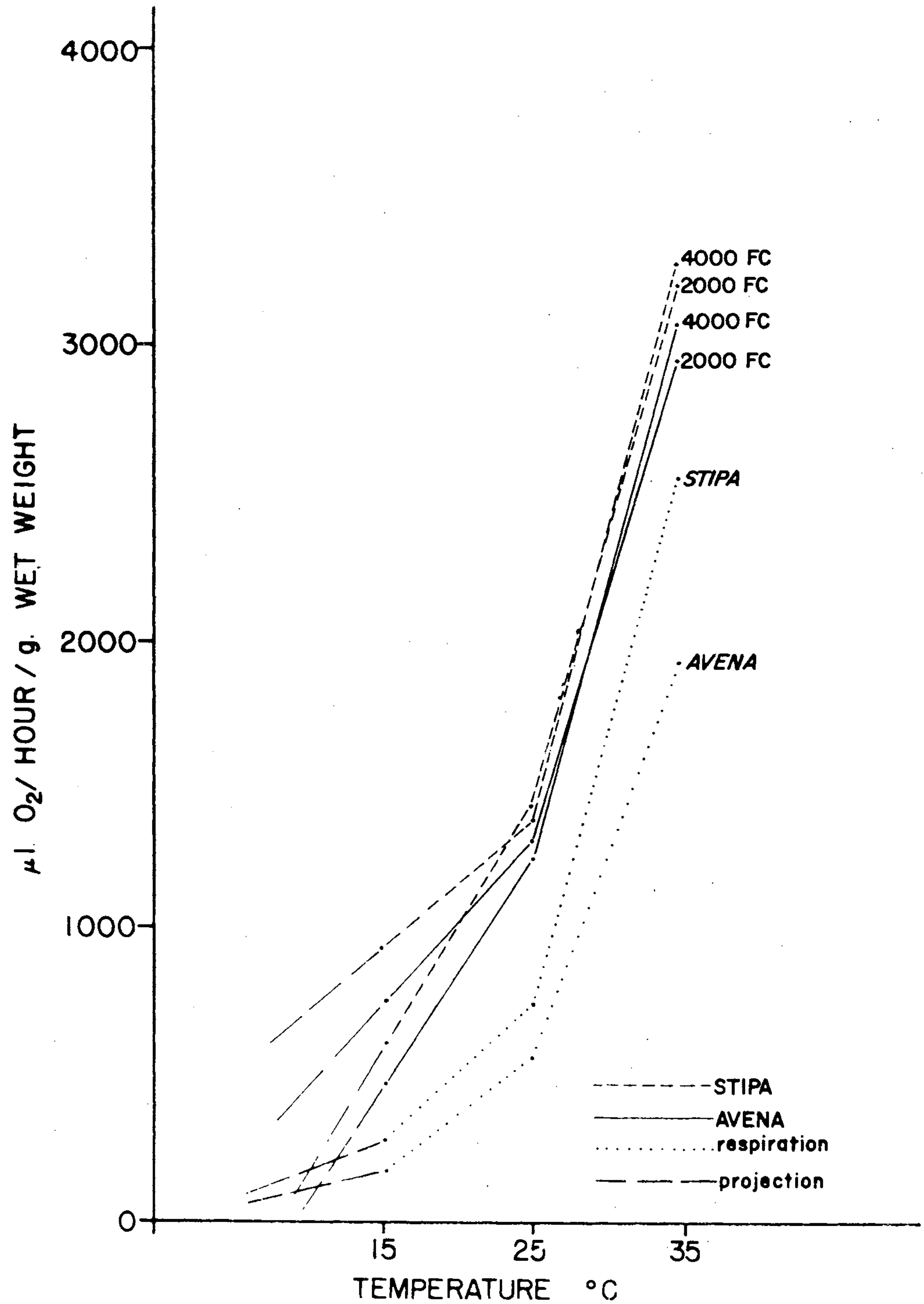

Figure 14. Relative Respiratory and True Photosynthetic Rates of <u>Stipa pulchra</u> and <u>Avena fatua</u>

The data suggest that Stipa is relatively more efficient at lower temperatures and Avena at higher temperatures. Since at a light intensity of 2000 foot candles and a temperature of 10°C both species approach their compensation points, little growth can be expected during the overcast and often cold midwinter season. At higher light intensities and/or temperatures photosynthesis is more rapid and similar for both species (Figure 15).

One might properly question whether the values established are absolute and whether they reflect the rates of the physiologically active portions of the blades. At present no techniques can enable the investigator to answer affirmatively on either count. Experimental conditions inevitably alter the activities of free living plants in ways which may be neither known nor measurable. Further, no tool exists which will enable measurement in leaves of rates for physiologically active cell constituents alone. Fresh weight was used because it was felt to provide a realistic means of comparing plants growing in a competetive relationship. Avena fatua does produce larger seedlings which grow more rapidly and are much taller at anthesis. As pointed out in the section on growth and germination, this vigor appears to result in the competetive exclusion of Stipa pulchra under certain climatic and edaphic conditions. Even though the methods outlined here have inherent limitations, the results seem to offer a partial explanation of this vigor in terms of greater photosynthetic efficiency in Avena fatua.

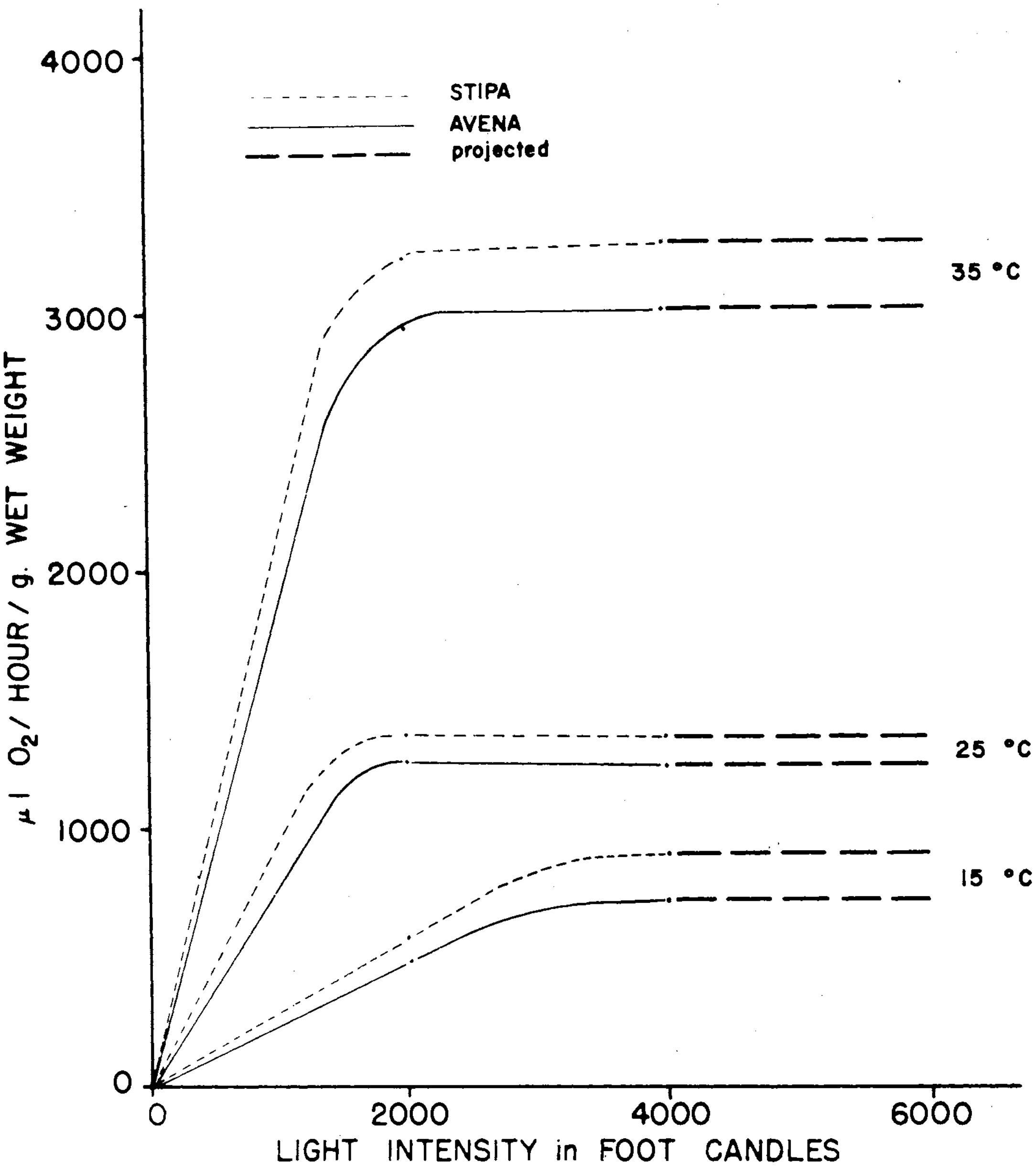

Figure 15. Relative Photosynthetic Rates of <u>Stipa pulchra</u> and <u>Avena fatua</u> at Different Light Intensities and Temperatures

Interrelationships

The methods and results outlined in the preceding pages give a clear indication of some of the physical and biological factors which are of importance in the dynamics of Stipa pulchra populations. As Billings (1952) pointed out in his analysis of the environmental complex, the consideration of single factors may lead to erroneous conclusions, for a change in the nature of any one may set off such a chain reaction in the ecosystem that it might well be termed a "trigger" factor. The dominance of the Mediterranean annual grasses, to the virtual exclusion of such native perennials as Stipa pulchra, was unquestionably triggered by overgrazing. Even so, the present distribution of that species just as surely reflects its environmental tolerances of the new ecosystem of which it is a part.

What are the tolerances of the local populations of Stipa pulchra in the study area? One of the most obvious can be seen in the relationship of spatial distribution to soil moisture. In the few feet across the ecotone between $Stipa_1$ and $Stipa_1$ Avena one encounters a complete change in the character of the community from a Stipa association to the California Annual Type. Soil moisture shows a similar change, with the $Stipa_1$ soil moisture maintaining a percentage almost twice that of the $Stipa_1$ Avena soil, and a reservoir of available water when the $Stipa_1$ Avena soil is below the permanent wilting point. This difference in soil moisture can in turn be related to soil structure. The Stipa soils studied are relatively high in colloidal clay, hold more water at field capacity, and can be expected to release it more slowly through the year. These same clay soils were found to have much more available phosphorus, and may be expected to have a high ion exchange capacity.

Germination of Stipa pulchra seed can also be related to soil moisture and soil nutrient supply. Though Stipa is dormant during the late summer, it remains green, and must inevitably use some water throughout the year. The small seedling, with its shallow root system, is subjected to considerable moisture stress. Where growth is limited by poor soils or severe competition, survival will depend on the supply of available water near the surface. Given equal water supplies, the much more vigorous growth of Stipa pulchra on $Stipa_1$ soil may indicate a higher phosphorus requirement than its annual competitors, at least for that particular soil. Growth is also affected by weather as it conditions physiological activity. Other factors being equal, Stipa was found to have a lower net photosynthetic rate than Avena fatua at most experimental temperatures and light intensities. This, in turn, was reflected in its much lower overall growth rate.

These interrelationships clearly illustrate some of the factors in the environmental complex of Stipa pulchra, but at the same time leave one with the feeling that much has yet to be learned. The most promising lines of future research seem to lie in the realm of comparative physiological ecology of competing species throughout the community.

CHAPTER IV

SUMMARY AND CONCLUSIONS

Among the grassland areas of the United States, or for that matter of the world, California is considered by many to be unique in that the perennial facies of the Valley Grassland, which are assumed to have been the climax vegetation over much of the state, have been almost entirely replaced by a relatively stable association of exotic annual grasses and forbs. Since this replacement began during the early days of Spanish exploration and settlement, we know very little of what actually happened. The foothills near Monterey provide an excellent opportunity for ecological analysis of isolated populations of the once dominant endemic perennial, *Stipa pulchra* Hitch. Three such sites were selected and studied over a period of two rain years with the intent of determining at least some of the environmental variables that delimit distribution in today's Valley Grassland Community.

An appreciation of the role of *Stipa pulchra* associations must rest in part upon a knowledge of the floristic history of the California Floral Province. Ample genetic and geologic evidence shows that the species represents a broad climatic and edaphic adaptation of an isolated relict of a population having northern affinities. It can be assumed to have become adapted to the developing Mediterranean climate under conditions of low grazing pressure for the great herds of grazing animals typical of other steppe-like communities have been unknown here in the Recent Epoch.

The weight of evidence suggests that aboriginal man had little large scale effect on vegetation in California. With the arrival of Spanish settlers in the late 1700s, the grassland associations were almost immediately subjected to intensive grazing pressure, supporting more cattle during the peak of expansion than they do today. Because these perennials were not adapted to such pressure, the range quickly declined. The simultaneous introduction of weedy Mediterranean annuals, pre-adapted to the California climatic pattern and with a reservoir of heterozygosity, made possible rapid adjustment to and dominance of the local grasslands. Competition for light and water between vigorous Mediterranean annuals and the endemic perennials, coupled with preferential grazing on Stipa by cattle, resulted in the destruction of bunches and the failure of reproduction such that Stipa pulchra disappeared over most of the range it may be assumed to have occupied.

The vegetational and environmental analyses undertaken in this study show clearly some of the factors limiting the success of the species today. In the past the Valley Grassland has been viewed from four somewhat subjective points of view. On the basis of presumed relicts in the central coast section of California and elsewhere, Clements (1920) concluded that a bunchgrass prairie dominated by *Stipa pulchra* was the climax under the valley climate. Cooper (1922) considered much of the grassland to be a fire subclimax, and Shreve (1927) thought of it as an edaphic climax on deeper soils. Wells (1962) concluded that the picture was not as simple as his predecessors had assumed, and that in the Central Coast Ranges disturbance by man was probably of primary importance in the establishment and maintenance of grassland associations. That these approaches to the problem were inadequate was established early in the course of research. Both laboratory and field methods were employed with intent to establish a balance between effective control and development under natural conditions. A two year series of such studies established the composition of the *Stipa* association and its sociological parameters. Perhaps most striking is the dominance of *Stipa pulchra* and the dense aerial cover it produces. *Stipa* seed was found to germinate well under all local conditions, and isolated seedlings grew vigorously when planted in the proper soil and provided with sufficient water. Conversely, when planted in poor soil or in competition with *Avena fatua* such seedlings scarcely grew at all, and seldom reached anthesis. Perhaps most significant was the clear and sharp limitation of *Stipa pulchra* to clay soils. Laboratory analysis indicated that these soils had a consistently higher percentage moisture and percentage available water than nearby soils dominated by annual grasses.

Further they were characterized by a much greater quantity of available phosphorus. Once established on these soils, Stipa competes well, and apparently precludes the dominance of Avena fatua and other large annual grasses. Be that as it may, manometric analysis of leaf sections from both species indicated relatively low apparent photosynthesis in Stipa at most temperatures and light intensities. This, coupled with the lack of competitive vigor in its seedlings explains, at least in part, why Stipa cannot reinvade the rich more friable soils on which it was once found, and on which it has been demonstrated to grow satisfactorily.

The findings outlined here indicate that Stipa pulchra may well have been the dominant grass through that part of the Valley Grassland and Foothill Woodland having agricultural type soils or heavy soils rich in mineral nutrients, but that well-drained sandy soils and those poor in mineral nutrients probably never supported such associations. Grazing and fire certainly have been factors in determining present distribution. Where Stipa has been destroyed on desirable sites by overgrazing or frequent burning, Mediterranean annuals now dominate. Certainly Stipa pulchra can return to protected sites, but the evidence indicates only to such areas as provide sufficient mineral nutrients and a supply of water through most of the year.

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APPENDICES

APPENDIX A

PHOTOSYNTHESIS OF AVENA FATUA AND STIPA PULCHRA AS O_2 EVOLVED PER 0.1 GM WET WEIGHT AT 4000 F.C. SUNLIGHT, DETERMINED WITH WARBURG MONOMETERS

TIME	TB		FLASK #3 AVENA			FLASK #4 STIPA			FLASK #6 AVENA			FLASK #7 STIPA		
15°C	Read'g	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.
1:22 pm	153	0	149	0		150	0		149	0		150	0	
:32	154	-1	160	+11	+10	157	+ 7	+ 6	162	+13	+12	160	+10	+ 9
:42	156	-3	166	+17	+14	166	+16	+13	170	+21	+18	170	+20	+17
:52	154	-1	162	+13	+12	167	+17	+16	168	+19	+18	169	+19	+18

Flask #3 Avena: μlO_2 = hkO_2 = 1.90 x 12 = 22.80/30 min. = 45.60/60 min.
Flask #4 Stipa: μlO_2 = 1.89 x 16 = 30.24/30 min. = 60.48/60 min.
Flask #6 Avena: μlO_2 = 1.82 x 18 = 32.76/30 min. = 65.52/60 min.
Flask #7 Stipa: μlO_2 = 1.85 x 17 = 31.45/30 min. = 62.90/60 min.

25°C	TB Read'g	TB Corr.	FLASK #3 AVENA			FLASK #4 STIPA			FLASK #6 AVENA			FLASK #7 STIPA		
12:03 pm	148	0	148	0		147	0		150	0		149	0	
:13	149	-1	157	+ 9	+ 8	155	+ 8	+ 7	158	+ 8	+ 7	160	+11	+10
:23	151	-3	165	+17	+14	163	+16	+13	165	+15	+12	166	+17	+14
:33	153	-5	172	+24	+19	166	+19	+14	173	+23	+18	173	+24	+19

Flask #3 Avena: μlO_2 = 1.83 x 19 = 34.77/30 min. = 69.54/60 min.
Flask #4 Stipa: μlO_2 = 1.83 x 14 = 25.62/30 min. = 51.34/60 min.
Flask #6 Avena: μlO_2 = 1.82 x 18 = 32.76/30 min. = 65.52/60 min.
Flask #7 Stipa: μlO_2 = 1.98 x 19 = 37.62/30 min. = 75.24/60 min.

35°C	TB Read'g	TB Corr.	FLASK #2 STIPA			FLASK #3 STIPA			FLASK #4 AVENA			FLASK #6 AVENA		
12:28 pm	151	0	148	0		150	0		148	0		150	0	
:33	150	+1	149			151	+ 1	+ 2	154	+ 6	+ 7	154	+ 4	+ 5
:38	148	+3	147			155	+ 5	+ 8	158	+10	+13	159	+ 9	+12
:43	148	+3	148			158	+ 8	+11	161	+13	+16	166	+16	+19
:48	148	+3	148			160	+10	+13	163	+15	+18	171	+21	+24

Flask #2 Stipa: LEAK
Flask #3 Stipa: μlO_2 = 1.77 x 13 = 23.01/20 min. = 69.03/60 min.
Flask #4 Avena: μlO_2 = 1.77 x 18 = 31.86/20 min. = 95.58/60 min.
Flask #6 Avena: μlO_2 = 1.76 x 24 = 42.24/20 min. =126.72/60 min.

PHOTOSYNTHESIS OF AVENA FATUA AND STIPA PULCHRA AS O_2 EVOLVED PER 0.1 GM WET WEIGHT AT 2000 F.C. SUNLIGHT, DETERMINED WITH WARBURG MONOMETERS

TIME	TB		FLASK #1 AVENA			FLASK #3 STIPA			FLASK #4 AVENA			FLASK #5 STIPA		
15°C	Read'g	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.
2:38 pm	149	0	149	0		147	0		148	0		149	0	
:48	150	-1	159	+10	+ 9	153	+ 6	+ 5	150	+ 2	+ 1	158	+ 9	+ 8
:58	151	-2	165	+16	+14	152	+ 5	+ 3	152	+ 4	+ 2	162	+13	+11
3:08	151	-2	166	+17	+15	154	+ 7	+ 5	157	+ 9	+ 7	162	+13	+11
:18	152	-3	168	+19	+16	158	+11	+ 8	157	+ 9	+ 6	165	+16	+13

Flask #1 Avena: μlO_2 = hkO_2 = 16 x 1.93 = 30.88/40 min. = 46.32/60 min.
Flask #3 Stipa: μlO_2 = 8 x 1.90 = 15.20/40 min. = 22.80/60 min.
Flask #4 Avena: μlO_2 = 6 x 1.89 = 11.34/40 min. = 17.01/60 min.
Flask #5 Stipa: μlO_2 = 13 x 1.91 = 24.83/40 min. = 37.25/60 min.

25°C	TB Read'g	TB Corr.	FLASK #1 STIPA			FLASK #3 STIPA			FLASK #4 AVENA			FLASK #6 AVENA		
4:02 pm	149	0	150	o		149	0		147	0		149	0	
:12	149	0	157	+ 7	+ 7	154	+ 5	+ 5	159	+12	+12	157	+ 8	+ 8
:22	149	0	161	+11	+11	160	+ 9	+ 9	161	+14	+14	161	+12	+12
:32	149	0	168	+18	+18	167	+16	+16	168	+21	+21	167	+18	+18

Flask #1 Stipa: μlO_2 = 18 x 1.87 = 33.66/30 min. = 67.32/60 min.
Flask #3 Stipa: μlO_2 = 16 x 1.83 = 29.28/30 min. = 58.56/60 min.
Flask #4 Avena: μlO_2 = 21 x 1.83 = 38.43/30 min. = 76.86/60 min.
Flask #6 Avena: μlO_2 = 18 x 1.82 = 32.76/30 min. = 65.52/60 min.

35°C	TB Read'g	TB Corr.	FLASK #2 STIPA		FLASK #3 STIPA		FLASK #4 AVENA		FLASK #6 AVENA	
4:40 pm	149	0	147	0	149	0	148	0	150	0
:50	149	0	155	+ 8	156	+ 7	160	+12	157	+ 7
:55	149	0	159	+12	159	+10	160	+18	161	+11
:60	149	0	160	+13	161	+12	172	+24	165	+15

Flask #2 Stipa: μlO_2 = 1.57 x 13 = 20.41/20 min. = 61.23/60 min.
Flask #3 Stipa: μlO_2 = 1.77 x 12 = 21.24/20 min. = 63.72/60 min.
Flask #4 Avena: μlO_2 = 1.77 x 24 = 42.48/20 min. =127.44/60 min.
Flask #6 Avena: μlO_2 = 1.76 x 15 = 26.40/20 min. = 79.20/60 min.

APPENDIX B

RESPIRATION OF AVENA FATUA AND STIPA PULCHRA AS O_2 CONSUMED PER 0.1 GM WET WEIGHT IN DARKNESS, DETERMINED WITH WARBURG MONOMETERS

TIME	TB		FLASK #2 AVENA			FLASK #3 AVENA			FLASK #4 STIPA			FLASK #7 STIPA		
15°C	Read'g	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.
5:20 pm	154	0	148	0		147	0		147	0		148	0	
:30	154	0	147	- 1	- 1	147	0		145	- 2		150	+ 2	
:40	152	+2	143	- 5	- 3	143	- 4	- 2	141	- 6	- 4	146	- 2	0
:50	151	+3	140	- 8	- 5	140	- 7	- 4	136	-11	- 8	139	- 9	- 6

Flask #2 Avena: $\mu l O_2 = hk_{O_2} = 5 \times 1.68$ = 8.40/30 min. = 16.80/hr

Flask #3 Avena: $\mu l O_2 = 4 \times 1.90$ = 7.60/30 min. = 15.20/hr

Flask #4 Stipa: $\mu l O_2 = 8 \times 1.89$ = 15.12/30 min. = 30.24/hr.

Flask #7 Stipa: $\mu l O_2 = 6 \times 1.98$ = 11.88/30 min. = 23.76/hr.

25°C	TB		FLASK #2 AVENA			FLASK #3 AVENA			FLASK #6 STIPA			FLASK #7 STIPA		
6:04 pm	154	0	147	0		147	0		148	0		149	0	
:14	156	-2	139	- 8	-10	139	- 8	-10	138	-10	-12	138	-11	-13
:24	155	-1	135	-12	-13	135	-12	-13	134	-14	-15	133	-16	-17
:34	156	-2	133	-14	-16	133	-14	-16	131	-17	-19	131	-18	-20

Flask #2 Avena: $\mu l O_2 = 16 \times 1.63$ = 26.08/30 min. = 52.16/hr.

Flask #3 Avena: $\mu l O_2 = 16 \times 1.83$ = 29.28/30 min. = 58.56/hr

Flask #6 Stipa: $\mu l O_2 = 19 \times 1.82$ = 34.58/30 min. = 69.16/hr.

Flask #7 Stipa: $\mu l O_2 = 20 \times 1.91$ = 38.20/30 min. = 76.40/hr.

35°C	TB		FLASK #2 AVENA			FLASK #3 AVENA			FLASK #6 STIPA			FLASK #7 STIPA		
6:44 pm	154	0	148	0		147	0		148	0		150	0	
:49	158	-4	128	-20	-24	127	-20	-24	122	-26	-30	131	-19	-25
:54	158	-4	120	-24	-28	119	-28	-32	113	-35	-39	118	-32	-36
:59	154	0	114	-34		113	-34		107	-41		107	-43	

Flask #2 Avena: $\mu l O_2 = 39 \times 1.57$ = 61.23/20 min. =183.69/hr

Flask #3 Avena: $\mu l O_2 = 37 \times 1.77$ = 65.49/20 min. =196.47/hr

Flask #6 Stipa: $\mu l O_2 = 46 \times 1.76$ = 80.96/20 min. =242.88/hr

Flask #7 Stipa: $\mu l O_2 = 48 \times 1.85$ = 88.80/20 min. =266.40/hr

RESPIRATION IN STIPA PULCHRA AND AVENA FATUA LEAF SEGMENTS AS CARBON DIOXIDE EVOLVED PER 0.1 GM WET WEIGHT IN WARBURG RESPIROMETERS, WITH DETERMINATION OF RESPIRATORY QUOTIENTS

RESPIRATION - Total Gas Exchange - 15°

TIME	TB		FLASK #2 STIPA			FLASK #3 STIPA			FLASK #6 AVENA			FLASK #7 AVENA		
	Read'g	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.
3:45 pm	154	0	148	0		147	0		148	0		149	0	
4:05	158	-4	152	+ 4	0	150	+ 3	- 1	151	+ 3	- 1	151	+ 2	- 1
:15	159	-5	153	+ 3	0	151	+ 4	- 1	152	+ 4	- 1	152	+ 3	- 2
:25	156	-2	149	+ 1	- 1	149	+ 2	0	148	0	- 2	147	+ 2	- 4
:35	155	-1	149	+ 1	0	147	0	- 1	148	0	- 1	148	+ 1	- 2
:45	154	0	148	0	0	146	- 1	- 1	147	- 1	- 1	147	- 2	- ?
:55	154	0	148	0	0	147	0	0	147	- 1	- 1	147	- 2	- 2

$\mu l CO_2$ evolved Flask #2 $= h - \frac{x_{O_2}}{k_{O_2}} \; k_{CO_2}$

$= (0 + 27/1.68)(1.82)$
$= 29.25$

$\mu l CO_2$ evolved Flask #6 $= h - \frac{x_{O_2}}{k_{O_2}} \; k_{CO_2}$

$= (-1 + 16/1.89)(2.02)$
$= 15.89$

RESPIRATION - Total Gas Exchange - 25°

TIME	TB		FLASK #3 STIPA			FLASK #4 STIPA			FLASK #6 AVENA			FLASK #7 AVENA		
	Read'g	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.
5:15 pm	153	0	147	0		147	0		148	0		149	0	
:25	155	-2	148	+ 1	- 1	149	+ 2	0	152	+ 4	+ 2	151	+ 2	0
:35	157	-4	150	+ 3	- 1	151	+ 4	0	155	+ 7	+ 3	152	+ 3	- 1
:45	158	-5	153	+ 6	+ 1	154	+ 7	+ 2	154	+ 6	+ 1	155	+ 6	+ 1
:55	157	-4	152	+ 5	+ 1	153	+ 6	+ 2	154	+ 6	+ 2	154	+ 5	+ 1

$\mu l CO_2$ evolved Flask #2 $= h - \frac{x_{O_2}}{k_{O_2}} \; k_{CO_2}$

$= (2 + 72.78/1.63)(1.63)$
$= 76.04$

$\mu l CO_2$ evolved Flask #7 $= h - \frac{x_{O_2}}{k_{O_2}} \; k_{CO_2}$

$= (2 + 55.36/1.91)(2.02)$
$= 62.57$

RESPIRATION - Total Gas Exchange - 35°

TIME	TB		FLASK #2 STIPA			FLASK #4 STIPA			FLASK #6 AVENA			FLASK #7 AVENA		
	Read'g	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.	Read'g	Change	Corr.
6:18 pm	148	0	149	0		148	0		148	0		148	0	
:23	143	+5	145	- 4	+ 1	145	- 3	+ 2	145	- 3	+ 2	145	- 3	+ 2
:28	144	+4	146	- 3	+ 1	147	- 1	+ 3	146	- 2	+ 2	146	- 2	+ 2
:33	145	+3	147	- 2	+ 1	147	- 1	+ 2	147	- 1	+ 2	146	- 2	+ 1
:35	142	+6	144	- 5	+ 1	145	- 3	+ 3	145	- 3	+ 3	144	- 4	+ 2

$\mu l CO_2$ evolved Flask #2 $= h - \frac{x_{O_2}}{k_{O_2}} \; k_{CO_2}$

$= (3 + 254.64/1.57)(1.65)$
$= 273.17$

$\mu l CO_2$ evolved Flask #7 $= h - \frac{x_{O_2}}{k_{O_2}} \; k_{CO_2}$

$= (6 \times 190.08/1.85)(1.93)$
$= 209.89$

<u>Respiratory Quotients (ratio of CO_2 per indicated flask and mean of O_2 consumed):</u>

15°C - Stipa Flask #2 = 29.25/27.00 = <u>1.08</u>

Avena Flask #6 = 15.89/16.00 = <u>0.99</u>

25° - Stipa Flask #2 = 76.04/72.78 = <u>1.05</u>

Avena Flask #7 = 62.57/55.36 = <u>1.13</u>

35° - Stipa Flask #2 = 273.17/254.64 = <u>1.07</u>

Avena Flask #7 = 209.89/190.08 = <u>1.10</u>

VITA

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