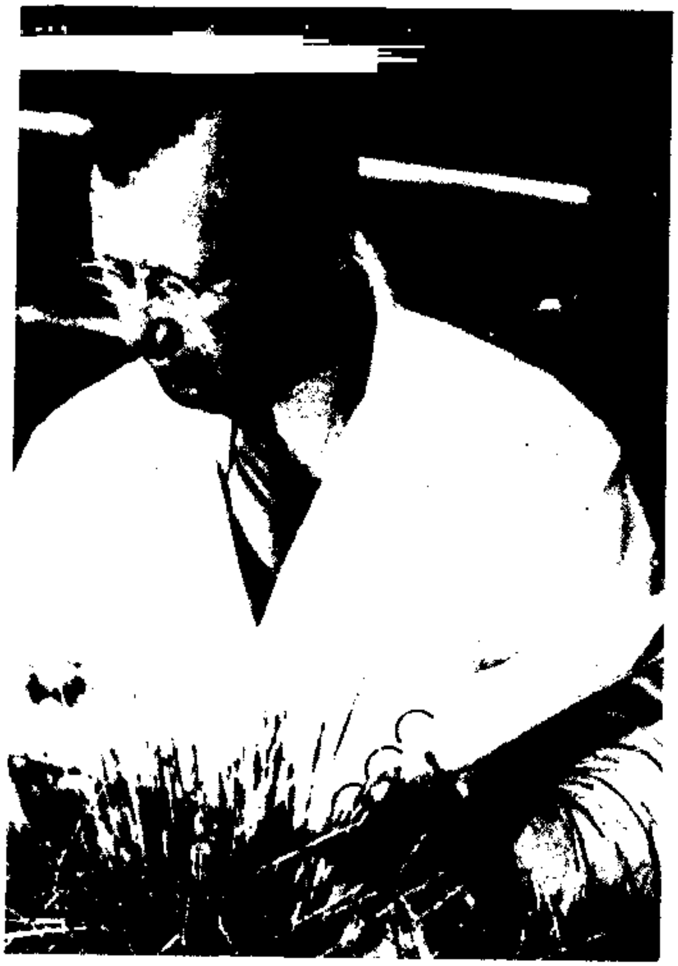
# EXPERIMENTAL STUDIES ON THE NATURE OF SPECIES. VI.



Dr. fens C. Clausen,
who initiated the present investigations and
carried much of the burden in their execution.

# EXPERIMENTAL STUDIES ON THE NATURE OF SPECIES

## VI. INTERSPECIFIC HYBRID DERIVATIVES BETWEEN FACULTATIVELY APOMICTIC SPECIES OF BLUEGRASSES AND THEIR RESPONSES TO CONTRASTING ENVIRONMENTS

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# PREFACE

This volume of the series *Experimental Studies on the Nature of Species* summarizes the results of interspecific-crossing experiments involving polyploid, facultatively apomictic species of grasses. The accumulated data place new light on the evolutionary significance of polyploidy and apomixis among higher plants, and outline the potentialities and limitations of such experiments for synthesizing new hybrid lines of agronomic value.

The genetic and cytologic complexities of those species that have evolved these reproductive devices tend to discourage experimental work designed to analyze their biological structure; yet such studies offer a challenge to plant biologists that cannot be ignored. Although the experimental work reported here was performed a number of years ago (1943-1960), the very extensive records that were preserved make possible now a comprehensive and critical evaluation of the results.

This endeavor was primarily the outcome of an idea sparked by the late Dr. Jens C. Clausen of the experimental taxonomy group of the Carnegie Institution's Department of Plant Biology. Although polyploidy and apomixis among higher plants were discussed in Volumes I and II of this series, the final impetus for initiating the extensive experimental work reported here was the pressure of World War II. At the start of the war, the experimental taxonomy group decided to devote some of its effort toward developing plants that might enhance world food supply. Since then, the pressure of increasing human populations everywhere has continued to accentuate the need for improved food production. It was Dr. Clausen's hope that by crossing facultatively apomictic grasses differing in desirable agronomic characteristics, "instant" new, self-reproducing "super-strains" having enhanced yield and tolerance to climatic extremes might be developed. Although this dream was not realized, a number of hybrid lines of considerable promise were synthesized and tested in a wide range of environments, and much was learned about biological relationships and breeding characteristics of partially apomictic species-complexes that we hope will be helpful to future investigators.

## ACKNOWLEDGEMENTS

The work summarized in this publication would not have been possible without the very extensive help of many people during the 16 years of active data gathering. Although we, the present authors, assume full responsibility for the contents of this volume, our contribution represents only a small fraction of the overall effort.

The late Dr. Jens Clausen, the prime initiator of the project, personally assumed many of the tasks of making interspecific crosses, supervising cytological studies, and studying the responses of hybrid lines and their parents at the many field test stations. He enlisted the aid of many collaborators both in the United States and in Europe. Prior to his death in November 1969, he worked on the analysis of the massive data that were accumulated, but was unable to bring the work to final publication. During 1943-1951, Dr. David Keck participated in field surveys of potential sources of breeding stocks and worked with other members of the Carnegie staff in observations of field tests. Dr. Paul Grun, Miss Marguerite Hartung, Miss Lois Cox, and Mr. Edward Triplett contributed to painstaking cytological studies, as well as to other phases of the work.

Our principal institutional collaborator was the U.S. Soil Conservation Service. Dr. J. M. Crist and Dr. A. L. Hafenrichter of the Pacific Division made available to us their extensive growing facilities of the regional nurseries as well as the thoroughly documented living collections of grass material for crossing experiments. Over a period of 15 years, Dr. Hafenrichter and his staff grew extensive, meticulously monitored plantings of numerous interspecific hybrids and their derivatives through as many as four generations at the various Soil Conservation Service nurseries. We are especially indebted to the following members of Dr. Hafenrichter's staff: Mr. John Schwendimen, Mr. Harold W. Miller, Me. H. Hoaglund, Dr. Lowell A. Mullen, Mr. Linn Guenther, Mr. Virgil B. Hawk, Mr. Paul Dickey, Mr. W. E. Chapin, Mr. Donald S. Douglas, and Mr. John Harris.

We are likewise indebted to Dr. A. A. Hanson of the Agricultural Research Service, Beltsville, Maryland, who organized and supervised a series of regional tests at state experiment stations at key locations throughout the United States during 1955-1958. Many cooperating agronomists provided help in establishing these field tests and in making them freely available to us for study. These collaborators include Dr. H. B. Musser, Pennsylvania State University, State College, Pennsylvania; Dr. T. Jackson Smith, Agricultural Experiment Station, Blacksburg, Virginia; Dr. E. L. Nielsin, University of Wisconsin, Madison; Dr. H. H. Kramer, Purdue University, Lafayette, Indiana; Dr. R. R. Buckner, Lexington, Kentucky; Dr. E. Marion Brown, Agricultural Experiment Station, Columbia, Missouri; Dr. H. D. Ellzey, Jr., Franklinton, Louisiana; Dr. K. L. Anderson, Agricultural Experiment Station, Manhattan, Kansas; Dr. J. R. Harlan, Oklahoma A & M College, Stillwater, Oklahoma; Dr. R. E. Stitt, Agricultural Experiment Station, Bozeman, Montana; Dr. H. H. Rampton, Agricultural Experiment Station, Corvallis, Oregon; Dr. H. L. Thomas, University of Minnesota, Minneapolis; and Dr. R. Merton Love, Department of Agronomy, University of California, Davis.

To our collaborators in Europe we are indebted for their keen interest and active participation in test plantings of many experimental hybrids at latitudes higher than are found in the United States and in localities with divergent climates. These include the late Dr. J. W. Gregor and Dr. R. Patricia J. Watson, Scottish Plant Breeding Station, Penlandfield, Roslin, Midlothian; Dr. Paul Solberg, Experimental Station for the Mountain Districts, Volbu, Valdres, Norway; Dr. Erik Akerberg, Director of the Uppsala branch of the Swedish Plant Breeding Association of Svalöf; and Drs. H. N. and K. J. Fransden of the Danish Cooperatives, 0toftegaard, Denmark. Dr. Ledyard Stebbins, University of California, Davis, and Dr. Olle Björkman, Carnegie Institution of Washington, reviewed the manuscript critically and contributed valuable suggestions, for which we are grateful.

The late Dr. H. A. Spoehr, former director of the Carnegie Department of Plant Biology, encouraged our experimental taxonomy group to embark on this program, and Dr. C. Stacy French, who succeeded him, continued his moral support. Finally, to Dr. Winslow Briggs, the present director, we owe our thanks for his encouragement in bringing this work to publication.

In the preparation of this manuscript, Mrs. Marylee H. Eldridge devoted much conscientious effort in the processing and interpreting of data. Miss Jennifer M. Wootton made many detailed drawings of parental and hybrid grasses, some of which are included in this volume. Mr. Merrill Adams drafted most of the graphs, and Mrs. Norma J. Powell did the final typing.

Voucher material along with original data relating to these investigations will be deposited in the Dudley Herbarium of Stanford University, now located at the California Academy of Sciences, Golden Gate Park, San Francisco.

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CARNEGIE INSTITUTION OF WASHINGTON
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*January 1982*

# CONTENTS

# I

# WORKING PRINCIPLES, METHODS, AND MATERIALS

# I

# WORKING PRINCIPLES, METHODS, AND MATERIALS

Initially, we attempted crossings within the genera *Agropyron, Elymus,* and *Poa,* all known to include species of important forage grasses. It soon became evident that if we were to make effective progress, it would be necessary to restrict our efforts to a single genus. The logical choice was the bluegrass genus *Poa,* containing approximately 200 named taxa widely distributed in regions of the world varying from cool-temperate to arctic, most of them extensively grazed by foraging animals. It was also necessary, in order to keep the investigations within feasible bounds, to restrict experimental crossings to relatively few species. Despite these limitations, the program in execution proved long and extensive.

CRITERIA FOR THE SELECTION OF TAXA USED IN THE CROSSING EXPERIMENTS. Since very little was known initially as to which interspecific combinations might be successful, we adopted the following general guidelines for the selection of parental materials:

1. Both parents should have desirable forage characteristics.
2. They should differ widely enough in morphological characteristics so that hybrids could be readily recognized.
3. The parents preferably should have originated from areas having contrasting climates.
4. The forms to be crossed should be reasonably apomictic in their seed production.

A fifth practical consideration was the ready availability of breeding stocks meeting the above requirements. The extensive living collections of diverse species and ecotypes of *Poa* maintained by the Soil Conservation Service of the United States Department of Agriculture, especially at the Western Regional Nurseries at Pullman, Washington, and Pleasanton, California, became our major source of parental breeding stock. Further additions included collections made by the Carnegie staff and by other contributors.

SPECIES USED IN INTERSPECIFIC HYBRIDIZATION. Crossing combinations were made mainly between species within three sections of the genus *Poa* as recognized by Hitchcock (1950), Le., the *Pratenses, Scabrelhe,* and *Ncvadenses.* A fourth group, represented by *Poa caespitosa* of the southern hemisphere in New Zealand and Australia, was included in later crossings. The species within the sections as recognized by Hitchcock are reasonably distinctive if one is considering the biological complexity of the entire genus, *Poa,* a feature that will be discussed at length in later pages.

Figure 1 is a generalized diagram indicating the principal interspecific crossing combinations that were made. It is purposely simplified, in that the lines connecting the pairs of "species" (represented by circles) indicate only that hybrid combinations were made between these complex entities. Virtually all the "species'* represented in figure 1 are themselves complexes composed of distinguishable ecotypes* and other variant forms.

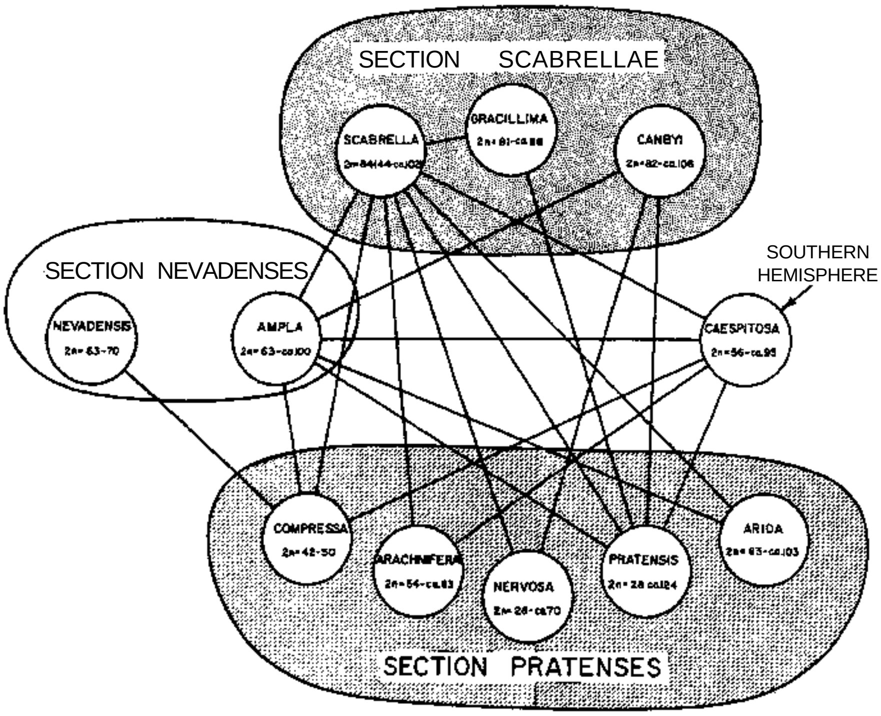

Figure 1. Simplified crossing diagram indicating the major taxa involved in making interspecific crossings in the bluegrass genus *Poa.*

INTRASPECIFIC VARIATION IN CYTOLOGICAL AND MORPHOLOGICAL CHARACTERISTICS. In figure 1 the somatic *(2n)* chromosome numbers for each species-complex are indicated as general ranges rather than a single number, since it is clearly established that individuals of *Poa* within a species may have very different chromosome numbers. Examples of such chromosomal variation are shown in figure 2, illustrating camera lucida drawings of somatic metaphase plates of root-tip cells with *Poa ampla, P. pratensis, P. arida,* and *P.*

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* The term "ecotype" as here used is a genetically differentiated and recognizably distinct form of a species associated with a difference in climatic or edaphic factors (Turesson, 1922, 1925).

*scabrella.* The three plants of *Poa ampla* for which chromosomes are shown in the extreme left row of figure 2 were morphological variants, or biotypes,[*] originating from a single local population endemic to the vicinity of Albion, Washington, collected by Dr. Lowell A. Mullen of the U.S. Soil Conservation Service. The range $2n$ = 56—145 is striking and perhaps somewhat unusual for a single local population of *Poa.* The population from which these plants were sampled consisted of field-grown seedlings taken from the original collection site. The prevailing chromosome number of the most frequently occurring "normal" type of this rather distinctive ecotype of *Poa ampla* is $2n$ = 64 (Hartung, 1946). An individual of the latter type was used in the crossings to be described in Chapter II. Detailed studies on chromosome number and meiotic pairing in parents and hybrid derivatives by Grun (1952, 1954, 1955a, 1955b) reveal the complexities of genome behavior in these polyploid grasses.

The variation in chromosome number in *Poa pratensis* shown in figure 2 (second row from left) is typical for this very widely distributed species. The two chromosome plates shown at the center and bottom are from two individuals, scarcely distinguishable from each other, growing in a meadow at elevation 1400 meters at the Carnegie Institution's Mather transplant station in Tuolumne County, California. Other individuals within this same population ranged in $2n$ = 49-69. A morphologically typical plant of this population with $2n$ = 54 chromosomes was used in a series of crossings with the Albion strain of *Poa ampla,* described in Chapter II. The somatic plate of *Poa pratensis* shown at the top of figure 2 is from a highly apomictic maritime ecotype originally collected from coastal bluffs overlooking the Pacific at Newport, Oregon, by the late W. L. Lawrence. This highly constant, freely seeding apomictic form proved to be a useful turf grass and was introduced into the commercial trade by the Ferry-Morse Seed Company of Mountain View, California, in about 1952-1953 under the trade name "C-l Newport Bluegrass." This strain was in 1977 still widely used in commercial lawn-grass seed mixtures.f This clone was used only to a limited extent in our crossing experiments.

Extensive cytological, embryological, and breeding studies on members of the *Poa pratensis* complex have been made by Scandinavian and other investigators. Miintzing (1933) uncovered the first real evidence of apomixis in *P. pratensis* and the related species P. *alpina.* He found that cultures of biotypes originating from different localities in northern Europe ranged in chromosome number *(2n)* from 49 to 82; within a given biotype from a single locality, seed progeny were found to vary in 2«, for example, in one biotype from 66 to 68,

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[*] The term "biotype" is used here to denote an individual variant within the same local population or ecotype and its offspring.

t Persona! communication to the authors from the Ferry-Morse Seed Company.

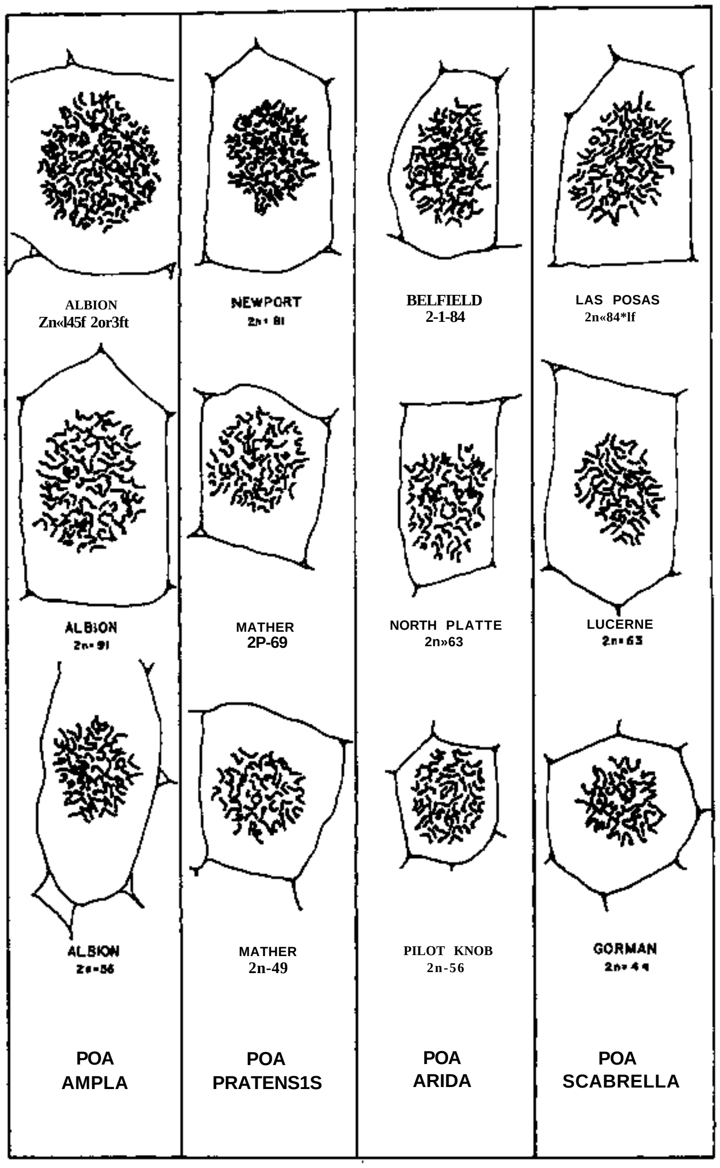

Figure 2. Camera lucida drawings of metaphase chromosome plates of root-tip cells of individual plants of *Poa* grown as seedlings at the Stanford nursery of the Carnegie Institution in 1944-1945. All drawings are at magnification approximately 1500 X. *Poa ampla:* upper, from plant No. 4274-18; center, from plant No. 4274-11; lower, from plant No. 4274-20. *Poa pratensis:* upper, from plant No. 4466-1; center, from plant No. 4253-7; lower, from plant No. 6411-11. *Poa arida:* upper, from plant No. 4616-11; center, from plant No. 4262-1; lower, from plant No. 4614-11. *Poa scabrella:* upper, from plant No. 4212-7; center, from plant No. 4217-17; lower, from plant No. 4495-1. For details of plant origins, see table 3.

compared with from 80 to 81 in another. In contrast, another form showing great morphological constancy yielded progeny which consistently had $2n$ = 49 chromosomes. On the basis of these and other studies with both sexual and apomictic forms of *Poa alpina* from Sweden and Switzerland, Miintzing (1940, 1966) concluded (1) that in at least some strains of P. *pratensis* and P. *alpina,* asexual reproduction is the prevailing mode of seed reproduction, and (2) in other strains sexual reproduction prevails (especially in P. *alpina);* sexuality is generally associated with lower chromosome numbers and morphological variability, while apomixis is mostly associated with higher chromosome numbers, aneuploidy, and morphological uniformity although aberrant types occur with varying frequency, depending upon the biotype.

These pioneer studies by Miintzing have been richly supplemented by subsequent contributions by him and other Scandinavian colleagues. The occurrence of pseudogamy in *Poa pratensis* and its importance for apomictic reproduction was demonstrated by Åkerberg (1936, 1942), who found that fertilization of the endosperm by foreign pollen stimulated the development of apogamous embryos. He also described the occurrence of polyembryony with the occasional production of twin seedlings from a single seed. The extreme polymorphism, variable chromosome number *(In* = 28-124),* and varying degrees of facultative apomixis, which altogether make the taxonomic delimitation of forms within *Poa pratensis* difficult, are also dealt with by this author.

The cytological and embryological studies by Kiellander (1941, 1942) and later by Nygren (1950) on *Poa pratensis* and other *Poa* species reveal with further clarity the complexity of alternate possibilities in the development of facultatively apomictic species. The excellent plates in Nygren's paper portraying many examples of various types of chromosomal behavior in *Poa* are highly revealing.

The balance between sexual and apomictic reproduction in *Poa pratensis* was analyzed by Grazi, Umaerus, and Âkerberg (1961) in a single clone and found to be both complex and delicate. Analyses of progeny tests in our investigations strongly indicate that this balance may be altered by environmental factors, as will be discussed in later chapters.

In figure 2, examples of variation in chromosome number in *Poa arida* and P. *scabrella* from different geographical areas indicate that the cytogenetic complexity so clearly established in *Poa pratensis* and its related forms also prevails in those other morphologically and geographically distinct entities of *Poa* that are characterized by high polyploidy and facultative apomixis.

Figure 3 illustrates examples of morphological variants within *Poa ampla*$_P$ *P. pratensis,* and P. *scabrella,* as seen when all are grown at Stanford. In these

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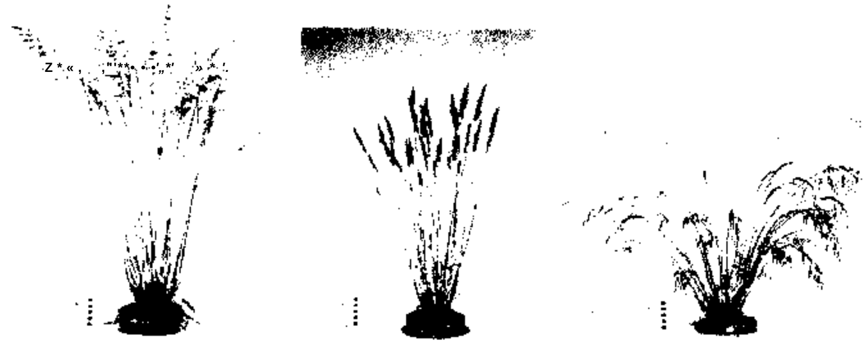
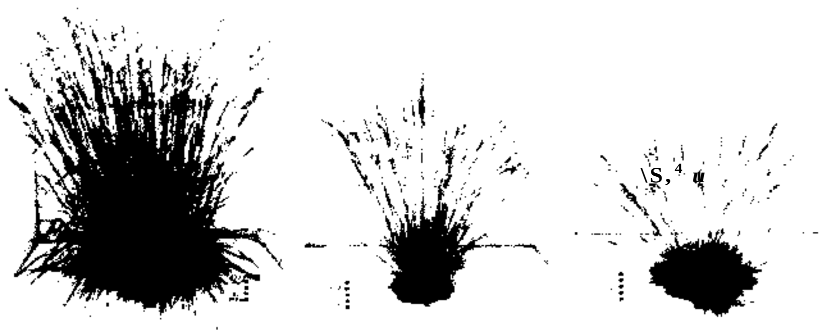
* The highest chromosome number reported in the genus ***Poa*** known to the authors i$ 2» ** 263—265 in *Pm iiicmsa* from the Auckland Islands (Hair and **Bcuzenberg,** 1961).



POA SCABRELLA



POA AMPLA

POA PRATENSIS

examples the different forms of each species can be recognized as distinct climatic races, or ecotypes, that have evolved in response to natural selection, as first elucidated by Turesson (1922, 1925) and substantiated by the extensive transplant and breeding experiments reported in Volumes I (1940), III (1950), and IV (1958) of the present series, as well as by other independent investigators (Stapledon, 1928; Cooper, 1954; Bradshaw, 1960; Gregor, 1939; Pegtel, 1976). Such genetically based ecotypic differences are clearly of importance in the synthesis of new interspecific hybrid derivatives suitable for different environments, and they will be dealt with in some detail in the following chapters describing different hybrid recombinations.

ABERRANTS AND OTHER SPONTANEOUS INTRAPOPULATION VARIANTS. In contrast with recognizable differences between climatically differentiated ecological races, or ecotypes, as illustrated in figure 3, are the more or less fequently occurring "off-types," or "aberrants," that appear in progenies of *Poa* from seed collected from individual plants that were self- or open-pollinated or from pooled samples of seed taken from different individuals of a local population. The embryological and cytological basis for the formation of such variants is inferred from the results of the studies reviewed above. The frequency of such aberrants within progenies is correlated with the number of sexually reproduced seeds. Such aberrants tend mostly to be less vigorous than material-type progeny reproduced by apomixis, although "plus aberrants" having enhanced vigor in a given environment compared with the prevailing apomictic type may occur. Aberrant progeny having chromosome numbers markedly lower or higher than the maternal parent may result from the deletion or addition of partial sets of genomes of the basic multiple of seven chromosomes prevalent in the genus *Poa.* The variants in chromosome number of *Poa ampla* illustrated in figure 2 are examples.

The distinction between genetically differentiated ecotypic differences and intrapopulation aberrants (which also may be genetically controlled) cannot be made with certainty based only on morphological or cytological differences. In the general overall biosystematic picture of relationships between and within

Figure 3. Examples of ecotypic variation within three sections of *Poa,* as expressed when grown in the same environment at Stanford. All plants are shown to the same scale; the black and white scale is 10 cm high, and each square is 1 cm. *Poa scabreila:* left, plant 4214-4 from near Watsonville, Santa Cruz County, California, at elevation 30 meters; center, 4217-12 from Lucerne, Lake County, California, at elevation 410 meters; right, 4493-1 from Margan Ranch, Riverside County, California, at elevation 100 meters. *Poa ampla:* left, plant 4273, line 1 (apomict of CIW 4183 from Albion, Whitman County, Washington, at elevation 610 meters; center, 4196-11, from Heise Hot Springs, E. Bonneville County, Idaho, at elevation 1525 meters; right, 4186-14 from near Enterprise, Wallowa County, Oregon, at elevation 1065 meters. *Poa pratensis:* left, plant 4252-11 from near Groveland, Tuolumne County, California, at elevation ^15 meters; center, 4466-1 from Newport, Oregon, near sea level; right, 4250-1 from near Abisko, Swedish Lapland, at elevation 420 meters.

species of *Poa,* however, this distinction is important in considering both evolutionary developments and practical aspects of plant breeding.

METHOD OF MAKING INTERSPECIFIC CROSSINGS. The method used by Dr. Clausen in making hybrids was simple. First, he attempted no crosses unless the proposed parents differed sufficiently in morphological characteristics so that there was a reasonable expectation that the resulting F, hybrids would be recognizable in early seedling stages. Moreover, it was essential that the flowering periods of the parental plants coincide or overlap sufficiently to ensure adequate cross-pollination when both parents were enclosed in a pollen-tight cage. When species differing in their flowering period were to be crossed, the. earlier parent was held in cold storage long enough to delay anthesis until the required time. In some instances the early-flowering parent was shipped as a vegetative clone from another regional nursery with a later growing season than the site where the crossings were made.

The controlled cross-pollinations were made at the Carnegie Institution's nursery at Stanford. Each morning during the flowering period, the inflorescences of the parental plants were shaken together freely in their pollen-tight cages to effect thorough mutual pollination.

No attempts were made to pollinate emasculated flowers because the statistical probability of obtaining hybrids in primary apomictically reproducing species would have been exceedingly small, especially since foreign pollen in pseudogamous apomictics would tend to stimulate the development of maternal replicates. Moreover, the tedious labor required would be prohibitive in cost.

The seed from both parents was harvested when mature and was sown in sterilized soil in flats in a greenhouse the next spring. Approximately five or six weeks after sowing, when the seedlings were about 1-2 cm high, they were pricked into larger flats approximately 2.5 cm apart. Each flat was examined daily for individuals showing vegetative characteristics, indicating that they might be hybrids. Often these could be recognized readily among the predominately uniform maternal-type plants resulting from apomictic reproduction. In most instances the frequency of hybrids in such a seedling population was very low, ranging from less than 0.0001 to as high as 0.05 percent The suspected hybrid individuals were marked individually and transplanted to soil in four-inch pots, where they were grown to semimature flowering stages, Cytological preparations were then made from root-tips and young flower buds. From four-inch pots the suspected hybrids were again transplanted into seven-inch clay pots and grown in a greenhouse or lathhouse, where they were observed at frequent intervals up to full flowering and seed maturity. At this stage, the plants in most instances could be positively identified either as true hybrids or as aberrants on the basis of both vegetative and flowering characters together with cytological information.

Individuals thus identified as F, hybrids were propagated vegetatively into clones if of sufficient vigor, or were placed in pollen-tight cages during their next flowering season for self-pollination. Their $F_2$ progeny grown from the resulting seed harvest were space-planted in field plots one meter apart for further study. The main purpose of such field plantings was to study the degree of constancy or variability among the progeny. From such tests the approximate degree of apomixis or sexuality of the parental $F_1$ hybrid could be determined. Figure 4 shows a view of the pollen-tight cages used in the crossings, and an example of a space-planted progeny test.

In many instances such $F_2$ progenies segregated, indicating a high degree of sexuality in the $F_1$ hybrids. Selected individual recombinations from such segregating $F_2$ populations were then isolated for further progeny testing in subsequent generations. A number of such recombinations were found to reproduce primarily by apomixis, showing a high degree of constancy among the maternal-like progeny. Such mainly apomictic-reproducing derivatives were found in $F_3$ or later generations. In following such steps, one could derive a series of morphologically distinct hybrid lines reproducing apomictically from a single original cross.

In space-planted progeny tests, usually from 90 to as many as 300 individuals were grown from seeds of a single individual plant. Such plantings were usually maintained for from two to five years. The adequate field space supplied by the Soil Conservation Service at their regional nurseries made such test plantings practicable.

Individual plants of hybrids or hybrid derivatives were routinely divided vegetatively as clones as soon as they were strong enough to withstand the shock of this operation. The propagules were then used either for transplant studies for testing in contrasting environments, mostly at the Carnegie altitudinal transplant stations at Stanford (elevation 30 meters), Mather (1400 meters), and Timberline (3050 meters). These stations are described in detail in Volume I of this series (Clausen, Keck, and Hiesey, 1940, pp. 4-15).

We kept detailed records of every individual in all of the numerous progeny tests. The frequency of morphologically constant maternal-like plants compared with "aberrant," or "off," types was determined and verified in repeated observations in later years. Some judgement could be made from the morphology of the aberrant plants, as to whether they were the product of sexual reproduction or chromosomal deviants from the maternal type. Cytological studies were often made on both "normal" and "aberrant" individuals, and from their chromosomal behavior deductions became possible.

FIELD TESTING OF HYBRID DERIVATIVES AND THEIR PARENTS. We devoted much effort to comparing parental lines and their hybrid derivatives in growth performance and survival, through field tests in widely different climates. In the earlier phases of the work (1944—1950), these tests were carried on mostly at the U.S. Soil Conservation Nurseries in the Pacific states and at the Carnegie Institution's altitudinal field stations at Stanford, Mather, and Timberline in

**Figure 4. Above, a battery of pollen-tight cages for making cross-pollinations. Below, space-planted segregating F, population at Stanford of *Pea ampla X P. pratensis* with cages over selected individual plants for further progeny testing.**

central California, described in earlier volumes of this series. In later years, after some 40 strains of stabilized, primarily apomictically reproducing strains were developed, the tests were expanded to include a number of experiment stations cooperating with the U.S. Agricultural Research Service under the direction of Dr. A. A. Hansen. These tests were set up as randomized plots of standard design sown with the seed from the apomictic lines. Some of the lines were also included in plantings in northern Europe, notably Scotland, Denmark, Norway, and Sweden, as mentioned in the preface to this volume. The data taken from these widespread plantings included measurements on overall plant dimensions, sizes of leaves, inflorescences and spikelets, vigor, seasonal development, and resistance or susceptibility to plant diseases.

Table 1 lists 26 stations from which substantial test data were obtained, their sponsorship, location, elevation, and their general climatic characteristics.

TABLE 1

COOPERATING EXPERIMENTAL TEST STATIONS

| Station Number | | Latitude | Longitude | Sponsors* and General Description |
|---|---|---|---|---|
| 1 | San Fernando, Ca. | 34° 16'N | 118° 36'W | SCS, Arid Mediterranean climate |
| 2 | Stanford, Ca. | 37° 26'N | 122° 06'W | CIW, Base station at elevation 30 meters |
| 3. | Sunol, Ca. | 37° 35'N | 121° 53'W | SCS, Dry hillside, central California |
| 4. | Mather, Ca. | 37° 53'N | 119° 52'W | CIW, Mid-altitude station at 1400 meters |
| 5. | Timberline, Ca. | 37° 57'N | 119° 17'W | CIW, Subalpine station at 3040 meters |
| 6. | Pleasanton, Ca. | 37° 40'N | 121° 52'W | SCS, Central California near coast |
| 7. | Davis, Ca. | 38° 33'N | 121° 45'W | UCD, Central Valley of California |
| 8. | Halls Flat, Ca. | 40° 25'N | 120° 46'W | CFR, Arid Great Basin (semi-desert) |
| 9. | Corvallis, Or. | 44° 38'N | 123° 15'W | ARS, Central Oregon valley |
| 10. | Pullman, Wa. | 46° 45'N | 117° 14'W | SCS, Palouse Prairie region |
| 11. | Lind, Wa. | 47° 02'N | 118° 37'W | SCS, Arid semi-desert |
| 12. | Bellingham, Wa. | 48° 49'N | 122° 29'W | SCS, Cool Northwest coast |
| 13. | Aberdeen, Id. | 42° 48'N | 112° 46'W | SCS, Interior Northwest |
| 14. | Tetonia, Id. | 43° 48'N | 113° 33'W | SCS, North Rocky Mts. at 1800 meters |
| 15. | Moccasin, Mt. | 46° 57'N | 109° 55'W | SCS, Central Montana plains |
| 16. | St. Paul, Mn. | 44° 40'N | 95° 23'W | ARS, Continental midwest |
| 17. | Columbia, Mo. | 38° 57'N | 92° 12fW | ARS, Central United States |
| 18. | Lafayette, In. | 40° 14'N | 86° 54'W | ARS, Central United States |
| 19. | Lexington, Ky. | 38° 04'N | 84° 42'W | ARS, South Central United States |
| 20. | Blacksburg, Va. | 37° 12'N | 80° 27fW | ARS, Southeastern United States |
| 21. | State College, Pa.f | 40° 48'N | 77° 52'W | ARS, Northeastern United States |
| 22. | Franklinton, La. | 30° 43'N | 90° irw | ARS, Southern coastal region |
| 23. | Penlandfield, Scotland | 55° 58'N | 3° 14'W | SPB, Cool coastal Europe |
| 24. | Volbu, Norway | 61° 08'N | 9° 15'E | EMD, Northern Europe at 651} meters |
| 25. | 0toftegaard, Denmark | 55° 41'N | 12° 10'E | DC, Central lowland Europe |
| 26. | Uppsala, Sweden | 59° 52'N | 17° 37'E | SPB, Northern continental Europe |

*SCS, U.S. Soil Conservation Service; CIW, Carnegie Institution of Washington; UCD, University of California, Davis; CFR, California Forest and Range Experiment Station, Berkeley; ARS, U.S. Agricultural Research Service Cooperating Station; SPB, Scottish Plant Breeding Station, Penlandfield; EMD, Experiment Station for Mountain Districts, Volbu» Norway; DC, Danish Cooperatives, 0toftegaard, Denmark; SPB, Swedish Plant Breeding Association of Svalöf, Uppsala Branch,

t Not used in field tests.

## TABLE 2

A SAMPLE OF DATA FOR RESPONSE INDEX DERIVATION FOR *Poa ampla* KAHLOTUS 4259-3

| Station | Width at Base, cm | Leaves | | Culms | | Vigor, 1-9 | Response Index, % |
|---|---|---|---|---|---|---|---|
| | | Longest, cm | Width, mm | Number of | Height, cm | | |
| Stanford | 11.6 ± OJ | 31 ± 1,2 | 3.4 ± 0.2 | 52 ± 10.1 | 65 ± 1.6 | 3.5 | 28 |
| Pullman | 16 ± 1.1 | 44 ± 1.9 | 2.0 ± 0.13 | 218 ± 30.6 | 91 ± 2.5 | 6.9 | 63 |
| Tetonia | 14 ± 0.58 | 53 ± 2.1 | 23 ± 0.12 | 180 ± 17.1 | 83 ± I.I | 8.3 | 57 |
| Blaeksburg | 5.5 ± 1.2 | 57,5 ± 4.4 | 2.8 ± 1.3 | 27.5 ± 13.6 | 88.5 ± 2.6 | 2.0 | 30 |

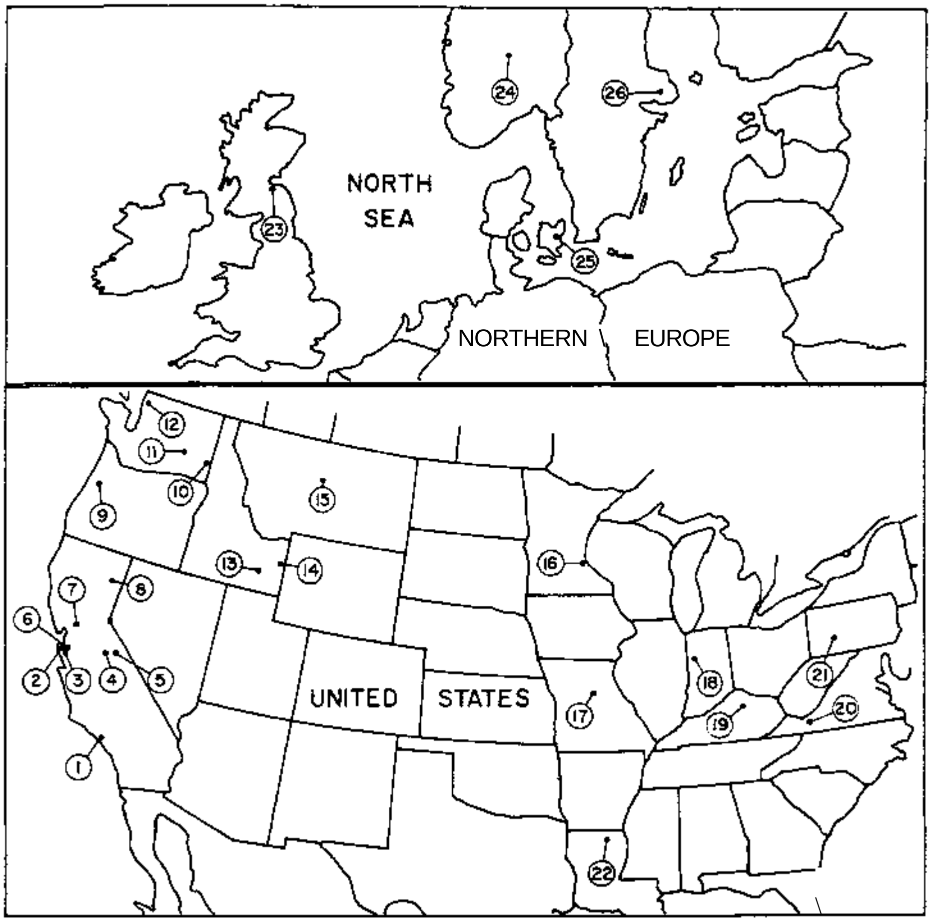


Figure 5. Geographical location of experimental test stations where parental and various interspecific hybrid derivatives of *Poa* were grown. The circled numbers refer to the sites listed and described in table 1.

The maps in figure 5 show their general locations: circled numbers refer to the stations listed in table 1.

We faced a major problem in summarizing the voluminous data in a clear form. An obvious approach was to compare the overall growth performance of hybrid derivatives with that of the parental lines in different environments. The evaluation of "growth performance," however, necessitates consideration of interactions between a number of factors. Any attempt to present in detail the variables that might be used to measure "growth performance" would result in an unwieldy manuscript.

We have attempted to resolve this problem by using a "response index," developed from several measures of overall growth performance applicable to all parental lines and hybrid derivatives in the different test environments. The response index employs both physical measurements and subjective evaluations from observations by members of the staff. We believe that this rather unorthodox treatment provides a reasonably true picture of the available data.

Six variables are used in computing the response index:

1. Width of plant at the base in cm
2. Length of longest leaf in cm
3. Width of longest leaf in mm
4. Length of tallest culm in cm
5. Number of culms per plant
6. Vigor and bulk of growth based on an arbitrary scale of 1 (low) to 9 (high).

Three-year means of these items on from 4 to 90 plants of each line (depending on the number of individuals in a given culture) are expressed as sums. To simplify graphing, the sums were divided by 6, the number of variables entering the response index.

An example of the computation of response index for a single parental line grown in four environments is shown in table 2. Diagrams depicting indexes of parental lines and hybrid derivatives are shown in figures 11-24, inclusive, in subsequent chapters.

ORIGIN OF SOURCE MATERIALS USED IN CROSSING EXPERIMENTS. Many collections of various species of *Poa* were grown in the gardens at Stanford to facilitate selection of the most promising individual plants for crossing. In table 3, left columns, are listed these materials and their origins in the order of their Carnegie accession numbers. This list, in addition to serving as a reference for later chapters dealing with specific crossing experiments, may serve to acquaint the reader with the genetic base on which the present investigations were conducted.

## TABLE 3

ORIGINAL SOURCE MATERIALS OF *Poa* GROWN AT STANFORD

| Carnegie Accession Number | Origin* | Chromosome Number *(In)* |
|---|---|---|
| | *Poa ampla* Merr. | |
| 4171 | SCS P-8942, 5 miles S of Ft. Klamath, Klamath Co., Or., 1280 m'[1] | 64 |
| 4172 | SCS P-2716, near Moro, Sherman Co., Or., 150 m | 63 |
| 4173 | SCS P-5731, 0.5 mile E of Condon Gilliam Co., Or., 760 m | -63 |
| 4174 | SCS P-7820, Cleman Mt., 15 miles NW of Wenas, Yakima Co., Wa., 1065 m | 63 |
| 4175 | SCS P-837, Wenatchee, Chelan Co., Wa., 208 m | 63 |
| 4176 | SCS P-999, Waterville, Douglas Co., Wa., 800 m | 62 |
| 4177 | SCS P-5728, 14 miles SE of Lind, Adams Co., Wa., 460 m | 63 |
| 4178 | SCS P-846, near Kahlotus, Franklin Co., Wa., 275 m | 64 |
| 4179 | SCS P-8916, 2 miles W of Barstow, N. Ferry Co., Wa., 610 m | -63 |
| 4180 | SCS P-4914, 8 miles SW of Spokane, Spokane Co., Wa., 580 m | 63 |
| 4181 | SCS P-998, Endicott, Whitman Co., Wa., 485 m | 63-64 |
| 4182 | SCS P-7772, 28 miles S of Rosalia, Whitman Co., Wa., 610 m | 63 |
| 4183 | SCS P-8903, 3 miles N of Albion, Whitman Co., Wa., 730 m | 63-64 |
| 4184 | SCS P-6116, near Clarkston, Asotin Co., Wa., 250 m | 63 |
| 4185 | SCS P-6252, Upper Ball Gulch near Pomeroy, Garfield Co., Wa, 610 m | 63 |
| 4186 | SCS P-8934, 6 miles NW of Enterprise, Wallowa Co., Or., 1065 m | 63 |
| 4187 | SCS P-8928, 15 miles NW of Cottonwood, Idaho Co., Id., 1220 m | -63 |
| 4188 | SCS P-5113, Cheyenne, Laramie Co., Wy. | 63 |
| 4196 | SCS P-6727, Heise Hot Spgs., E. Bonneville Co., Id., 1525 m | 70-71 |
| 4197 | SCS P-6716, 3 miles SE of Newdale, Madison Co., Id., 1525 m *(juncifolia)* | 61 |
| 4199 | SCS P-6774, Henry Lake, Fremont Co., Id., 2120 m | -63 |
| 4473 | CIW, near Susanville, Lassen Co., Ca., 1340 m | 64 |
| 4474 | SCS P-6774, Henry Lake, Fremont Co., Id., 2140 m | ... |
| 4586 | Porter 3308, Medicine Bow Mts., Albany Co., Wy., 2740 m | 64 |
| 4587 | Porter 3528, Medicine Bow Mts., Albany Co., Wy., 2900 m | ... |
| 4588 | NGP D-617, Torrington, Goshen Co., Wy., | ... |
| 4591 | Porter 3249, Pole Mtn. Region, Albany Co., Wy., 2560 m | ... |
| 4645 | Cottam 2976, Clear Creek, Boxelder Co., Utah, 1530 m | ... |
| 4646 | Hull 9574, 9 miles E of Wells, Elko Co., Nc, 2440 m | ... |
| 4655 | Mullen 19-45-43, 2 miles S of Bridgeport, Mono Co., Ca., 1970 m | ... |
| | *P. arachnifera* Torr. | |
| 4248 | SCS P-3179, Stillwater, Payne Co., Ok., | ... |
| 4434 | J. Harlan, near Fargo, Ellis Co., Ok., 610 m | 54-56 |
| 4435 | J. Harlan, near Woodward, Woodward Co., Ok. (from bulk seed sam.) | ""-63 |
| | *P. arida* Vasey | |
| 4262 | SCS P-7936, North Platte, Lincoln Co., Nb., 860 in | 63 |
| 4431 | J. Harlan, Albuquerque, Bernalillo Co., N.M. | 63 |
| 4432 | J. Harlan, Indian Ck., near Woodward, Woodward Co., Ok. (sandy bottom) | -64 |
| 4433 | J. HarSan, near Fargo, Ellis Co., Ok., 610 m | 64 |
| 4613 | NGP, D-970, Glenrock, Natrona Co., Wy., 1530 m | 64 |
| 4616 | NGP, D-965, Belfield, Stark Co., N.D., 795 m | 84 |
| | *P. caespitosa* Forst. | |
| 4680 | CSIRO, Canberra, A.C.T., Australia | 56-68 |
| 6494 | L. B. Moore, Awatere Valley, Marlborough, New Zealand, 150 m | 95 ± 5 |
| 6495 | L. B. Moore, Acheron River, Marlborough, New Zealand, 855 m | ... |

*(Cmtimmed on next page)*

TABLE 3

(CONTINUED)

| Carnegie Accession Number | Origin* | Chromosome Number |
|---|---|---|
| 6496 | L. B. Moore, Cat Creek, Tarndale, Marlborough, New Zealand, 960 m | ... |
| 6497 | L. B. Moore, Cow Creek, Alma River, Marlborough, New Zealand, 975 rn | ... |
| 6498 | L. B. Moore, Carter's Saddle, Clarence River, Marlborough, New Zealand, 1220 m | ... |
| | P. *canbyi* (Scribn.) Piper | |
| 4201 | Stebbins No. 3308, near Glen Alpine, El Dorado Co., Ca., 2100 m | -84 |
| 4202 | SCS P-5748, 6 miles E of Austin, Grant Co., Or., 1300 m | ... |
| 4203 | SCS P-6114, 5 miles SE of Goldendale, Klickitat Co., Wa., 610 m | ... |
| 4204 | SCS P-3974-1, Goldendale, Klickitat Co., Wa. | -86 |
| 4205 | SCS P-8906, 11 miles S of Chewelah, Stevens Co., Wa., 580 m | -82 |
| 4206 | SCS P-851, Blue Mts.; Columbia Co., Wa. | 84 |
| 4207 | SCS P-2588, Mt. Misery, Garfield Co., Wa. | 84 |
| 4208 | SCS P-6336, Craigmont, Lewis Co., Id., 1100 m | ... |
| 4209 | SCS P-6229, 12 miles S of Horse Shoe Bend, Boise Co., Id., 820 m | -82 |
| 4210 | SCS P-6214, 12 miles W of Dubois, Clark Co., Id., 1525 m | -83 |
| 4211 | SCS P-6326, near Galletin Gateway, Galledn Co., Mt., 1525 m | 84 |
| 4224 | CIW, Yosemite Cr., Mariposa Co., Ca., 2250 m | -94 |
| 4230 | SCS P-6003-4, Kiger Creek, Steens Mts., Harney Co., Or. | 85 |
| 4233 | SCS P-5980, Emmett, Gem Co., Id., 700 m | 84 |
| 4515 | CIW, near Susanville, Lassen Co., Ca., 1340 m | ... |
| 4518 | CIW, Yosemite Creek, Mariposa Co., Ca., 2250 m | 93 |
| 4520 | CIW, above Tenaya Lake, Mariposa Co., Ca., 2530 m | ... |
| 4590 | Porter No. 3510, Pole Mt. region, Albany Co., Wy., 2500 m | -72 |
| 5851 | CIW, Scott Mtn. Summit, Siskyou Co., Ca., 1640 m | ... |
| | *P. compressa* L. | |
| 4260 | SCS P-410-1, from Chorsum, Turkey, through U.S. Bureau of PL Inds. | 50 |
| 4532 | CIW, 2 miles SW of Crescent Mills, Plumas Co., Ca., 1070 m | 42 |
| | *P. confinis* Vasey | |
| 4246 | SCS P-8399, Warrenton, Clatsop Co., Or., 3 m | 42 |
| | *P. cusicfyi* Vasey | |
| 4531 | CIW, near Satdey, Sierra Co., Ca., 1530 m | 42 |
| | *P. douglasii* Nees. | |
| 4533 | CIW, Cape Mendocino, Humboldt Co., Ca., 3 m | 28 |
| | *P. epilis* Scribn. | |
| 4241 | CIW, Slate Creek Valley, Mono Co., Ca., 3110 m | ~70 |
| 4242 | Stebbins No. 3313, Desolation Valley, El Dorado Co., Ca., 2500 m | ... |
| 4243 | SCS P-27434, Sutherland Camp, Steens Mts., Harney Co., Or. | ~84 |
| | *P.fibrata* Swallen | |
| 4534 | Cal. Forest & R. Exp. Sta., W of Eagle Lake, Lassen Co., Ca., 1740 m | 64 |
| | *P. glaudfotk* Scribfi. + Will. | |
| 4611 | Porter No. 3506, Pilot Knob, Albany Co., Ca., 2850 m | 56 |
| 4612 | NGP, No. D-968, Glenrock, **Natrona** Co., Wy., 1550 m | 5(1 4- / |
| | *P. gmdllima* Vasey | |
| 4226 | CIW, Slate Creek Valley, **Mono** Co., Ca., **3200 m** | **~84** |
| 4227 | Stebbins No. 3312, S of Fallen Leaf Lake, El Dorado Co., Ca., 2500 m | -91 |

*(Comtmued om mxt **ptge)***

TABLE 3

(CONTINUED)

| Carnegie Accession Number | Origin* | Chromosome Number |
|---|---|---|
| 4240 | Stebbins, No. 3163, above Fallen Leaf Lake, El Dorado Co., Ca., 2160 m | 86 |
|  | *P. juncifblia* Scribn. |  |
| 4589 | Porter No. 3475, 15 miles W of Laramie, Albany Co., Wy., 2280 m | 84 |
|  | *P. leibergii* Scribn. |  |
| 4244 | CIW, Slate Creek Valley, Mono Co., Ca., 3200 m | ~81 |
|  | *P. longifolia* Trin. |  |
| 4245 | SCS P-417, from Armenia, U.S. Bureau of Plant Industry No. 108, 531 | 43 |
|  | *P. macrantha* Vasey |  |
| 4247 | SCS P-4140, Warrenton, ClatsopCo., Or., 3 m | 28 |
|  | *P. nervosa* (Hook.) Vasey |  |
| 4255 | CIW, Yosemite Creek, Mariposa Co., Ca., 2260 m | 63 |
| 4256 | CIW, Tuolurnne Meadows, Mariposa Co., Ca., 2620 m | 62 |
| 4257 | CIW, Slate Creek Valley, Mono Co., Ca., 3110 m | 63 |
| 4468 | CIW, Yosemite Creek Grade, Mariposa Co., Ca., 2130 m | ... |
| 4469 | CIW, Tuolumne Meadows, Mariposa Co., Ca., 2620 m | ... |
| 4470 | CIW, Slate Creek Valley, Mono Co., Ca., 3050 m | ... |
| 4471 | CIW, Carnegie Timberline Station, Mono Co., Ca., 3050 m | ... |
| 4472 | CIW, above Carnegie Timberline Station, Mono Co., Ca., 3200 m | 70 |
|  | *P. nevadensis* Vasey ex Scribn. |  |
| 4475 | CIW, Warren Creek, Mono Co., Ca., 2740 m | 63 |
| 4476 | CIW, Mohawk Valley, Plumas Co., Ca., 1350 m | 62 |
| 4477 | CIW, near Westwood, Lassen Co., Ca., 1530 m | ~65 |
| 4478 | CIW, 5 miles E of Westwood, Lassen Co., Ca., 1580 m | 63 |
| 4479 | SCS P-7584, Hart Mtn. Pass, Lake Co., Or., 1830 m | ... |
| 4480 | SCS P-8941, Summer Lake, Lake Co., Or., 1340 m | ... |
| 4481 | SCS P-2646-1, Seneca, Grant Co., Or., 1070 m | ... |
| 4482 | SCS P-2646-2, near Seneca, Grant Co., Or., 1070 m | ... |
| 4483 | SCS P-6349, 13 miles NE of Blackfoot, Bingham Co., Or., 1220 m | ... |
| 4656 | CIW, 4 miles S of Leevining, Mono Co., Ca., 1950 m | ... |
| 4189 | SCS P-5755, 10 miles SE of Mitchell, Wheeler Co., Or., 820 m | 64 |
| 4190 | SCS P-2646, Seneca, Grant Co., Or., 1065 m | 62-63 |
| 4191 | SCS P-8941, Summer Lake, Lake Co., Or., 1340 m | -66 |
| 4192 | SCS P-7584, Hart Mtn. Pass, Lake Co., Or., 1830 m | 63 |
| 4193 | SCS P-7743, Steens Mts., Harncy County, Or. | ... |
| 4194 | SCS P-6281, 1 mile S of Riddle, S. Owyhee Co., Id., 1710 m | 63 |
| 4195 | SCS P-6349, 13 miles N of Blackfoot, Bingham Co., Id., 1220 m | 63 |
| 4198 | SCS P-8804, Tetonia, Tcton Co., Id., 1890 m | 63 |
| 4200 | SCS P-6439, 4 miles N of Winchester, Lewis Co., Id., 1100 m | 70 |
|  | *P. pratensis* L. |  |
| 4249 | SCS P-3128, Selected strain from Cent. Exp. Farm, Ottawa, Canada | 70 |
| 4250 | CIW, S of Abisko, Sweden, at 68°21$^f$ N. Lat., 420 m (ssp. *aipigtna)* |  |
| 4252 | CIW, near Groveland, Tuolumne Co., Ca., 915 m | % |
| 4253 | CIW, Mather, Tuolumne Co., Ca., 141X1 m | 68 |
| 4254 | CIW, Cottonwood Meadow, Mariposa Co., Ca., 18311 m | ~67 |
| 4258 | CIW, Leevining Creek, Mono Co., Ca., 224(1 m | *m* |

*[Continued on next page)*

TABLE 3

(CONTINUED)

| Carnegie Accession Number | Origin* | Chromsome Number |
|---|---|---|
| 4259 | CIW, 4 miles S of Leevining, Mono Co., Ca., 2070 m | 64 |
| 4436 | CIW, 1 mile N of Hume, Fresno Co., Ca., 1670 m | 67 |
| 4437 | CIW, near Groveland, Tuolumne Co., Ca., 915 m | 50 |
| 4438 | CIW, Mather, Tuolumne Co., Ca., 1400 m | 68-69 |
| 4439 | CIW, Mather, Tuolumne Co., Ca., 1400 m | 68 |
| 4440 | CIW, Mather, Tuolumne Co., Ca., 1400 m | 49 |
| 4441 | CIW, Mather, Tuolumne Co., Ca., 1400 m | ... |
| 4442 | CIW, Cottonwood Meadow, Mariposa Co., Ca., 1830 m | ... |
| 4443 | CIW, Cottonwood Meadow, Mariposa Co., Ca., 1830 m | ... |
| 4444 | CIW, Crane Flat, Mariposa Co., Ca., 1890 m | -56 |
| 4445 | CIW, Slate Creek Valley, Mono Co., Ca., 3050 m | -73-74 |
| 4446 | CIW, Warren Creek, Mono Co., Ca., 2740 m | 68-76 |
| 4447 | CIW, Leevining Grade, Mono Co., Ca., 2660 m | 54 |
| 4448 | CIW, near Leevining, Mono Co., Ca., 2240 m | ... |
| 4449 | CIW, near Leevining, Mono Co., Ca., 2240 m | ... |
| 4450 | CIW, near Leevining, Mono Co., Ca., 2240 m | ... |
| 4451 | CIW, 4 miles S of Leevining, Mono Co., Ca., 2070 m | 49 |
| 4452 | CIW, 4 miles S of Leevining, Mono Co., Ca., 2070 m | ... |
| 4453 | CIW, N of Mono Lake, Mono Co., Ca., 1980 m | 50 |
| 4454 | CIW, Mono Lake, Mono Co., Ca., 1980 m | ... |
| 4455 | CIW, 4 miles NE of Columbia, Tuolumne Co., Ca., 730 m | ... |
| 4456 | CIW, Avery, Calaveras Co., Ca., 1070 m | ... |
| 4457 | CIW, Goodycars Bar, Sierra Co., Ca., 730 m | ... |
| 4458 | CIW, 4 miles W of Sierra City, Sierra Co., Ca., 1095 m | 56 |
| 4459 | CIW, 2 miles NW of Battley, Sierra Co., Ca., 1610 m | ... |
| 4460 | CIW, Feather River Inn, Plumas County, Ca., 1360 m | ... |
| 4461 | CIW, Quincy, Plumas Co., Ca., 1065 m' | ... |
| 4462 | CIW, 2 miles E of Westwood, Lassen Co., Ca., 1530 m | 58 |
| 4463 | CIW, 3 miles SE of Peanut, Trinity Co., Ca., 795 m | ... |
| 4464 | CIW, Norse Butte, Trinity Co., Ca., 1220 m | ... |
| 4465 | Lawrence No. 5206-B, Blodgett, Benton Co., Or., 150 m | —70 |
| 4466 | Lawrence No. 5204-B, Newport, Lincoln Co., Or., near sea level | 81 |
| 4467 | Lawrence No. 5203-B, Boiler Bay State Park, Lincoln Co., Or., near sea level | 84 |
| 4653 | CIW, Monte Rio, Sonoma Co., Ca., 92 m | ... |
| 4654 | Kellog No. 4495, Aurora Canyon, Mono Co., Ca., 2280 m | ... |
|  | *P. rhyzomata* Hitchc. |  |
| 4609 | Stcbbins & Beetle 3263, Hamburg, Siskiyou Co., Ca., 520 m | 28 |
| 4610 | Beetle No, 3651, 9 miles E of Buroey, Shasta Co., Ca. | ... |
|  | *P. scabrelk* (Thurb.) Benth ex Vasey |  |
| 4212 | 8CS P-1KH0, near Somis (Las Posas), Ventura Co., Ca., 175 m | 82 |
| 4213 | SCS P-l 1789, NE of King City, Monterey Co., Ca., 122 m | 8? |
| 4214 | SCS P-IOW, Watsonville, Santa Cruz Co., Ca., 30 m | 82 |
| 4215 | SCS P-12529, Mr, Hamilton, Santa Clara Co., Ca., 850 m | 84 |
| 4216 | SCS P-116I7, near Livermorc, Alameda Co., Ca,, inner coastal valley | ... |
| 4217 | SCS P-l2517, Lucerne, JUkt Co., Ca,, 410 m | -68 |
| 4218 | SCS P-12341, NW of Wilfo, Mcndocino Co., Ca., inner coastal valley | 84 |
| 421^ | SCS P-12343, Sherwood Valley, Mendocino Co., Ca., inner coastal valley | 63 |
| *42211* | Stehbim, Yager Creek, Humboldt Co,, Ca., outer coastal area | ... |

*(Continued on next page)*

TABLE 3

(CONTINUED)

| Carnegie Accession Number | Origin* | Chromosome Number |
|---|---|---|
| 4221 | SCS P-12509, Monolith, Kern Co., Ca., Tehachapi Mm. area | ... |
| 4222 | CIW, Mather, Tuolumne Co., Ca., 1400 m | 84 |
| 4223 | CIW, near Mather, Tuolumne Co., Ca., 1460 m | *M* |
| 4228 | SCS P-12716, E of Anderson, Shasta Co., Ca., 180 m | 84 |
| 4229 | SCS P-11891, 4 miles W of Red Bluff, Tehema Co., Ca., 120 m | 84 |
| 4488 | CIW, 10 miles SE of Paicines, San Benito Co., Ca., 335 m | ... |
| 4489 | CIW, Paicines, San Benito Co., Ca., 198 m | ... |
| 4490 | CIW, Clear Lake Highlands, Lake Co., Ca., 500 m | 84 |
| 4491 | CIW, 8 miles NE of Ukiah, Mendocino Co., Ca. | ... |
| 4493 | CIW, 5 miles SE of Dorland Ranch, Riverside Co., Ca. | ... |
| 4494 | CIW, 10 miles N of Abbeville, Riverside Co., Ca., Temescal Canyon | ... |
| 4495 | CIW, 8 miles N of Gormon, Los Angeles Co., Ca., 1160 m | 44 -4- / |
| 4496 | CIW, 8 miles N of Woodlake, Tulare Co., Ca., 214 m | ... |
| 4497 | CIW, 4.6 miles S of Badger, Tulare Co., Ca., 650 m | ... |
| 4498 | CIW, 2.5 miles N of Pinehurst, Fresno Co., Ca., 1680 m | ... |
| 4499 | CIW, 1 mile N of Hume, Fresno Co., Ca., 1680 m | ... |
| 4500 | CIW, E of Groveland, Tuolumne Co., Ca., 1220 m | ... |
| 4501 | CIW, Mather, Tuolumne Co., Ca., 1400 m | ... |
| 4502 | CIW, 4 miles NE of Columbia, Tuolumne Co., Ca., 730 m | ... |
| 4503 | CIW, near Columbia, Tuolumne Co., Ca., 730 m | ... |
| 4504 | CIW, near Avery's Station, Calaveras Co., Ca., 1100 m | ... |
| 4505 | CIW, 2.4 miles E of Pilot Hill, El Dorado Co., Ca., 304 m | ... |
| 4506 | CIW, 12 miles N of Auburn, Nevada Co., Ca., 426 m | ... |
| 4507 | CIW, 3 miles E of Downieville, Sierra Co., Ca., 975 m | ... |
| 4508 | CIW, 2 miles NW of Sattley, Sierra Co., Ca., 1620 m | ... |
| 4509 | CIW, 1 mile N of Quincy, Plumas Co., Ca., 1070 m | "~B8 |
| 4510 | CIW, 2 miles W of Platina, Shasta Co., Ca., 885 m | 61-63 |
| 4511 | CIW, 3 miles W of Wildwood, Trinity Co., Ca., 1035 m | ~84 |
| 4512 | CIW, Norse Butte, Trinity Co., Ca., 1220 rn | ... |
|  | *P. secunda* Presl. |  |
| 4225 | CIW, Slate Creek Valley, Mono Co., Ca., 3200 m | ^" |
| 4231 | SCS P-6002, 15 miles W of Fossil, Wheeler Co., Or., 790 m | 86 |
| 4232 | SCS P-6037, 5 miles S of Ritzville, Adams Co,, Wa., saline gravel | ... |
| 4334 | SCS P-2731, 35 miles E of **Mayfield,** Elmore Co., Id., 820 m | ~87 |
| 4335 | SCS P-6274, Duck Valley, S **Owyhcc** Co., Id., 1650 m | ^ |
| 4236 | SCS P-6209, American River Falls, Power Co., Id., 1320 m | »4 |
| 4237 | SCS **P-5881,** Dillion, Bcaverhcad Co., Mt., 1550 m | 85-87 |
| 4239 | SCS P-6005, 16 miles S of Pilot Rock, Umatilla Co., Or., 760 m | ~74 |
| 4487 | CIW, Panoche Pass, San Benito Co., Ca., 365 rn | ... |
| 4523 | CIW, Slate Creek Valley, Mono Co., Ca., 32<M) m | ... |
| 4527 | CIW, near Sattley, Sierra Co., Ca. 1530 m | ... |
| 4528 | CIW, S end of Lake Almanor Plumas Co., Ca., 1 MO m | ... |
| 4529 | CIW, 8.5 miles W of **Susan\iile,** Lassen Co., Ca., 1465 m | ... |
| 4530 | CIW, 2 miles W of Beegum. Shasta Co., Ca., 73H in | im_^ |

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•**SCS** = US Soil Conservation Service Number; CIW « Canteyt Institution Collea^n; Mil* Northern Great Plains Field Station; **CSIRO** - *CotttmmnxtJth* Sucntifu. and Industrial RI-MMK Organization, Canberra, Australia. Co. « County· Elevation in ratters.

# II

# CROSSINGS BETWEEN POA AMPLA MERR. AND POA PRATENSIS L.

# II

# CROSSINGS BETWEEN POA AMPLA MERR. AND POA PRATENSIS L.

Among the more successful interspecific combinations were those between various forms of *Poa ampla* and *P. pratensis.* Although reciprocal crossings were routinely attempted in all instances, Fj hybrids were obtained only with *Poa ampla* as the female parent. The primary reason for this result, we believe, is that the forms of P. *pratensis* used as parents had higher degrees of apomixis than the *P. ampla* parents. It is conceivable that with other forms of these two species, hybrids might also have been obtained on P. *pratensis.*

Table 4 lists the attempted crossings between *Poa ampla* and P. *pratensis,* and the number of $F_x$ hybrids, if any, obtained in each attempt. It is evident from this table that the majority of crossing attempts were unsuccessful, and that the self-reproducing apomictic hybrid derivatives that were obtained were derived from only a few combinations. Figure 6 summarizes these crossings. Results from the more successful hybridizations are described in some detail in this chapter to illustrate various aspects encountered in these studies.

## POA AMPLA KAHLOTUS 4178-1 x P. PRATENSIS ATHABASCA 4249-1

This example (CIW culture 4537, table 4) is fairly representative of combinations between different forms of *Poa ampla* and P. *pratensis* although, as will become evident later, the results from each individual cross differed from the others in important respects.

### *The Poa ampla parent*

The original seed stock from which the parental individual used in this crossing was collected on July 3, 1934, by Professor E. R. Bogush, then curator of the herbarium at Washington State University at Pullman, Washington. The collection site was a steep north slope near Kahlotus, Franklin County, about 25 miles south of Lind. This *Poa* was associated with *Artemisia* and *Chrysothamnus* in a sand-dune region and was noted as growing in "isolated bunches 3 dm tall."

The original two ounces of seed collected was planted in 1935 at the U.S. Soil Conservation Service station at Pendleton, Oregon, from which a subsequent generation was harvested and planted in 1937 at the Pullman nursery.

TABLE 4

HYBRID COMBINATIONS ATTEMPTED BETWEEN *Poa ampla* X *P. pratensis*

| Parental Strains | | | CIW Culture No. | No. Plants Grown | No. of Maternals | No. of Aberrants | No. of F, Hybrids | No. of Apomictic Lines |
|---|---|---|---|---|---|---|---|---|
| Albion 4183-2, *2n* * 70 | X | ssp. *alpigena* Lapland 4250-1. *In* • 74 | 4273 | 226 | 170 | 49 | 7 | 10 |
| Reciprocal | | | 4272 | 53 | 14 | 39 | 0 | 0 |
| Albion 4183-1, *2n* * 63 | X | Mather 4253-4, 2» = 68 | 4535 | 1142 | 1004 | 81 | 57 | 15 |
| Reciprocal | | | 4536 | 222 | 211 | 11 | 0 | 0 |
| Albion 4183-1, *2n* » 63 | X | Athabasca 4249-1, *In* = 70 | 4729 | 520 | 435 | 79 | 6 | 2 |
| Condon 41734, *In* =* 3 | X | Athabasca 4249-1, *In* = 70 | 4727 | 590 | 583 | 0 | 7 | 0 |
| Heise Hot Springs 4196-12, 2» - 70 | X | Newport 4466-1, *In* = 81 | 4731 | 3132 | 3075 | 0 | 57 | 2 |
| Reciprocal | | | 4732 | 60 | 60 | 0 | 0 | 0 |
| Kahlotus 4178-1, *In* » 64 | X | Athabasca 4249-1, *In* = 70 | 4537 | 404 | 340 | 48 | 16 | 12 |
| Reciprocal | | | 4538 | 1062 | 1046 | 16 | 0 | 0 |
| Morro 4172-1, 2» * 63 | X | ssp. *alpigena* Lapland 4250-1, *In* = 74 | 4271 | 16 | 10 | 3 | 0 | 0 |
| Reciprocal | | | 4270 | 102 | 65 | 97 | 0 | 0 |
| Morro 4172-1, 2» * 64 | X | Mather 4532*2, *In* = 68 | 4539 | 75 | 46 | 19 | 0 | 0 |
| Reciprocal | | | 4540 | 1056 | 1012 | 44 | 0 | 0 |
| Morro 4172-1, *In* = 64 | X | Leevining 4258-3, *In* = 68 | 4541 | 3 | 2 | 1 | 0 | 0 |
| Reciprocal | | | 4542 | 1056 | 1038 | 18 | 0 | 0 |
| Wenatchee 4175-11, 2» = 63 | X | Athabasca 4249-1, *In* = 70 | 4728 | 192 | 189 | 0 | 3 | 0 |

A third seed generation was planted in a nursery row at Pullman in 1941. This row planting was uniform in habit, morphological characters, and seasonal timing, and grew as a sturdy, fine-stemmed bunchgrass. Two individuals from this planting were shipped live to Stanford in November 1943 and were propagated as vegetative clones under the Carnegie accession numbers 4178-1 and" 4178-2.

Seeds harvested from the open-pollinated nursery row at Pullman in 1941 were also sown at Stanford in 1944, and a resulting population of 30 space-planted individuals were grown in the Stanford garden and observed over a period of several years. This maternal-like apomictic population was relatively uniform, among the earliest of the *Poa ampla* forms to flower at Stanford (May 3-10), and produced from 80 to 250 culms per plant ranging from 60 to 90 cm in height. In this population were also a few weak subnormal maternal-like plants classed as "aberrants." By mid-July the normal maternal-like plants were in mature fruit and had started to wither in dormancy; by late summer new rosette leaves had started to develop, to be followed by continued active growth during the winter and to culminate in vigorous development of culms during the next spring. This strain of *Poa ampla* was, however, subject to rust infection at Stanford, especially during the second and later years.

### *The Poa pratensis parent*

The parental clone 4249-1 was shipped to Stanford from the Soil Conservation Service nursery at Pullman in May 1943. It was among a number of vigorous individuals grown at Pullman from seed supplied by the Central Experimental Farm at Ottawa, Canada, in 1936. According to information supplied by Dr. T. M. Stevenson,* Dominion Agrostologist, this seed originated from a single plant selection made by Dr. L. A. Kirk in 1913 and was believed to have been collected from native plants in either northern Alberta or northern Saskatchewan. The Kirk selection was licensed in Canada under the commercial name "Delta" and was subsequently grown extensively in the United States.

Commercial Delta is composed of a mixture of biotypes, as is evident in space-planted progeny test plots at Stanford, Pullman, Purdue, and other experiment stations. For example, a sample of foundation seed of Delta, kindly sent to us by Dr. T. M. Stevenson in 1956, was grown at Stanford. Among a population of 89 space-planted individuals, 46 were uniform and exactly comparable with the very uniform seed progeny of the self-pollinated clone 4249-1 used in our crossing experiments. The remaining 43 plants were variable and generally later in flowering when grown in the Stanford environment. In similar test plantings at Pullman, Washington, and Purdue (near

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* Letter from Dr. Stevenson to Dr. Jens Clausen, May 15, 1944.

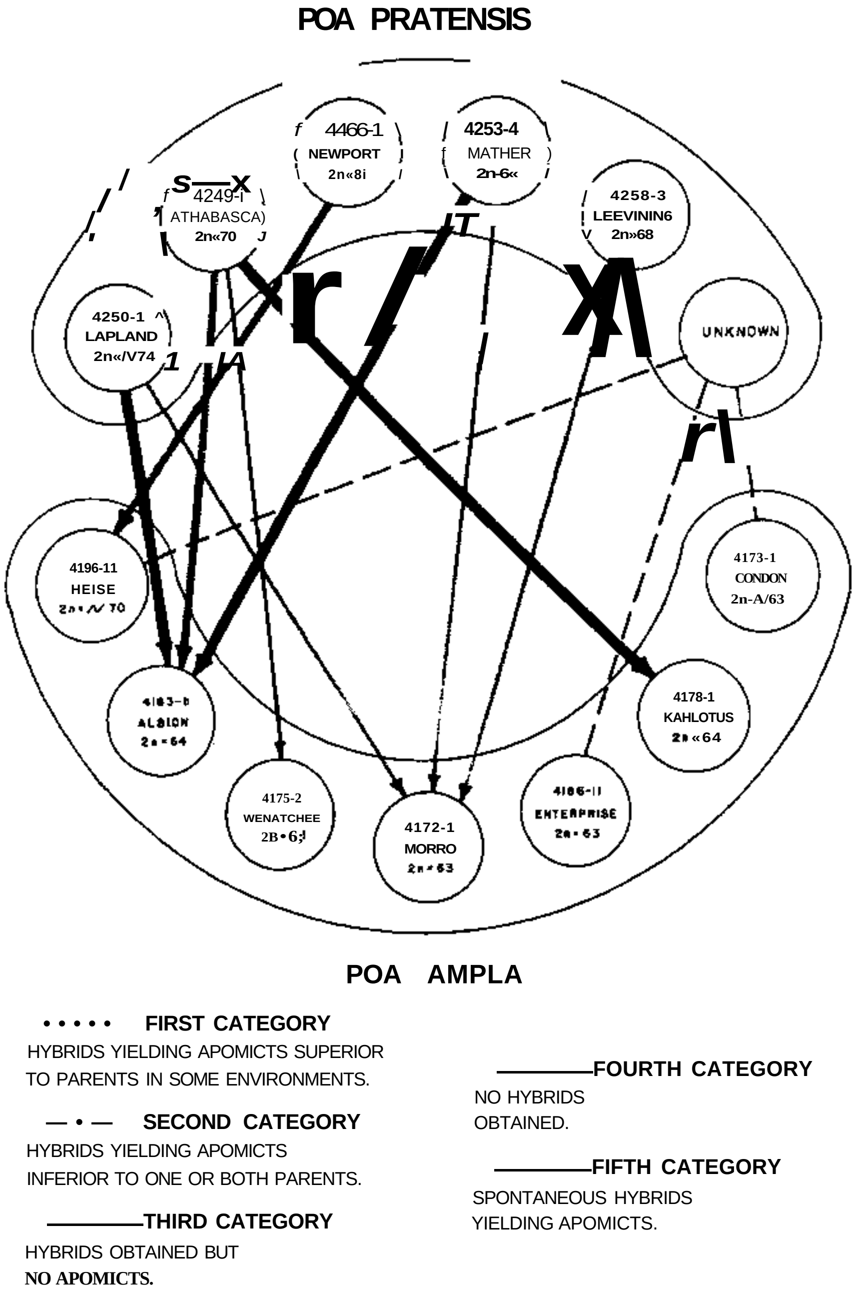


Figure 6. Summary of crosses between different forms of *Poa ampla* Merr. (lower) and P. *pratensis* L. (upper). Arrows point to the female parent. The numbers inside the circles representing parents refer to Carnegie culture numbers (tables 2 and 3); somatic *(2n)* chromosome numbers are also shown for each parental plant. Further details are given in text.

Lafayette, Indiana), variation was also observed, and was especially marked at Purdue. At each of these contrasting stations, however, plants of the same uniform and recognizable biotype represented by the clone 4249-1 and its offspring were present.

From such space-planted field tests we concluded that the clone 4249-1 is highly apomictic and that its seed progeny consists of a high percentage of a single biotype together with a low frequency of relatively weak aberrants. We refer to this apomictic biotype as the "Athabasca" strain.

Another conclusion is that the biotypic variation within commercial Delta may be masked by phenotypic modifications in different environments. This variation was apparently not evident at the Experimental Farm at Ottawa and became apparent only when the plants were grown further south. This opinion was shared by Dr. R. W. Vicar, Head, Departmental Research of the Genetics and Plant Breeding Institute, Ottawa, expressed in his letter to Dr. Jens Clausen on May 27, 1960.

TABLE 5

CHARACTERS DISTINGUISHING PARENTS AND AN $F_t$ HYBRID

| 4178-1 *Poa ampla* Mcrr. Kahlotus | 4537-9, F, Hybrid | 4249-1, *Poa pratensis* L. Athabasca |
|---|---|---|
| Bunchgrass | Bunchgrass | Rhizome grass |
| Glacus herbage | Glauscent herbage | Green herbage |
| Long panicles (27-30 cm) | Short panicles | Short panicles (12-15 cm) |
| Lemmas smooth | Lemmas intermediate | Lemmas floccose |
| *In* = 64 | *In* = -83 | *In* = 70 |
| —75% apomictic | Sexual | ~95% apomictic |
| Culms tall, spreading | Culms intermediate | Culms shorter, erect |
| Rust-susceptible | Rust-susceptible | Rust-resistant |
| Dies at Timberline | Survives at Timberline | Survives at Timberline |
| Winter-active at Stanford | Winter-active at Stanford | Winter-dormant at Stanford |

The superior growth and forage characteristics of the Athabasca biotype when grown at both Pullman and Stanford made it a logical choke for crossing experiments. The strong production of rhizomes, abundance of rosette leaves and numerous erect culms (200-300 per plant), and freedom from rust were among its desirable features.

### *Differences between Poa ampla Kahlotus 4178-1 and P. pratensis Athabasca 42494*

Table 5 summarizes the principal differences between the two parents and one of their Fj hybrids, 4537-9„ which was intermediate in some characteristics. Figure 7 shows the parents and the same F| hybrid when grown in the same

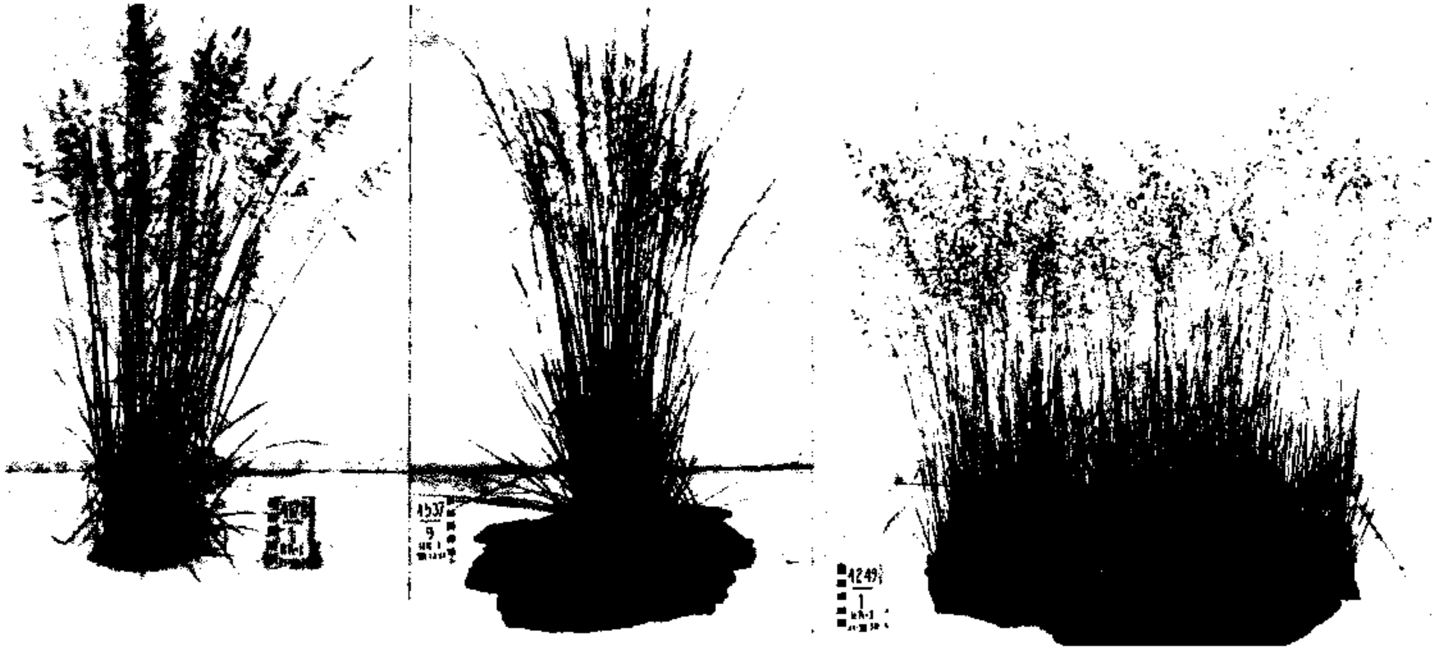


Figure 7, Poa a m ^ Kahlotus 4178-1 (left), *P. pmtensis* Athabasca 4249-1 (right), and one of their F, hybrids, 4537-9 (center), all grown at the Mather transplant station at elevation 1400 meters on the western slope of the Sierra Nevada, California. The photographs were taken on June 21, 1958. The black and white scale is 10 cm high; each square is 1 cm. Note the difference in lateral spread between the parents and the semi-bunchgrass habit of the hybrid. See also table 5 for listings of the characteristics of these same parents, and figure 8 for drawings of details of spikelets, lemmas, and ligules.

garden at the Mather transplant station at elevation 1400 meters on the western slope of the Sierra Nevada. In figure 8 are detailed drawings of spikelets, lemmas, and ligules of these same individuals.

*Results from crossing*

After mass pollination of the two parents at Stanford in 1944, as described in Chapter I, the seedling progeny of both were grown. Among 1062 seedlings harvested on the *Poa pratensis* parent, all were uniformly of the maternal type except for 16 aberrants which were variants of P. *pratensis* that presumably arose from chromosomal irregularities.

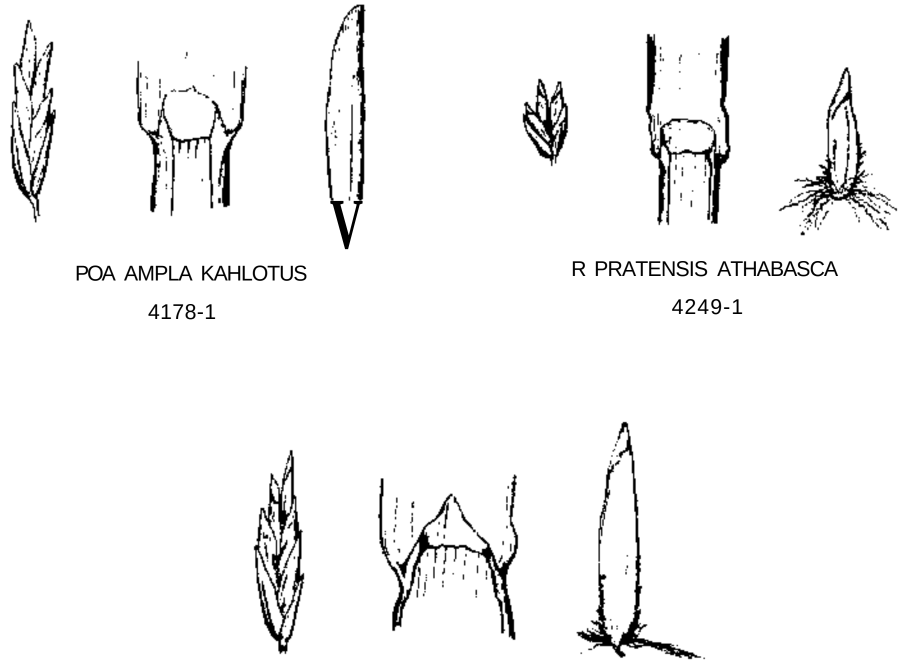


Figure 8. Drawings of details of spikelets,. lemmas, and ligules of the parents and an F$_s$ hybrid of *Poa ampia* Kahlotus X *P, pratensis* Athabasca shown at the same scale. See also table 5 and figure 7.

Although the *P. amph* parent suffered considerable rust damage in the Stanford environment, 404 seedlings were grown from it; 48 of these were

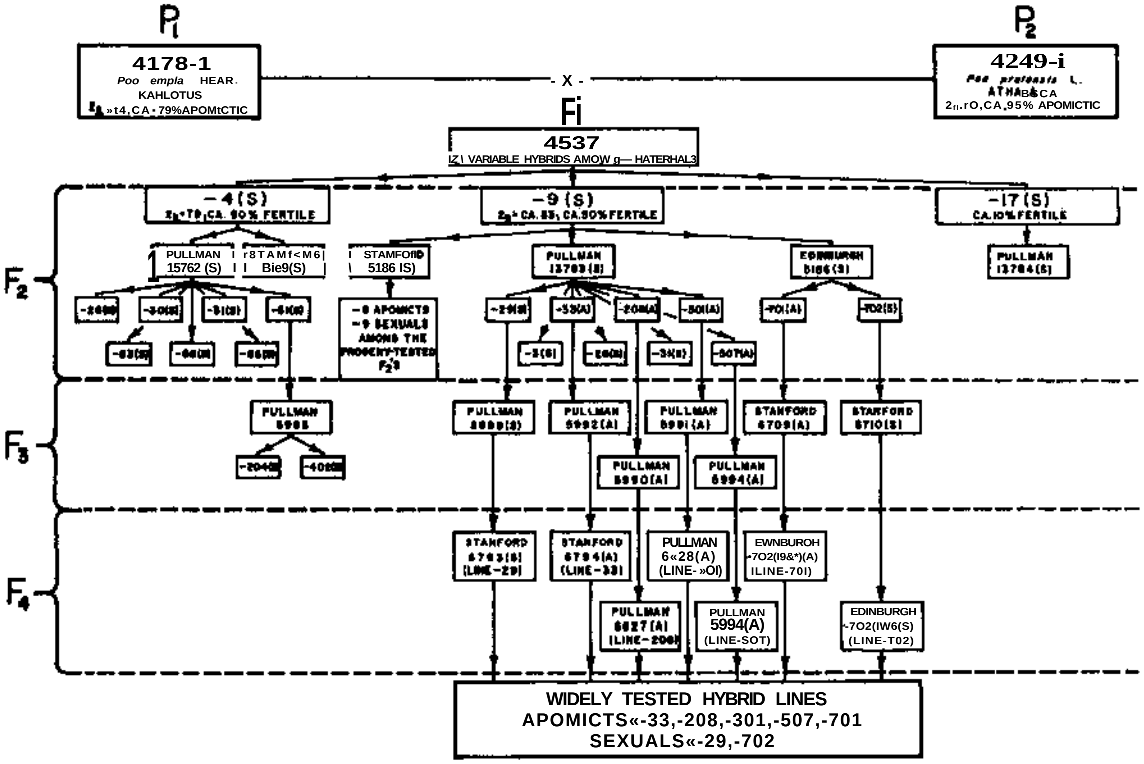


Figure 9. Pedigree showing origin of the most widely tested apomictic hybrid derivatives stemming from the cross *Poa ampla* Kahlotus X P. *pratensis* Athabasca. Subnumbers (preceded by a dash) refer to individual plants; (S) = sexual, (A) = apomictic. Progeny tests were made at Pullman, Washington, Stanford, California, and Edinburgh, Scotland, as indicated.

mostly weak aberrants of the maternal type, but 16 were $F_1$ hybrids, as was shown by morphological marker characters. The frequency of the $F_1$ hybrids harvested on *Poa ampla* was, therefore, a little over 5%, contrasted with 0% for *P. pratensis,* which clearly was highly apomictic. The 340 remaining maternal-like individuals harvested on *P. ampla* were of normal vigor.

The 16 $F_1$ individuals were highly variable, differing from each other markedly in vigor, chromosome number, fertility, and morphological characters. The variability among the $F_1$ progeny was evidently due to the highly irregular distribution of chromosomes during meiosis, characteristic of both P. *ampla* and *P. pratensis* (Grun, 1954, 1955a). The three most vigorous $F_1$ hybrids were 4537-4, -9, and -17, all of which were sexual, yielding highly segregating $F_2$ progeny. Likewise, none of the other $F_1$ hybrids were apomictic. Selections were then made among the $F_2$ segregants for vigorous individuals to be included in further progeny tests, and the results from some of these trials were more encouraging.

A total of 12 apomictic lines were derived, all from selected $F_2$ segregants of the single $F_1$ hybrid 4737-9. The selected $F_2$ individuals were progeny-tested in spaced plantings at Stanford, Pullman, and Edinburgh. The pedigree shown in figure 9 indicates the relative frequency of apomictic derivatives compared with sexually reproducing progeny among $F_2$ segregants. The segregating progenies, while mostly highly variable, were often composed of a high proportion of weak individuals.

Exceptions to this rule were found, for example, in lines -29 and -702 (see bottom of figure 9), both of which were derived from the sexual $F_1$ hybrid 4537-9. These two lines consisted of relatively vigorous plants through the $F_4$ generation, and showed minor variations of recombinations of the original parents within a narrow range. The range of phenotypic variability observed within these two lines differed when grown at Stanford, Pullman, and Edinburgh; variability range was greatest at Stanford, least at Edinburgh (see Watson and Clausen, 1961). Stanford is the most arid of these three environments, contrasted with the more humid and cooler climate at Edinburgh, which is more favorable for the growth of most members of the genus *Poa.* Differences between minor genetic variants tend to be masked when the plants ire observed in a more favorable environment.

Figure 10 shows one of the apomictic $F_3$ populations (culture No. 6658) Jhat were progeny-tested in the Stanford garden. The 12 apomictic derivatives liffered from one another in chromosome number, morphological charactersties, and growth responses when grown in contrasting environments, but all lad features recombining in various degrees the characters of the original >arents. In table 6 are listed the 12 apomictic lines derived in the $F_5$ generation **rom** the $F_1$ hybrid 4537-9 and an impression of their overall growth responses **vhen** grown as vegetatively cloned transplants at the contrasting altitudinal tations at Stanford, Mather, and Timberline; comparative data is given for he parents and their $F_1$ progenitor. The range in chromosome number, 2«

TABLE 6

MEAN PERFORMANCE OF PARENTS AND APOMICTS FROM *Poa ampla* RAHLOTUS X *P. pratensis* ATHABASCA AT CONTRASTING ALTITUDINAL STATIONS*

| | | Responses at Transplant Stations | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Stanford (30 meters) | | | Mather (1400 meters) | | | Timberline (3050 meters) | | |
| Line Number | Chromosome Number, *In* | Width, cm | Culm Ht., cm | Index Value | Width, cm | Culm Ht$_M$ cm | Index Value | Width, cm | Culm Ht., cm | Index Value |
| 4I784P.) | 64 | 8 | 62 | 20 | 9 | 76 | 26 | NS\| | NS | 0 |
| 4249-l($P_2$) | 70 | 20 | 52 | 22 | 89 | 76 | 96 | 14 | 30 | 11 |
| 4537~9(F,) | -83 | 12 | 48 | 16 | 12 | 72 | 24 | 6 | 0 | 1 |
| 5I86-20CF,) | 87 | 32 | 47 | 22 | 75 | 76 | 59 | 23 | 33 | 14 |
| 5186-23(F,) | 82-85 | 26 | 47 | 20 | 50 | 68 | 61 | 29 | 32 | 16 |
| 5186-123($F_S$) | -72 | 31 | 44 | 20 | 63 | 71 | 76 | 25 | 31 | 14 |
| 5186-309^) | 102 | 28 | 56 | 24 | 67 | 84 | 84 | 28 | 43 | 18 |
| 5l86-3il(Fj) | -84-85 | 34 | 59 | ***36*** | 58 | 85 | 88 | 23 | 39 | 16 |
| 5186-323CFJ) | 81 | 28 | 38 | 18 | 31 | 62 | 31 | 42 | 39 | 20 |
| 5186-418($F_3$) | ... | NS | NS | 0 | 7 | 49 | 15 | NS | NS | 0 |
| 5I86'70l(Fi) | 86 | ***37*** | 40 | 24 | 81 | 82 | 93 | 34 | 28 | 14 |
| 13783-33(F,) | 68 | 32 | 45 | 22 | 68 | ***73*** | 72 | 19 | 22 | 10 |
| 13783-208($F_J$) | 70 | 19 | 57 | 18 | 47 | 78 | 54 | 14 | 34 | 11 |
| 13783-301($F_3$) | 80 | 32 | 47 | 29 | 81 | 80 | 112 | 24 | 26 | 12 |
| 13783-5O7($F_3$) | -70 | 32 | 70 | 31 | 62 | 88 | 59 | 5 | 41 | 12 |

* All data averaged from three years' measurements (1957-1959).

t NS = nonsurvivor.

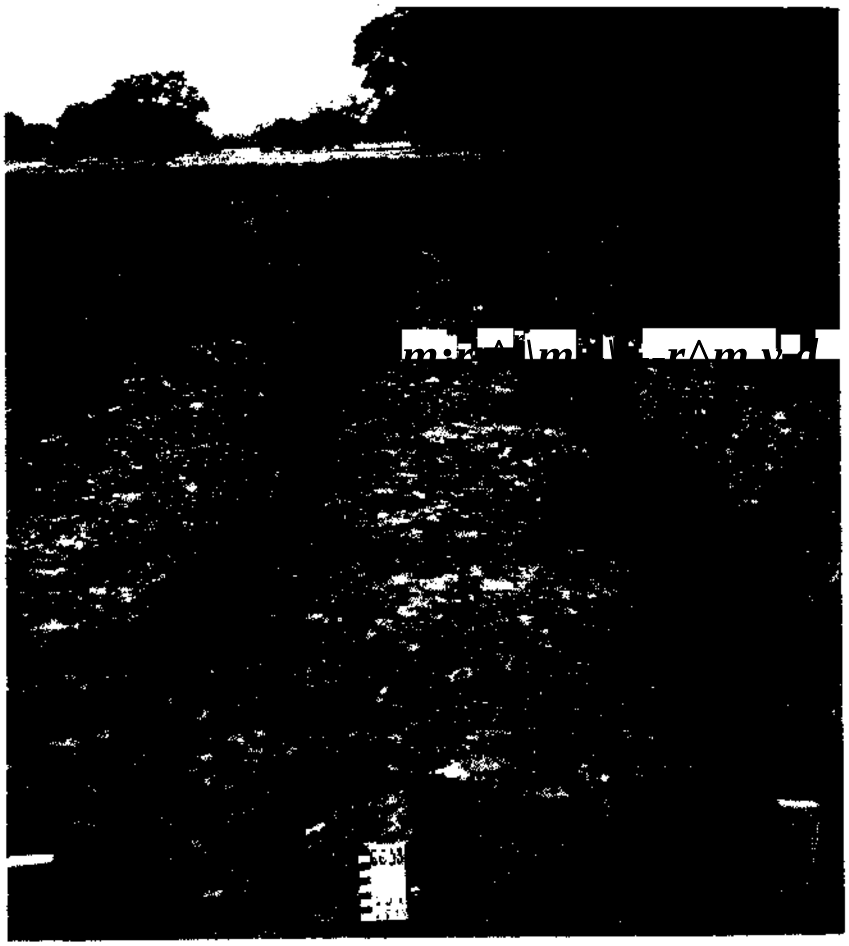
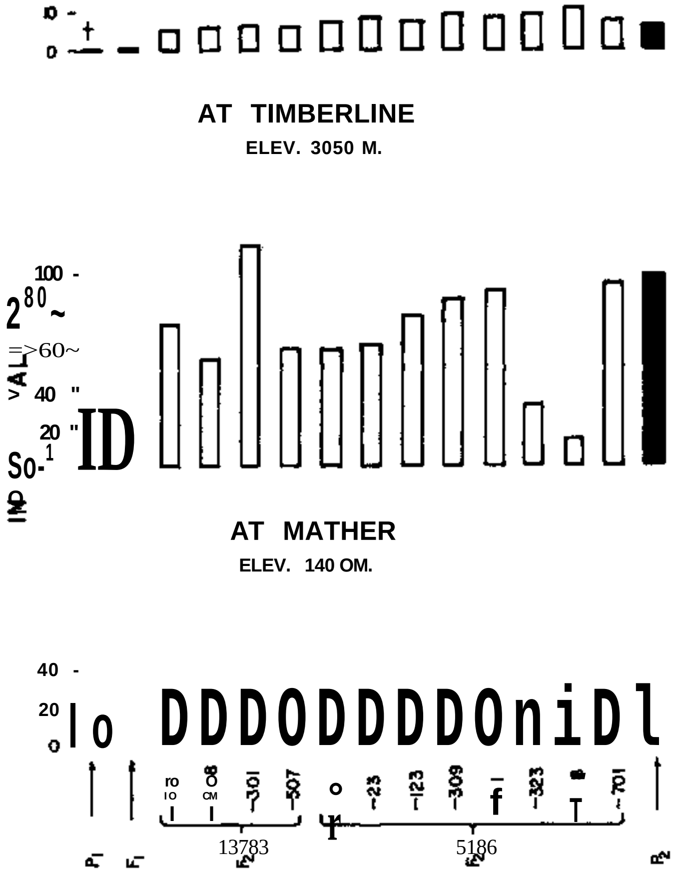


Figure 10. View of space-planted progeny tests in the Stanford garden of *Poa amph* Kahlotus X *P. pratensis* Athabasca. The two rows in the center are culture 6658, one of the uniform apomictic lines derived from the Fj hybrid 4537-9. The black and white scale is 10 cm high. The photograph was made on May 3, 1955.

= 70-102, in the apomicts is not surprising in view of the characteristic meiotic irregularity in *Poa* hybrids. Of particular interest is that one apomict (line 13783-301) outperformed both of the original parents at all three transplant stations, and that several others, including lines 5186-309, -311, -701, and 13783-33, had a higher range of tolerance to the contrasting climates than either parent. On the other hand, the line 5186-418 performed poorly.

These comparisons are more clearly shown by the histograms in figure 1L The overall better performance of both parents and the apomicts ai Mather



AT STANFORD

ELEV. 30 M.

Figure II. Histograms of response index values showing average growth performance of parents, the $F_s$ hybrid 4537-9, and apomictic derivatives of the cross *Poa ampla* Kahlotus 4178-I ($P_1$) X *P. pratauis* Athabasca 4249-1 ($P_2$) when grown as vegetatively cloned propagules at the altitudinal transplant stations at Stanford, Mather, and Timberline. Crosses indicate non-survivors. The response index values (indicated by the scale at the left) were obtained by averaging measurements at each station for three years (1957-1959, inclusive) for the following characters: (1) Width of plant at base in cm, (2) Length of longest basal leaf in cm, (3) Width of longest basal leaf in mm, (4) Height of tallest culms in cm, (5) Number of culms per plant, (6) Relative overall bulk in growth measured on a scale of 1 (low) to 9 (high). See Chapter I for details.

compared with those at Stanford and Timberline is also evident. The characteristic differences between the parents and also between the various apomicts come to fullest expression at this mid-altitude station. It is especially noteworthy that the sexual F, hybrid 4537-9, which gave rise to all of these apomictic lines through its $F_2$ segregants, was itself a relatively poor performer at all three altitudes, although it did barely manage to survive at Timberline over a winter, something which the P. *ampla* parent failed to do.

The four apomictic lines 13783-33, -208, -301, and -507 were selected for testing at the cooperating stations of the Agricultural Research Service and other agencies listed in table 1 and mapped in figure 5. In these broad regional tests, the parental and apomictic derivatives were grown from seed in randomized test plots at each station. The growth performance of the apomicts and the parents at many of these test stations is summarized in figure 12. The histograms of this figure are constructed from response index values based on the means of six corresponding variables determined at each station during 1956-1958, as explained in Chapter I.

The greater tolerance of the *Poa pratensis* parent to widely different climates compared with the *P. ampla* parent is apparent in figures 11 and 12. At the southernmost site at Franklinton, Louisiana, at 30°50'N, however, P. *pratensis* as well as *P. ampla* and the four apomicts failed to survive. Further north at Blacksburg, Virginia (38°12'N), where the *pratensis* parent performed fairly well and *ampla* poorly, the apomict -*33* was outstanding, greatly exceeding both parents. At Lexington, Kentucky (38°02'N), in an area noted for its bluegrass pastures, the *P. pratensis* parent was extremely vigorous, contrasting with poor performance of *P. ampla*. There, the *pratensisAik.t* apomict -33 performed well, but not as well as the P. *pratensis* Athabasca parent, and the *ampla-li\ae* apomicts -208 and -507 lagged. In the highly continental climate at Purdue, Indiana (40°25'N), and at St. Paul, Minnesota (44°57'N), characterized by cold, severe winters and hot summers, *Poa ampla* failed to survive, but the P. *pratensis* parent grew satisfactorily, as did the four apomictic derivatives, especially line -33, which well exceeded even the *pratensis* parent.

At Pullman, Washington (46°35'N), both of the parental lines thrived but were outperformed by their *ampla-likc* apomictic derivative, line -208. The Pullman plantings were made in the region from which the *ampla* parent originated, so it is not surprising that this parent attained its maximum development there. The markedly strong inhibiting effect on the growth of both parents and the apomicts at the arid test station at Lind, Washington, is clearly evident. The poorer performance of the parents and apomicts at Stanford, Pleasanton, and Davis in California compared with Pullman, Washington, is also apparent from the histograms, even though irrigation was practiced at all these stations. In the nonirrigated test plots at HalPs Flat in an arid region east of Mt. Lassen, California, both the parents and the apomicts made very restricted growth, yet did manage to survive.

At the stations in northern Europe listed in table 1, both of the parental lines and their hybrid derivatives were tested. At Penlandfield, Scotland (56°58'N), *Poa ampla* Kahlotus prospered, even surpassing somewhat its performance at Pullman, Washington; but at Uppsala, Sweden **(59°52'N),** and at Volbu, Norway **(61°08'N),** this strain failed to survive. In contrast, *Poa pratensis* Athabasca

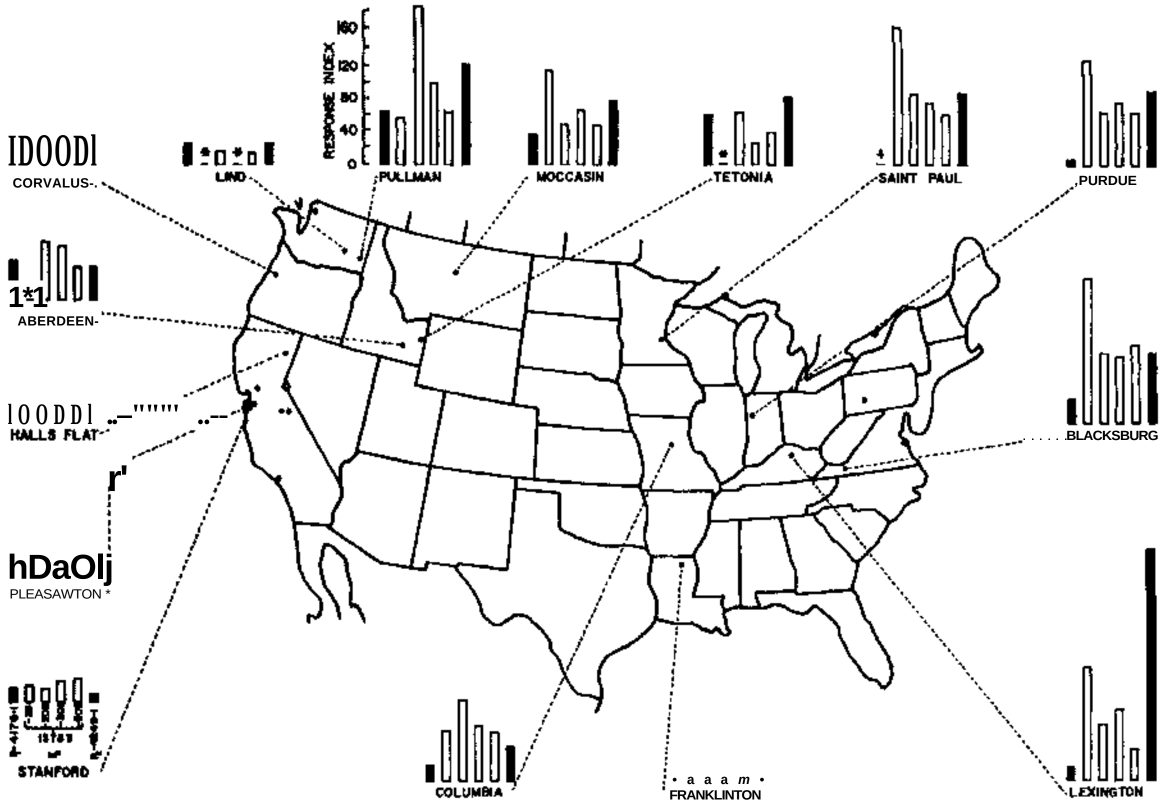


Figure 12. Histograms of response index values indicating relative growth performance of the parents and apomictic derivatives from the cross *Poa ampla* Kahlotus 4178-1 (P,) X *P. pratensis* Athabasca 4249-1 ($P_2$), when grown in randomized seeded test plots at various experiment stations in the United States, as indicated. See table 2 for details about the test stations. The responses of the parental lines are indicated by the solid black columns, the tpomicts by open columns. Line numbers are shown under the histogram columns for Stanford. Crosses indicate nonsurvivors; stars, absence of data. The response index values, indicated by the scale at the left for the Pullman station, were computed by averaging measurements from each station for the years 1958-1960, inclusive, for each of the six characters listed in the legend of figure 11. (See Chapter I.)

and the apomicts -33, -208, -301, and -597 thrived well at all three of these stations.

A comparative statistical analysis of the growth performance of both parental strains and a number of their hybrid derivatives at Penlandfield, Scotland, at Pullman, and at Stanford was made by Dr. Patricia Watson in Scotland in collaboration with the late Dr. Jens Clausen (Watson and Clausen, 1961). The main objective of this study was to determine the extent to which differences in phenotypic expression of both apomictic and sexual progenies differ when grown in contrasting climates. These studies were conducted between 1950 and 1959. Appreciable differences in growth responses of apomictic progenies of the same parentage were evident at the contrasting environments, especially at Stanford. Sexual segregating progenies of this same parentage likewise displayed a greater range of phenotypic diversity at Stanford. Thus, genetic variability masked in the more favorable environments came to light at Stanford. The phenotypic modifications in the apomictic lines were uniform, while the sexual lines were extremely variable. This was most apparent in leaf color, culm length, leaf length, and development of rhizomes.

On the basis of the widespread transplant and field tests, the apomictic hybrid lines 13783-33, -208, and -507 were considered to have potential value as agronomic forage grasses.

### *Summary of results from the cross Poa ampla Kahlotus* X P. *pratensis Athabasca*

The major findings from this cross between these two contrasting and predominantly apomictic polyploid species follow:

1. The frequency of $F_t$ hybrids occurring on P. *ampla* Kahlotus as the female parent was approximately 5%; the remaining progeny were either maternal-like replicates, or weak aberrants.
2. The 16 Fj hybrids that were obtained varied widely in both morphological features and in vigor, but all had recombinations of the characteristics of the parents.
3. Progeny tests of the more vigorous $F_t$ hybrids revealed all to be sexual, yielding highly segregating $F_2$ progeny.
4. From $F_2$ segregants of one of the Fj hybrids, 12 self-reproducing apomictic lines were derived in the $F_2$ generation. Extensive progeny tests on two other $F_2$ hybrids failed to yield any other apomictic derivatives.
5. In extensive growth performance tests of parental and selected $F_2$ apomictic derivatives in widely different environments, the performance of some of the apomicts when grown in some climates was superior to that of the parents.
6. The possibility of synthesizing agronomically useful new hybrid strains through the above interspecific combination is clear.

## POA AMPLA ALBION 4183-1 X P. PRATENSIS MATHER 4253-4

The parents of this combination (CIW culture No. 4535 of table 4) represent distinctive ecotypes of the two species, in contrast with the preceding cross. The frequency of Fj hybrids obtained on the maternal parent was higher, and some of the F,'s, unlike those from the Kahlotus-Athabasca combination, proved to be directly apomictic. Among the sexual F,'s, however, $F_2$ segregants were likewise found, which gave rise to new apomictic recombinations. Some of these were widely field-tested, and several proved to have potential agronomic value.

### *The Poa ampla Albion parent*

This distinctive tall form of *Poa ampla* (figure 3, middle row at the left) was collected by Dr. L. A. Mullen of the Soil Conservation Service on July 5, 1940, a few miles north of Albion, Whitman County, Washington, at elevation 730 meters, in deep loam soil associated with other native herbaceous species. This form is among the tallest and most robust of the species, which with its distinctive blue-glaucus leaves and stems has been aptly named "big bluegrass." The original seeds collected by Dr. Mullen were sown at the Pullman nursery. From the resulting planting, two individuals were shipped as live transplants to Stanford in May 1943 and assigned the Carnegie accession numbers 4183-1 and -2. The vegetative propagules of these two clones were used in the crossing and transplant experiments.

### *The Poa pratensis Mather parent*

This was one of a series of transplants of native *Poa pratensis* dug in a meadow at the Carnegie transplant station at Mather, elevation 1400 m, on the western slope of the Sierra Nevada in 1943. The individual used in this cross, 4253-4, was a typical representative of the Mather population. Like the Athabasca form of *P. pratensis* used in the preceding cross, the Mather parent proved to be widely tolerant when tested in different climates and also was quite highly apomictic.

### *Comparison between characteristics of the parents*

The contrast in morphological characteristics and seasonal growth responses between the parents of this cross were as striking as in the *P. ampla* Kahlotus X *P. pratensis* Athabasca combination. The major differences are summarized in table 7. Physiologically, *Poa ampla* Albion differed from the Kahlotus form used in the preceding cross in that growth and flowering of the Albion clone is more favored by cooler night temperatures, as shown by controlled growth experiments at the former Earhart Laboratory at the California Institute of

Technology at Pasadena (Hiesey, 1953). In field tests, likewise, the Albion form performed better in the colder, more continental climates such as at Uppsala, Sweden, and at the Timberline transplant stations, while Kahlotus was favored by milder climates such as at Edinburgh, Scotland, and Bellingham, Washington. Corresponding comparative growth experiments in both the laboratory and field revealed a wide range of tolerance to environmental differences, for both the Mather and Athabasca forms of *Poa pratensis*.

### *Results from crossing experiments*

The parental plants were mutually pollinated in a pollen-tight cage at Stanford during their overlapping flowering periods in May 1944. Twenty-one inflorescences of P. *ampla* 4183-1 were mutually pollinated with numerous inflorescences of P. *pratensis* 4253-4, and seeds on both were harvested when mature. We obtained from P. *ampla* approximately 4000 apparently viable seeds, which were sown the following season at Stanford under the culture number 4535. Among 1142 plants that were grown from this harvest, 131 were classed as aberrants, 954 as maternal-like apomicts, and 57 as Fj hybrids. These were readily distinguished in early seedling stages from the maternals primarily through their more decumbent growth habit and their shorter, darker green leaves.

TABLE 7

CHARACTERISTICS DISTINGUISHING *Poa ampla* ALBION 4183-1 AND *Poa pratensis* MATHER 4253-1 AS SEEN AT STANFORD

| *Poa ampla* Albion 4183-1 | *Poa pratensis* Mather 4253-4 |
|---|---|
| Strict bunchgrass | Strongly rhizomatous grass |
| Herbage blue-glaucus | Herbage dark green |
| Culms tall, strict, to 150 cm | Culms shorter, somewhat divaricate, to 70 cm |
| Panicles long, open, 25-30 cm | Panicles short, more congested, 10-15 cm |
| Lemmas smooth | Lemmas floccose |
| *In* = 63 | *In* = 68 |
| ~-*84% apomictic | —88% apomictic |
| Winter-active at Stanford | Winter-dormant at Stanford |
| Rust-susceptible | Rust-resistant |

The Fj hybrids varied among themselves in chromosome number, degree of fertility, degree of apomixis or sexuality, color of herbage, leaf dimensions, degree of production of rhizomes, and the amount of pubescence on spikelets and lemmas, but all had characteristics intermediate between the parents. None were as vigorous in growth as the P. *pratensis* parent, but some were comparable in vigor with the *P. ampla* parent at this low-altitude station.

Table 8 lists the F, hybrids individually with some of their characteristics, including their responses as vegetatively cloned transplants at the altitudinal

TABLE 8

$F_t$ HYBRIDS OF *Poa ampla* ALBION X *P. pratensis* MATHER

| F, Hybrid Number | Chromosome No,, *In* | Fertility, % | Apomictic or Sexual | No. of Culms* |  |  | No. of Apomictic Derivativesf |
|---|---|---|---|---|---|---|---|
|  |  |  |  | Stanford | Mather | Timberline |  |
| 4535-1 | 66 | 40 | Sexual | 11.0 | 8.3 | 1.6 | 0 |
| -2 | 96 | 20 | 58% apomictic | 29.6 | 62.0 | 12.1 | 2 |
| -3 | ... | ... | Not tested | 3.1 | 27.6 | 23.0 | 0 |
| ~4 | 63 | ... | Sexual | 38.0 | 47.0 | 21.3 | 3 |
| -5 | 93 | ... | 47% apomictic | 16.3 | 22.3 | 4.6 | 2 |
| -6 | -96 | 35 | 60% apomictic | 28.3 | 28.0 | 15.3 | 1 |
| -7 | ... | ... | Not tested | 0.3 | 10.3 | 20.0 | 0 |
| -8 | ... | 75 | Not tested | 23.3 | 10.3 | 16.6 | 0 |
| -9 | -104 | 80 | Sexual | 9.6 | 21.3 | 13.6 | 0 |
| -10 | ... | 50 | Not tested | 2.6 | 12.3 | 16.6 | 0 |
| -11 | ... | 88 | Not tested | 13.6 | 15.6 | 20.0 | 0 |
| -12 | ... | *77* | Not tested | 3.3 | 14.6 | 12.0 | 0 |
| 43 | ... | 84 | 56% apomictic | 6.0 | 6.0 | 17.3 | 0 |
| -14 | ... | ... | Not tested | 7.0 | 16.0 | 4.0 | 0 |
| -15 | ... | 75 | Not tested | 10.3 | 19.0 | 8.0 | 0 |
| *A6* | ... | 80 | Not tested | 4.0 | 10.0 | 12.3 | 0 |
| -17 | -94 | ... | Sexual | 3.0 | 32.0 | 17.0 | 0 |
| -18 | ... | 50 | 40% apomictic | 21.3 | 10.3 | 15.2 | 1 |
| -19 | -97 | 35 | 60% apomictic | 17.3 | 46.6 | 28.6 | 1 |
| -20 | ... | 80 | Not tested | 10.6 | 13.3 | 6.3 | 0 |
| -21 | 94 | 80 | 35% apomictic | 12.0 | 42.3 | 15.6 | 1 |
| -22 | ... | 75 | Not tested | 3.0 | ... | 8.6 | 0 |
| -23 | ... | ... | Not tested | 0.0 | 6.0 | 7.6 | 0 |
| -24 | ... | ... | Not tested | 0.3 | ... | 14.6 | 0 |
| -25 | ... | ... | Not tested | 1.0 | 8.6 | 16.0 | 0 |
| -26 | -100 | 67 | 90% apomictic | 8.6 | 40.0 | 27.0 | 1 |
| -27 | ... | ... | Not tested | 3.6 | ... | 9.6 | 0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| -21 | -104 | 75 | Sexual | 16.0 | ... | 33.6 | 0 |
| -19 | 92 | 40 | 42% apomictic | 24.6 | 11.0 | 16.6 | 1 |
| 40 | ... | ... | Not tested | 8.6 | 11.6 | 13.0 | 0 |
| 41 | 94 | 33 | Sexual | 10.3 | 46.3 | 24.6 | 0 |
| 42 | ... | 67 | Not tested | 203 | 37.6 | 13.0 | 0 |
| 43 | ... | 40 | Not tested | 2.0 | 10.3 | 1.0 | 0 |
| 44 | ... | ... | Not tested | 3.3 | 21.6 | 16.3 | 0 |
| 45 | 96 | ... | Not tested | 2.5 | 32.0 | 22.6 | 0 |
| 46 | ... | ... | Not tested | 0.0 | 2.3 | 1.3 | 0 |
| ~$7 | ... | ... | Not tested | 0.0 | 2.0 | 2.6 | 0 |
| 4$ | -94 | ..* | Sexual | 4.6 | 31.3 | 20.6 | 0 |
| 49 | ... | ... | Not tested | 3.1 | 26.0 | 1.0 | 0 |
| -40 | ... | 20 | Sexual | 4.6 | 23.0 | 18.6 | 0 |
| 41 | ... | ... | Not tested | 3.0 | 19.0 | 7.3 | 0 |
| -42 | ... | ... | Not tested | 0.0 | 4.0 | 11.5 | 0 |
| -43 | ... | ... | Not tested | 0.6 | 1.0 | 0.0 | 0 |
| -44 | 70 | 67 | Sexual | 7.6 | 31.0 | 9.0 | 0 |
| 45 | -91 | 16 | 80% apomictic | 48.0 | 29.3 | 16.0 | 1 |
| -46 | ~99 | 50 | Sexual | 19.3 | 21.6 | 20,6 | 1 |
| •47 | ... | ... | Not tested | 0.3 | 12.3 | 5.3 | 0 |
| -48 | ... | ... | Not tested | 3.0 | 6.0 | 11.0 | 0 |
| 49 | ••• | ... | Not tested | 3.0 | 14.6 | 6.6 | 0 |
| -50 | 100 | 77 | 85% apomictic | 9.6 | 13.0 | 8.0 | 1 |
| -11 | -117 | 75 | 40% apomictic | 2.0 | 2.0 | 6.0 | 2 |
| 42 | -70-74 | 75 | Sexual | 18.3 | 11.3 | 0.0 | 3 |
| 43 | ... | 75 | Not tested | 14,3 | 0.0 | 1.3 | 0 |
| 44 | -61 | 86 | Sexual | 18,3 | 19.6 | 10.0 | 0 |
| 45 | ... | ... | Not tested | 1.3 | 9.6 | 25.0 | 0 |
| 46 | ... | ... | Not tested | 0.0 | ... | 5.0 | 0 |
| 47 | ... | 50 | Sexual | 27.0 | 5.3 | 10.3 | 0 |

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* Mean data from three years (1946-1948).

t Set Table 9 for details.

stations at Stanford, Mather, and Timberline. Also indicated are those F, hybrids from which apomictic derivatives were obtained either directly or through the $F_2$ or $F_3$ generations.

*Apomictic lines tested in different environments*

Altogether, 15 apomictic lines derived from the cross *P. ampla* Albion 4183-1 X P. *pratensis* Mather 4253-4 were selected for testing at the various field stations. These apomicts are listed in table 9, which also indicates the origin of each line and some of its features.

The histograms in figure 13 show the overall relative growth performance of these apomictic lines when grown as vegetatively cloned transplants at the altitudinal stations at Stanford, Mather, and Timberline over a three-year period.

TABLE 9

APOMICTIC LINES DERIVED FROM *Poa ampla* ALBION X R *pratensis* MATHER

| Line Number | Origin | % Apomixis | Chromosome Number, *In* |
|---|---|---|---|
| 4535-6 | Direct $F_1$ apomict | 82 | 95-97 |
| 4535-26 | Direct F, apomict | 92 | -100 |
| 4535-45 | Direct $F_l$ apomict | 67 | 90-92 |
| P-597I-2G8 | $F_3$ from 4535-2 | 96 | 75-77 |
| P-5971-408 | $F_3$ from 4535-2 | 80 | 86 |
| P-13775-202 | F, from 4535-4 | 82 | ... |
| P-13775-211 | $F_3$ from 4535-4 | 68 | 67 |
| P-13775-212 | F, from 4535-4 | 95 | 56-57 |
| P-13822-304 | FJ from 4535-51 | 88 | ... |
| P-13823-706 | F, from 4535-5 | 96 | 55-57 |
| P-13823-409 | $F_3$ from 4535-51 | 92 | 82 |
| P-13833-211 | $F_3$ from 4535-52 | 80 | 99 |
| P-B833-3II | Fj from 4535-52 | 81 | -100 |
| P-13833-701 | $F_3$ from 4535-52 | 84 | -100 |

From figure 13 it is evident that growth performance of the hybrid apomictic derivatives at the three altitudes varied appreciably. The line 13833-701 outperformed somewhat both of the parents at all three stations, whereas lines 4535-26 and -45 proved to be inferior to either parent at all altitudes. In general, the responses of most of the apomictic lines can be characterized as intermediate between the parents. These results, although not surprising, were contrary to the original hope that the apomicts would generally surpass the parental lines when grown in a wide range of climates.

The relative growth performance of the parental lines and seven of the apomictic lines when grown from seed in randomized test plots at the various stations cooperating with the Agricultural Research Service is indicated in figure 14 by the histograms showing "response index" values computed as

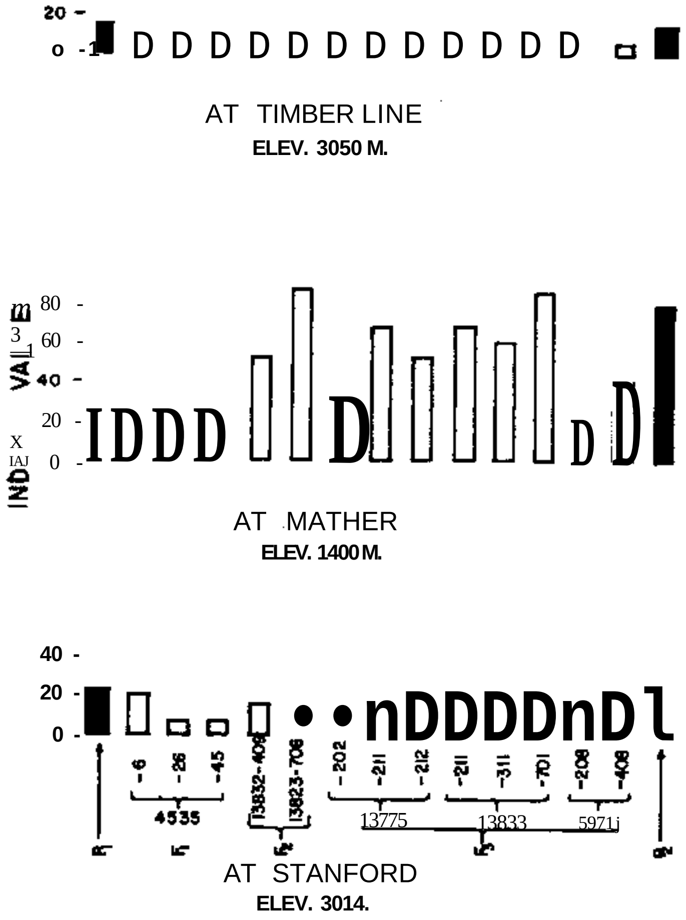


Figure 13. Histograms of response index values indicating average growth performance of the parents and apomictic hybrid derivatives from the cross *Poa amph* Albion 4183-1 (P,) X P. *pratensis* Mather 4253-4 ($P_2$) when grown as vegetatively cloned transplants at the altitudinai stations at Stanford, Mather, and Timberline. The solid black columns represent the parents, the open columns the apomictic hybrid derivatives. The index values ^indicated by the scale at the left) were computed as described in Chapter I. Line numbers are shown under the histogram columns for the Stanford station.

explained in Chapter I. The data from both figures arc therefore comparable.

The regional tests reveal a number of interesting facts. As in the preceding *Poa amph* Kahlotus X P. *pratensis* Athabasca combination, both parents and all of the apomictic lines failed to survive at the southernmost station, in Franklinton, Louisiana. At Blacksburg, Virginia, the *Poa prattnsis* Mather parent thrived, in contrast with the considerably poorer performance of the

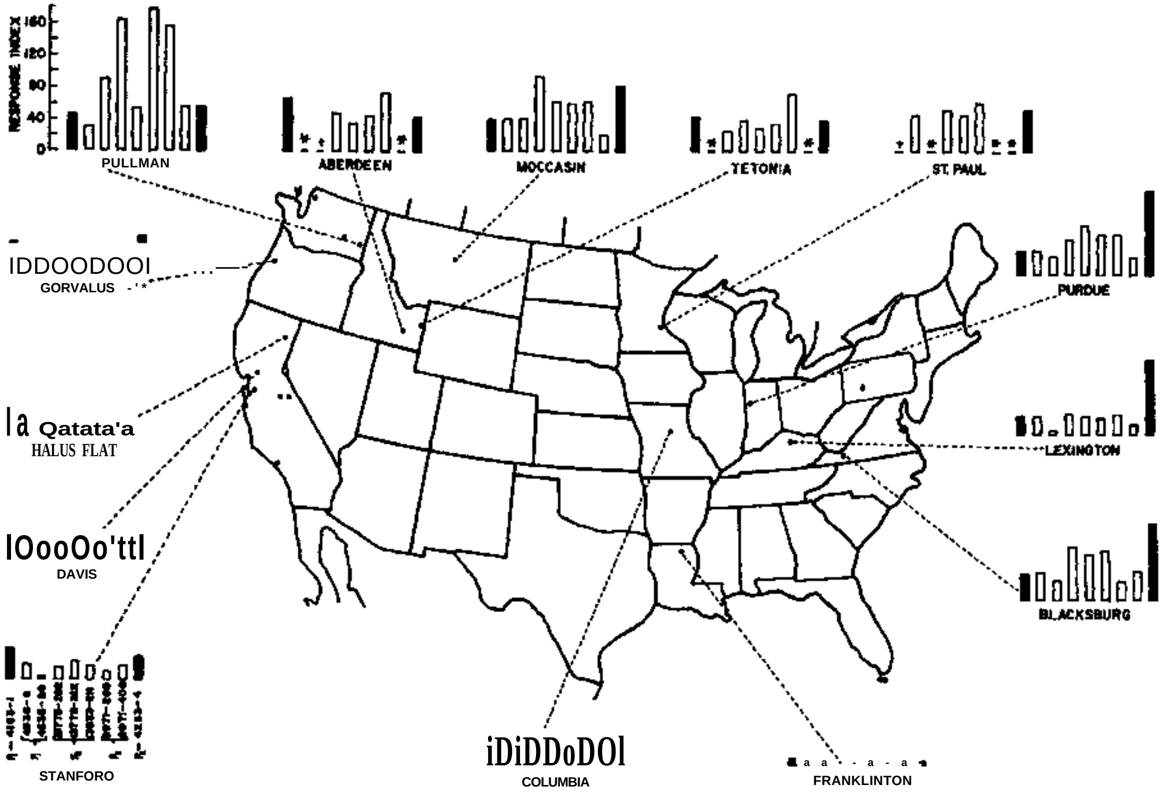


Figure 14. Histograms of response index values indicating average relative growth performance of seven hybrid apomictic lines derived from the cross *Poa ampla* Albion 4183-1 (P,) X *P. pratensis* Mather 4253-4 ($P_2$) compared with the parental lines when grown in randomized seeded test plots at various experiment stations in the United States, as indicated. See table 1 for details about the test stations.

The parental lines are indicated by the solid black columns, hybrid derivatives by open columns. Line numbers are shown under the histogram columns for Stanford. Crosses indicate nonsurvivors; stars, absence of data. The response index values (indicated by the scale at the left for Pullman) were computed by averaging measurements from the plots at each station for the years 1958-1960, inclusive, for six characteristics listed in Chapter I.

*P. ampla* Albion parent—a pattern parallel to the responses of the respective parental strains used in the *P. ampla* Kahlotus X *P. pratensis* Athabasca cross. The apomicts from *ampla* Albion and *pratensis* Mather, however, failed to perform as well at Blacksburg as the apomicts in the former cross. At Lexington, Kentucky, the apomicts of the *ampla* Albion X *pratensis* Mather combination likewise lagged considerably behind the performance of those derived from *ampla* Kahlotus X *pratensis* Athabasca. At Purdue, Indiana, the performance of the parents and apomicts was rather similar in both crosses to those observed at Blacksburg, Virginia, except that the *Poa ampla* Albion strain survived the cold winter better at Purdue than did the P. *ampla* Kahlotus strain.

Figure 15. A test planting of the apomictk line 13775-202, an $F_2$ derivative of *Poa ampk* Albion 4183-1 X *P. pratensis* Mather 4253-4 grown at the U.S. Soil Conservation nursery at Pullman, Washington. The photograph was taken on April 6, 1952, two years after planting. Culms averaged 82-90 cm in height, See figures 13 and 14 for the performance of this line in other environments.

In the more severe climate at St. Paul, Minnesota, *ampk* Albion failed to survive, whereas *pratensis* Mather thrived there fairly well although outperformed by *pratensis* Athabasca used in the former cross. In view of these results, it is interesting that the apomicts from the *ampk* Albion X *pratensis* Mather combination at St. Paul were notably poorer in overall performance than the apomicts from *ampk* Kahlotus X *pratensis* Athabasca, probably because of the influence of the male parent.

At Pullman, Washington, the growth of the apomicts 5971-208, 13833-211, and 13775-202 of the *ampla* Albion X *pratensis* Mather combination greatly exceeded the growth of both parental strains. Figure 15 shows a view of the apomict 13775-202 growing in the Pullman nursery. The responses of this line varied widely at the various test stations, as shown by the histograms, a result also typical of the other apomicts *of the ampla* Albion X *pratensis* Mather parentage. Also, the poor development of these hybrid derivatives at Stanford, Davis, and Hall's Flat, all in California, reflect their limited tolerances to these more arid climates.

The apomicts from the *ampla* Albion X *pratensis* Mather combination were not as widely and systematically tested at the northern European test stations as were those from the *ampla* Kahlotus X *pratensis* Athabasca combination, so that the available data add little significant information to that obtained from the North American regional tests.

### *Summary of results from crossing Poa ampla Albion 4183-1* X *P. pratensis Mather 4253-4*

The principal features emerging from the studies of this hybrid combination may be summarized as follows:

1. Mutual mass pollination between an individual of P. *ampla* Albion and another of *P. pratensis* Mather resulted in 57 $V_x$ hybrids harvested on *P. ampla* as the female parent; no Fi hybrids were obtained on *P. pratensis.*
2. The Fj hybrids displayed variation among themselves in morphological characters and in their growth responses when transplanted as vegetative clones at Stanford, Mather, and Timberline.
3. Three of the $F_x$ hybrids proved to be directly apomictic and were tested in contrasting field stations together with 12 other apomictic lines derived from either $F_2$ or $F_3$ segregants of sexual Fj hybrids.
4. The self-perpetuating apomictic hybrid derivatives differed widely from each other in morphological characteristics, chromosome numbers, and growth responses in contrasting habitats. Some exceeded both parents in performance in some climates.
5. The possibility of synthesizing new hybrid lines of agronomic value from the above combinations seems to be clear.

## POA AMPLA ALBION 4183-2 X P. PRATENSIS SSP. ALPIGENA LAPLAND 42504

In this cross (CIW culture No. 4273 of table 4), the parental lines represent the most contrasting forms of the *Poa ampla* X *P. pratensis* series; the apomictic lines derived from them differed markedly from the patterns encountered in the previous two combinations.

### *The parental lines*

The *Poa arnpla* parent was of the same Albion strain employed in the previous cross with *P. pratensis* Mather, but a different individual, 4183-2, whose chromosome number was *In* = 70 rather than 63, as in the plant 4183-1 used in the cross with *P. pratensis* Mather.

Seeds of *Poa pratensis* ssp. *alpigena* were originally collected by Dr. Jens Clausen in August 1936 in Swedish Lapland on the east side of Abiskojokk, south of Abisko (68°02'N), at an elevation of 420 meters. This form was associated with *Deschampsia caespitosa* (L) Beauv. in openings of a forest of *Betula pubescens* Ehrh., and in its natural habitat this *Poa* produced culms 50-60 cm tall. Seedlings of this collection were grown at Stanford in 1937, and two of them were selected for cloning and assigned the Carnegie accession numbers 4250-1 and 4250-2. The first of these was used as a parent in the crossing experiments.

TABLE 10

DIFFERENCES BETWEEN *Poa ampla* 4183-2 AND *P. pratensis* SSP. *alpigens* LAPLAND 4250-1 AS EXPRESSED AT * STANFORD

| *Poa ampla* Albion 4183-2 | *Poa pratensis* ssp. *alpigena* Lapland 4250-1 |
|---|---|
| Densely tufted bunchgrass | Extensively spreading rhizome grass |
| Herbage blue-glaucus | Herbage dark green |
| Leaves 30-50 cm long, 4-6 mm wide | Leaves to 20 cm long, 2.5-3 mm wide |
| Culms 85-150 cm high, erect | Culms 20-25 cm high, spreading |
| Inflorescences long with erect branchlets | Inflorescences short with horizontal branchlets |
| Lemmas smooth | Lemmas floccose |
| 2» = 70 | *In* ^ -74 |

This *alpigena* form of *Poa pratensis* when grown at Stanford was considerably earlier in flowering and more dwarf in stature than strains of this species-complex from more southern latitudes, as illustrated in figure 3 (lower row to the right). The freely spreading rhizomes of ssp. *alpigena* facilitated its vegetative progagation.

Table 10 lists the principal contrasting morphological differences between *Poa ampla* Albion 4183-2 and P. *pratensis* ssp. *alpigena* Lapland 4250-1 when both are grown at Stanford. At northern latitudes, such as at Volbu, Norway, this form developed considerably taller culms and longer and wider leaves than when grown at Stanford.

### *Results from crossing*

In June 1943, five inflorescences of *Poa ampla* Albion 4183-2 were individually mutually mass-pollinated with *P. pratensis* ssp. *alpigena* 4250-1 in a pollen-tight cage in a greenhouse at Stanford. Upon harvesting at maturity, approximately 500 well-filled seeds were obtained on *P. ampla* along with a great number of empty, aborted ones. When the seeds were sown at Stanford in February 1944, a total of 305 plants germinated; of these, 226 survived up to July 1945. Among the survivors, 170 proved to be typical maternal-type apomicts of *Poa ampla* Albion, 49 were classed as aberrant forms of *ampla* resulting from sexual selfing (mostly weak individuals), and 7 were recognized as interspecific hybrids.

Only 53 plants germinated from the seeds harvested on *Poa pratensis* ssp. *alpigena,* none of which were F, hybrids with *P. ampla.* This progeny was variable but consisted only of individuals of the *alpigena* type. Many were too weak to survive in the Stanford garden through even a single year, indicating that this form of *P. pratensis* is genetically unsuited for continuous long-term survival in the Stanford environment, in contrast with the much more successful performance of seedlings of the Athabasca and Mather forms *of* this species.

TABLE 11

F, HYBRIDS AND APOMICTIC DERIVATES FROM *Poa ampla* ALBION 4183-2 X P. *pratensis* SSP. *alpigena* LAPLAND 4250-1

| Culture Number | Chromosome Number, *In* | Reproductive Characteristics | Description | Number of Apomictic Derivatives |
|---|---|---|---|---|
| 4273-1 | 72 | Sterile | Weak, alpigena-like | 0 |
| 4273-7 | 68 | Sterile | Weak, glaucus form | 0 |
| 4273-8 | 70 | 88% apomictic | Weak, semi-glaucus | 4 |
| 4273-9 | ***63*** | 83% apomictic | Intermediate between parents | 5 |
| 4273-13 | 70 | Sexual | Dwarf, ascending-divaricate | 1 |
| 4273-15 | 63 | Sterile | Weak, intermediate | 0 |
| 427346 | 72 | Nearly sterile, sexual | Low, spreading | 0 |

### *Characteristics of the* F, *hybrids*

The seven Fj hybrids from this combination were mostly weaker than those from the two previous crosses between *Poa ampla* and *P. pratensis,* but were equally highly variable among themselves in vigor of growth and in floral and vegetative characters. Table 11 lists the hybrids individually and indicates the origin of the apomictic lines derived from them. Some of the apomicts were widely tested in comparison with the parents, both in the United States and in northern Europe.

The Fj hybrid 4273-8 was a weak, dwarf, semi-glaucus plant with short rhizomes and was approximately 70% apomictic. This individual was so weak that it was grown only at Stanford. Among the nonapomictic progeny from

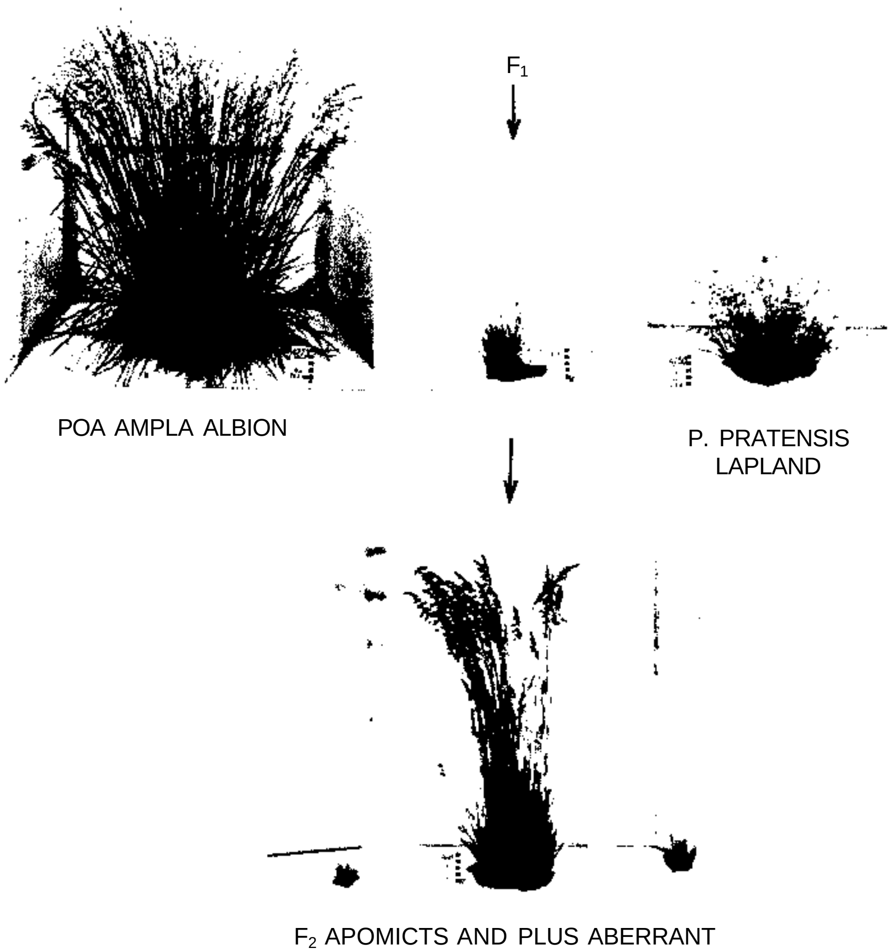


Figure 16. *Poa ampla* Albion (left), *P. pratensis* ssp. *alpigma* Lapland (right), and a partially apomictic F, hybrid (center). Below, a vigorous $F_2$ aberrant plant (center) between typical self-replicating Fj apomicts. All were grown in the Stanford garden. The black and white scale is 10 cm high. The aberrant, itself apomictic, gave rise to line 4683-1, which was widely field-tested. See figures 17 and 18, which show performances in contrasting climates.

this Fj hybrid in the $F_2$ generation, however, were several from sexual recombinations that were strikingly more vigorous than this F, parent. Among these were some which, on further progeny testing, proved to be strongly apomictic.

A spectacular example is illustrated in figure 16, which shows the original parents, the Fj hybrid 4273-8, and a sample of its apomictic progeny including the outstandingly vigorous $F_2$ plant 4683-1, all grown at Stanford. This *F*:

TABLE 12

APOMICTIC LINES FROM *Poa ampla* ALBION 4183-2 X P, *pratensis* SSP. *alpigena* LAPLAND 4250-1

| Line Number | Generation of Origin | Chromosome Number, *In* | Description | General Performance |
|---|---|---|---|---|
| 4273-8 | Direct Fj apomict | 73 | Weak, dwarf, short rhizomes | Poor in environments tested |
| 4683-1 | $F_2$ of line 4273-8 | 70 | Tall, vigorous form with rhizomes, 88-97% apomictic | Widely tolerant, mostly vigorous |
| 4683-2 | $F_2$ of line 4273-8 | 70 | Low, divaricate, some rhizomes, 90% apomictic | Weak |
| 4683-4 | $F_2$ of line 4273-8 | 63 | Male sterile | Vigorous |
| 4273-9 | Direct F, apomict | 63 | Semi-giaucus, short rhizomes | Moderately vigorous, widely tolerant |
| 46844 | $F_2$ of line 4273-9 | 85 ± 1 | 82% apomictic, culms 60-70 cm high, moderate rhizomes | Rather weak, but moderately tolerant |
| 4684-5 | $F_2$ of line 4273-9 | ... | 76% apomictic | Leafy, tolerant, vigorous |
| P43945-410 | $F_3$ of line 4273-9 | 66 | Highly rhizomatous, leafy, few culms | Moderately vigorous |
| P43545413 | F, of line 4273-9 | ... | 69% apomictic, stiff glaucus leaves, culms 60-70 cm high | Not vigorous, small range of tolerance |
| P4353641 | $F_2$ of 4273-13 | 66 | Intermediate | Good general performance |
| P43948-204 | $F_3$ of 427343 | -97 | Few rhizomes, numerous culms, leafy | Moderately tolerant and vigorous |

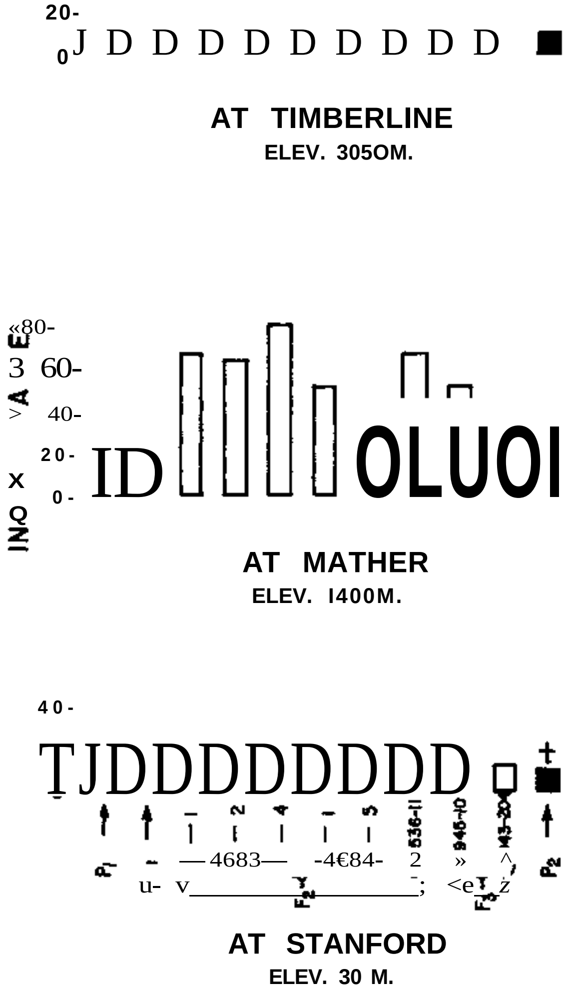


Figure 17. Histograms indicating relative growth performance of the parents, *Poa amph* Albion 4183-2 (P,) and P. *pratensis* ssp. *alpigma* Lapland 4250-1 ($P_2$), and an $F_s$ hybrid (4232-9), in comparison with apomictic hybrid derivatives when grown as vegetatively cloned transplants at the altitudinal stations at Stanford* Mather, and Timbedme. The solid black columns indicate the parents, the open columns the hybrid derivatives. Cross indicates nonsurvivor. The response index values (shown by the scale at the left) were computed from averaged values of six key characters, as explained in Chapter I. See tables 10 and 11 for origins and characteristics of hybrid derivatives (identifiable by the line numbers indicated, above, for the Stanford station).

plant proved to be approximately 90% apomictic and was widely field-tested in contrasting environments, where it made a creditable showing.

Table 12 lists the apomictic derivatives originating from the cross *Poa amph* Albion X P. *pratensis* ssp. *alpigena* Lapland, their lineages, chromosome num-

Figure 18. Histograms indicating relative growth performance of the parents, *Poa ampla* Albion 4183-2 (Pj) and *P. pratensis* ssp. *alpigena* Lapland 4250-2 ($P_2$), and apomictic hybrid derivatives when grown in randomized seeded test plots at various stations in the United States, as indicated. The solid black columns represent the parents, open columns apomictic hybrid lines. Crosses indicate nonsurvivors; stars, absence of data. The response index values (indicated by the scale at the left for Pullman) were computed as explained in Chapter I. The line numbers of the apomicts are indicated by the key for the Stanford station. See table 1 for details about the test stations, and tables 10 and 11 for origins and characteristics of the various lines.

bers, and some of their characteristics. As is evident from the table, the apomictic lines differed widely from each other and demonstrate the range of types that may be obtained from a single cross.

### *Responses of the apomicts in different environments in comparison with the parents*

The histograms in figure 17 show the relative growth performance of vegetatively cloned parents and their apomictic derivatives when grown at the altitudinal transplant stations at Stanford, Mather, and Timberline. As in the previous graphs, the heights of the histograms represent response index values computed from the means of six basic measurements of growth performance over three years, 1956-1958. The overall performance of both parents and the apomicts of this combination was markedly better at Mather than at either Stanford or Timberline, and also the relative differences in growth between the parents and the various apomictic lines were most clearly expressed at Mather. It is especially noteworthy that all the apomicts except the F, line 4273-9 outperformed both parents at this mid-altitude station.

At Stanford some of the apomictic lines, notably 4683-1, -4, 4684-5, and 13536-11, likewise performed better than the parents, although the F, line 4273-9 and the $F_3$ line 13943-204 lagged behind the most vigorous parent, *Poa ampla* Albion. In the subalpine climate at Timberline none of the apomicts grew better than the parents.

In the regional field tests (figure 18) the comparison between the apomictic derivatives and the parental lines is less complete, largely because the *Poa pratensis* ssp. *alpigena* parent was not included at many of the stations because it produced insufficient seed (cf. the histograms in figure 18). At Lexington, Kentucky, the apomictic line 13536-11 was conspicuously successful and greatly outperformed the *P. ampla* Albion parent there. A similar growth pattern was observed at Blacksburg, Virginia, and at Purdue, Indiana. One of the most striking growth differentials was observed at St. Paul, Minnesota, where the *Poa ampla* Albion parent failed to survive and *P. pratensis* ssp. *alpigena* achieved only limited growth in contrast with the apomictic lines 4683-1, 4684-5, and 13536-11, which were far more successful than either parent. Response patterns rather similar to those at St. Paul were also found at Moccasin and Pullman except that at the latter two stations the *Poa ampk* Albion parent was a vigorous survivor. At Corvallis, Oregon, and at Hall's Flat and Pleasanton in California, none of the apomictic lines tested equaled the performance of the *Poa ampk* parent; the *P. pratensis* ssp. *alpigena* line was a nonsurvivor at the two latter stations.

Figure 19 shows a space-planted block of the apomictic line BV48-2M at the Pullman,. Washington, nursery in 1953. The typical open inflorescences and numerous semi-erect culms of this derivative were also charactemtii' of

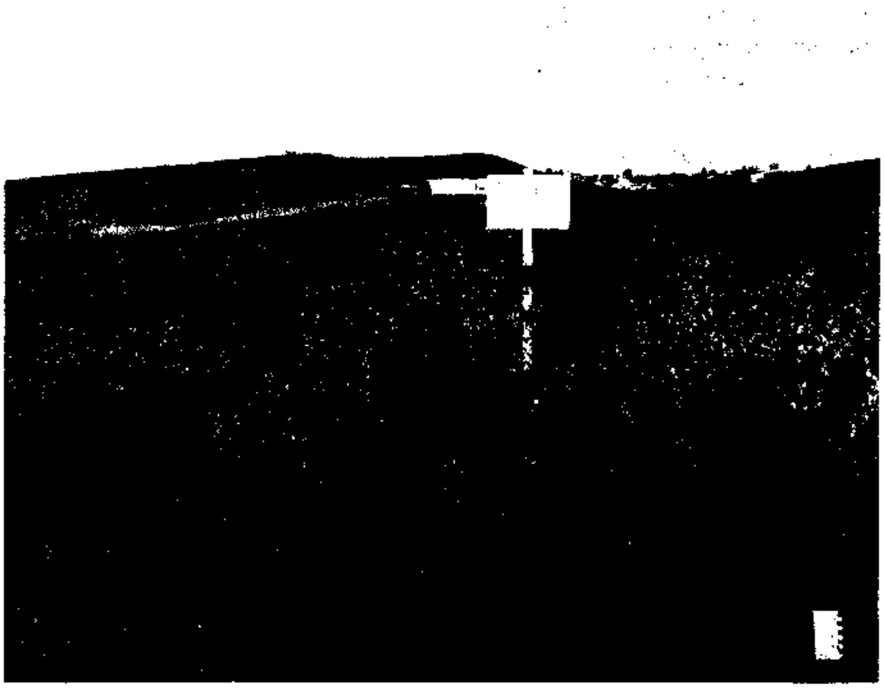


Figure 19. Space-planted test plot of the apomictic line 13948-204 derived from the cross *Poa ampla* Albion 4183-2 X P. *pratensis* ssp. *alpigena* Lapland 4250-1 at the U.S. Soil Conservation nursery at Pullman, Washington. The photograph was taken on June 14, 1952, a year after planting. The black and white scale in the foreground is 10 cm high. See table 11 and figures 17 and 18 for data on the origin and relative growth performance of this line in contrasting climates.

the other apomicts of this hybrid combination, including lines 4683-1 and 4273-9 at Pullman.

### *Responses of the parental and apomictic lines at northern European stations*

Although the data obtained from the northern European stations are extensive, they could not in all cases be obtained at stages in plant maturity comparable with those obtained in the United States. Therefore these data cannot be compared directly in graphic form. The studies made over a five-year period can, however, be briefly summarized.

At the cool-temperate maritime climate at Edinburgh (Penlandfield), Scotland (55°58'N), the parental *Poa pratensis* ssp. *alpigena* thrived considerably better than in the arid Mediterranean climate at Stanford, but was nevertheless outperformed by the more southern forms of *Poa pratensis* from Athabasca and Mather, and especially by the coastal form from Newport, Oregon (4466-

1). The *Poa ampla* Albion parent likewise thrived at Edinburgh, although the Kahlotus form of this species exceeded it in performance. The apomictic derivatives, lines 4683-1, 4273-9, and P-13536-10 all grew well, with characteristics intermediate to those of the parents, but none of them exceeded in growth both parental forms at Edinburgh.

At Volbu, Norway (61°08'N), the parental *Poa pratensis* ssp. *alpigena* attained its best growth at any of the field stations tested; there, space-planted apomictic progeny produced vigorous plants having culms 60-70 cm tall and many leaves from actively spreading rhizomes. The *Poa ampla* Albion parent grew moderately well, producing stems from 85 to 95 cm high and a fair number of leaves, but few tillers. The hybrid apomictic derivative line 4683-1 was remarkably successful at Volbu, being highly leafy with many rhizomes and numerous culms, and it was favored by Dr. Solberg as a promising forage grass. Line 4273-9 was likewise vigorous and leafy but rather stemmy, a characteristic doubtless inherited from *Poa ampla* Albion. Less productive on a dry-weight basis was P-13536-10, which had fewer and shorter leaves than the former two apomictic lines, yet performed reasonably well. It is of special interest that at Volbu the apomictic derivatives of the combination *Poa ampla* Albion X *P. pratensis* Mather were considerably less successful than the apomicts of the same interspecific combination using P. *pratensis* ssp. *alpigena* Lapland as the male parent.

In the more continental northern climate at Uppsala, Sweden (59°52'N), the same *Poa pratensis* ssp. *alpigena* line grew relatively poorly, producing mostly scattered culms 28-45 cm high with relatively few leaves. The apomictic hybrid line 4683-1 made a creditable showing in comparison with the parents, producing stems to 80 cm high with numerous leaves and active rhizomes. This line, however, was too stemmy to be considered a desirable forage type. Line 4273-9 was somewhat less productive but more leafy, while line 13536-10 tended to have many culms 60—65 cm high but few leaves. The apomict 4683-1 at Uppsala also tended to be stemmy, showing a strong influence from the *Poa ampla* Albion parent. Neither the parents nor their apomictic derivatives were competitive with the local forms of *Poa pratensis* grown for forage in the Uppsala area.

### *Summary of data from the cross Poa ampla Albion 4183-2* X P. *pratensis ssp. alpigena Lapland 4250-1*

The hybrid derivatives of this cross between these most contrasting forms of *Poa ampla* and P. *pratensis* differed from those of the two preceding crosses mostly in their differences in tolerance when grown in contrasting climates. In overall breeding characteristics, the data from the various crosses between *Poa ampla* and P. *pratensis* reveal rather parallel features. The results from crossing *Poa ampla* Albion X P. *pratensis* ssp. *alpigena* Lapland may be summarized as follows:

1. The seven Fj hybrids obtained differed individually from each other in well-marked characteristics and were mostly weaker than the parents when grown at Stanford.

2. An especially conspicuous plus variant in an $F_2$ population originating from one of the weak partially apomictic $F_{\{}$ hybrids proved to be itself apomictic, and it gave rise to a line widely tested in a number of environments.

3. Eleven apomictic hybrid lines were tested in different climates in comparison with the growth responses of their parents.

4. Several apomicts outperformed both parents in some but not all the environments tested.

5. The genetic influence of the male parent, *Poa pratensis* ssp. *alpigena* Lapland, was especially evident in the performance of the apomicts in cold-temperate northern Europe climates in comparison with apomicts from the two preceding *P. arnpla-pratensis* combinations.

## OTHER COMBINATIONS OF POA AMPLA X P. PRATENSIS

Among the hybridizations listed in table 4 are several of sufficient interest to be reviewed briefly.

PoA AMPLA HEISE HOT SPRINGS 4196-12 X P. PRATENSIS NEWPORT 4466-1. This combination was made in the hope that by combining a relatively high altitude form of *Poa ampla* from the interior northern Rocky Mountains with a vigorous maritime form of *P. pratensis* native to ocean-facing bluffs of the Pacific Coast, agronomically desirable apomictic derivatives might be obtained having a wide range of tolerance to different climates. The results were not as successful as had been hoped, but it is nevertheless of interest to review the data obtained for possible reference in future investigations.

### *The Poa arnpla parent*

A sister plant of the individual 4196-12 used in this cross grown at Stanford is illustrated in figure 3 (center plant of middle row). As can be seen in this figure, in comparison with the *P, ampla* Albion plant shown the ecotype represented by Heise Hot Springs has shorter and more slender culms, is narrower at the base, and has fewer, shorter leaves. Mr. Worley of the Soil Conservation Service collected the original native seed of this form during the summer of 1938 at elevation 1525 meters at Heise Hot Springs in E. Bonncville County, Idaho, in association with *Artemisia tridentata* and *Agropyron spicatum.* He considered this plant to be a form of *Poa nevadensis* Vasey ex Scribn. When grown at the Soil Conservation Service nursery at Pullman, Washington, it thrived and produced a uniform culture with stems up to 90 cm tall Seeds harvested from this Pullman planting were sown at Stanford in January 1944, as culture No. 4196. The 29 space-planted individuals grown there were uniformly true to type except for four aberrants. At Stanford the growth of this culture was reasonably vigorous but suffered from rust damage, although not as much as other forms of *Poa ampla* in this garden. The individual plant 4196-12 used in the crossing was typical of this form of *Poa ampla.*

*The Poa pratensis parent*

A transplant originally dug from a native population along an ocean-facing bluff at Newport, Lincoln County, Oregon, in June 1944 by the late Professor William L. Lawrence was vegetatively cloned at Stanford; it proved to be an especially vigorous form *ofPoa pratensis* and was ultimately used as a successful commercial turf grass, as described on page 5. This clone, 4466-1 (figure 3, center plant of bottom row), proved to be tolerant to a wide range of contrasting climates and was especially successful at Edinburgh, Scotland, where it was considered to be a desirable forage grass. It was likewise an outstanding performer at Volbu, Norway.

TABLE 13

DIFFERENCES BETWEEN PARENTAL LINES

| *Poa ampla* Hcisc Hot Springs 4196-12 | *Poa pratensis* Newport 4466-1 |
|---|---|
| Strict bunchgrass | Vigorously spreading rhizome grass |
| Herbage glaucus | Herbage dark green |
| Culms erect, slender, to 80 cm high | Culms divaricate, 50-60 cm high |
| *In* = 70 | *In* = 81 |
| Lemmas smooth | Lemmas with long, curly pubescence |
| Winter-active, summer-dormant at Stanford | Active both in winter and summer at Stanford |

Table 13 summarizes the principal differences between the parental individuals used in this cross, as expressed when both were grown at Stanford.

*Results from crossing*

After mass cross-pollination in pollen-tight cages at Stanford in 1944, a total of 190 inflorescences of the *Poa ampla* parent yielded approximately 5000 apparently viable seeds. From these, 3132 seedlings were grown, 55 of which proved $F_{\{}$ hybrids (ca. 1.8%). The hybrids were distinguished without difficulty in early seedling stages from the maternal-like *ampla* individuals, mainly because of the relatively wider, darker green leaves of the hybrids and their more divaricate habit. The variability among the F| hybrids was, nevertheless, in marked contrast with the uniform maternal-type apomicts.

Among the hybrids, 16 were especially vigorous and surpassed the maternal P. *ampk* parent in growth at Stanford, 29 were of intermediate vigor, and 10

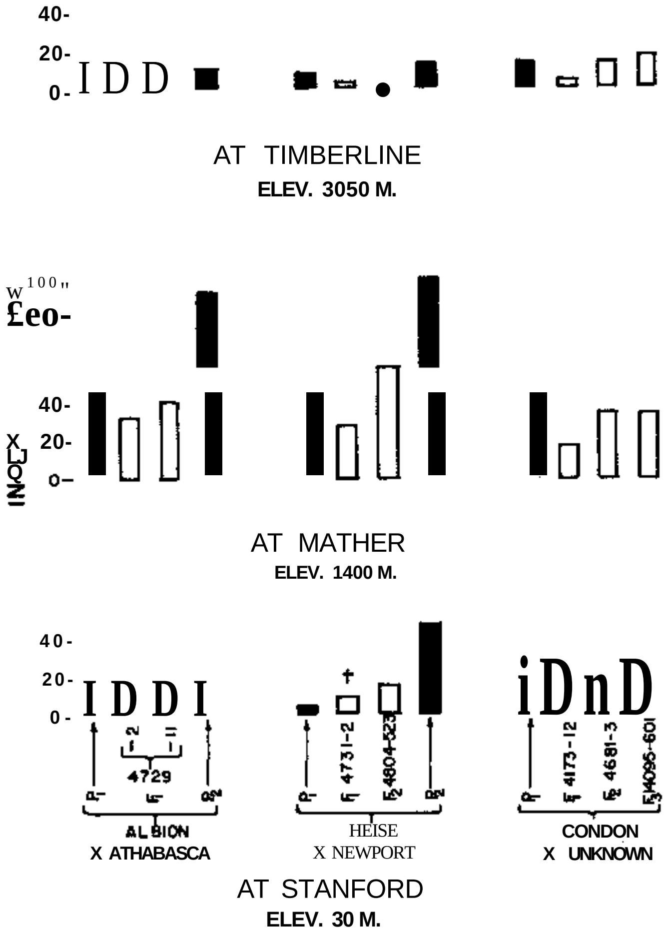


Figure 20. Histograms of response index values indicating relative growth performance of parents and apomicts of crosses between *Poa ampla* and *P. pratensis* when grown as vegetatively propagated transplants at the altitudinal stations at Stanford, Mather, and Timberline. Parents ($P_1$, $P_2$) are indicated by black columns; hybrids, by open columns. Response index values were computed as described in Chapter I. See text and tables 12 and 13 for details on the origin and characteristics of the parental and hybrid lines.

were weak. Chromosome counts made on three of the more vigorous $F_1$ hybrids ranged in $2n$ = 75-79. The hybrids as a whole were disappointing because of their sterility. For example, a vigorous plant, 4131-2, having $2n$ = 75 chromosomes, proved to be only 3.5% fertile, and there was extreme variability in an $F_2$ population of 195 individuals grown at Stanford from this plant, indicating sexual segregation. Among this $F_2$ population was plant 4804-

523, which on progeny testing proved to be approximately 90% apomictic in the $F_3$ generation. This apomictic line was the only one of this hybrid combination included in the widespread field tests in the United States and Europe. The line 4804-523 was considerably inferior in growth performance in all these tests to the *Poa pratensis* Newport parent, which proved to be an unusually tolerant and vigorous form, often equalling and sometimes exceeding the Athabasca and Mather strains used in the previous crossing combinations. The histograms in the center of figure 20 indicate the growth responses of the parents, the $F_1$ hybrid 4731-2, and the $F_2$ apomict 4804-523, when growing as cloned transplants at Stanford, Mather, and Timberline.

The high hopes that originally prompted this crossing combination were not realized primarily because of the low fertility of the $F_1$ hybrids that were produced. The fact that at least one reasonably successful apomict was obtained suggests the possibility that another effort using somewhat different strains of the parental ecotypes might yield more promising hybrid apomicts.

## POA AMPLA ALBION 4183-1 X P. PRATENSIS ATHABASCA 4249-1.

### *The parents*

The *Poa ampla* Albion parent in this combination was a clone of the same individual used in the previous cross, *Poa ampla* Albion X P. *pratensis* Mather. The *P. pratensis* Athabasca parent was a clone of the same plant used in the cross *Poa ampla* Kahlotus X *P. pratensis* Athabasca. The contrasting characters between these parents can be visualized by referring to the preceding pages describing these combinations.

### *Results from crossing*

The parental lines were cross-pollinated in the usual manner in pollen-tight cages at Stanford in 1944. Among 508 seedlings grown at Stanford from the maternal parent, *Poa ampla* Albion, seven individuals proved to be $F_1$ hybrids with *P. pratensis* Athabasca. Two of these, plants 4729-2 and -11, proved to be partially apomictic, with chromosome numbers of $2n = \sim 103$ and $\sim 75$, respectively. Other $F_1$ hybrids that were progeny-tested proved to be sexual.

The apomictic line 4729-2 was approximately 51% apomictic, with seed fertility of approximately 45%. This line was not widely tested, since its growth performance at the altitudinal transplant stations, as shown by the histograms of response indexes at the left of figure 20, did not surpass those of either parent. The other apomict, line 4729-11, was more highly fertile and approximately 87% apomictic; it performed somewhat better at the altitudinal transplant stations, as also shown by the histograms at the left of figure 19. This line made its best showing at Pullman, Washington, Moccasin, Montana, Pleasanton, California, and Blacksburg, Virginia, but at none of these places did it exceed both parents in performance. This line was not grown at the European test stations.

POA AMPLA CONDON X UNKNOWN P. PRATENSIS. A strain of *Poa ampla* from near Condon, Gillian County, Oregon, at elevation 760 meters, collected by the U.S. Soil Conservation Service, was grown at their Pullman, Washington, nursery. There it grew as an impressively vigorous bunchgrass with slender, open culms from 80 to 195 cm high, and uniform in habit, color of herbage, and time of flowering. One individual from this Pullman planting was shipped in 1943 to Stanford, where it was assigned the Carnegie accession number 4173-1. Open-pollinated seeds from this strain collected at Pullman were also grown at Stanford.

TABLE 14

DIFFERENCES BETWEEN *Poa ampla* CONDON AND A SPONTANEOUS F, HYBRID WITH *Poa pratensis* AS SEEN AT STANFORD

| *Poa ampla* Condon 4173-1 | Hybrid with Unknown *P. pratensis,* 4173-12 |
|---|---|
| Strict bunchgrass | Bunchgrass type with short rhizomes |
| Herbage glaucus | Herbage dark green |
| Leaves to 45 cm long, 4 mm wide | Leaves to 26 cm long, 4 mm wide |
| Culms slender, open inflorescences | Culms heavier with more compact inflorescences |
| Lemmas smooth | Lemmas curly-pubescent |
| Late flowering, May 16-30 | Earlier flowering, April 18-30 |
| Rust-susceptible at Stanford | Semi-rust-resistant at Stanford |
| *In* = --63 chromosomes | *In* = ~98 chromosomes |

Both the cloned transplant and the seedlings made an impressive showing at Stanford, although after the second year this strain, like other forms of Poa *ampla,* suffered from rust damage on stems and leaves. Among a population of 30 otherwise uniform space-planted seedlings grown at Stanford was an outstanding variant that was recognized as a hybrid with some form of *Poa pratensis.* Since this individual, 4173-12, arose from seed harvested at Pullman, it was assumed to be a spontaneous Fj hybrid arising from open-field pollination at the Pullman nursery. Table 14 lists the principal differences between the Condon strain and its assumed F} hybrid with *Poa pratensis.*

The *Poa ampla* Condon plant 4173-1 proved to be approximately *73%* apomictic and had a fertility of approximately 50%, which was sufficient to produce an abundance of viable seed on its numerous slender culms. It was tested extensively at the various field stations in the United States and Europe.

The assumed spontaneous Fj hybrid with *P. pratensis,* 4173-12, proved to be sexual and only about 5.5% fertile. The variation among its $F_2$ progeny covered a wide range in such characters as degree of rhizome development, color of herbage (glaucus to green), height and number of culms per plant, and detailed inflorescence characters. Among a population of 240 $F_2$ individuals grown at Stanford were a number of promising individuals that were progeny-tested in the $F_3$ and $F_4$ generations in search of apomictic derivatives. Among 15 individuals tested, only one, 4681-3 with $2n = {\sim}78$ chromosomes, was found to be apomictic, with a fertility of approximately 81%, giving rise to line 4681-3. This apomict was widely compared in field tests with *Poa ampla* Condon, and it proved to be a moderately successful performer. The histograms in figure 20 (right) indicate the relative growth performance of this apomict and the parental Condon line, together with the spontaneous Fj hybrid 4173-12 grown as cloned transplants at the altitudinal stations at Stanford, Mather, and Timberline. Also shown are the responses of the $F_3$ plant 14095-601, a vigorous individual selected at Pullman that proved to be sexual.

In the randomized seeded test plots of the cooperating stations of the U.S. Agricultural Research Service, the performance both of the *Poa ampla* Condon line and the $F_2$ hybrid apomict 4683-1 varied markedly between the test stations. At Pullman, Washington, both the parent and the apomict achieved excellent growth, but the apomict outperformed the parental strain in response index by a factor of three. At St. Paul, where *ampla* Condon failed to survive the winters, the apomict made excellent growth, as it did also at Blacksburg, Virginia, and Purdue, Indiana, where *ampla* Condon did poorly. At Lexington, Kentucky, the apomict far surpassed the Condon strain, a response consistent with other *ampla-pratensis* combinations at this station. As might be anticipated, both failed at Franklinton, Louisiana.

At Edinburgh, Scotland, both *Poa ampla* Condon and the apomict 4681-3 attained consistently good growth, but their performance was not competitive with local grass strains. At Uppsala, Sweden, *ampla* Condon, like the Albion strains, grew with considerable vigor, but the apomict was a disappointment.

## CONCLUSIONS FROM THE RESULTS OF CROSSING VARIOUS FORMS OF POA AMPLA AND POA PRATENSIS

Taken together, the results from crossing the various forms of *Poa ampla* and *P. pratensis* demonstrate that it is feasible to synthesize an almost unlimited number of self-perpetuating new hybrid derivatives having characteristics recombining the characters of the parental forms used. Moreover, it is possible to secure such apomictic forms within a relatively few generations. The selection of the parental forms to be crossed is highly important and should be kept in mind in synthesizing lines for particular agronomic uses in given climates. With the extremely wide possibilities for selection among Fj, $F_2$, $F_3$, and later-generation derivatives exhibiting facultative apomixis combined with sexual recombination, a single cross may be used to derive a large number of new lines for selection by the plant breeder.

# III

# INTERSPECIFIC CROSSINGS INVOLVING POA SCABRELLA

# Ill

# INTERSPECIFIC CROSSINGS INVOLVING POA SCABRELLA

We attempted to cross various forms of *Poa scabrella* with other species of *Poa*, especially *Poa pratensis* (cf. figure 21), in the hope of obtaining apomictic hybrid derivatives capable of outperforming the generally drought tolerant races of the *scabrella* complex, which constitute an important component of native forage grasses prevalent in the semi-arid foothill regions of California. Combinations with *Poa pratensis* were emphasized, with the thought that this rhizome-producing species combined with the bunchgrass habit characteristic of the various forms of *scabrella* might result in hybrid derivatives with enhanced productivity and a capacity to succeed in Mediterranean-type climates. Crosses between *Poa scabrella* and other species of *Poa* were also made, not only to explore the agronomic possibilities of various combinations but also to throw light on the biosystematic relationships between different species of *Poa*.

## POA SCABRELLA-PRATENSIS COMBINATIONS

Table 15 lists the crossings attempted between *Poa scabrella* and *P. pratensis*. The most prominent feature shown is, perhaps, the failure in most of the attempts to obtain even F, hybrids. In only several combinations were self-perpetuating apomictic hybrid derivatives realized, but the characteristics and growth performance of these apomicts in contrasting climates is of interest in comparison with those from the *arnpla-pratensis* combinations described in Chapter II.

As in the *arnpla-pmtensis* crosses, $F_\}$ hybrids were obtained only when *Poa pratensis* served as the male parent, *P. scabrella* the female. Faïlure to obtain hybrids in the reciprocal direction was probably because of the higher degree of apomixis in the forms of P. *pratensis* than in the *P. scabrella* parents.

The forms *ofPoa scabrella* used were native to the California foothill regions and were typically winter-active and summer-dormant in response to the normal cycle of precipitation in these areas. Like *Poa amph*$_f$ these forms of *P. scabrella* are bunchgrasses, but they differ in having less bulk in growth and generally fewer culms and leaves per plant. Also, forms of *Poa ampla* native to the Pacific Northwest are normally winter-dormant and summer-active in their native habitats, but when transplanted to the milder Mediterranean-type climate at Stanford they often become winter-active and at least partially summer-dormant. The review of the more successful *scabrella-pra-*

TABLE 15

HYBRID *Poa* COMBINATIONS ATTEMPTED, *Poa scabrella* X *P. pmtensis*

| Parental Strains | CIW Culture No. | No. Plants Grown | No. of Maternals | No. of Aberrants | No. of F, Hybrids | No. of Apomictic Lines | |
|---|---|---|---|---|---|---|---|
| Las Posas 4212-7, *In* * 84 X | Athabasca 4249-1, *In* = 70 | 4553 | 2940 | 2735 | 195 | 10 | 3 |
| Reciprocal | | 4554 | 75 | 70 | 5 | 0 | 0 |
| Las Posas 42124,*2n* = -84 X | ssp. *alpigena* Lapland 4250-1, | 4555 | 860 | 778 | 80 | 2 | 1 |
| Reciprocal | *In* = 74 | 4556 | 210 | 147 | 63 | 0 | 0 |
| Las Posas 4212-3, *In* = **84 X** | | 4557 | 1380 | 1166 | 194 | 20 | 7 |
| Reciprocal | Mather 4253-4, *In* = 63 | 4558 | 180 | 163 | 17 | 0 | 0 |
| Las Posas 4212-4, 2» = **82 X** | | 4559 | 1307 | 1090 | 210 | 7 | 3 |
| Reciprocal | Leevining 4259-3, *In* = 68 | 4560 | 210 | 194 | 16 | 0 | 0 |
| Las Posas 4553 X | | 4747 | 384 | 362 | 22 | 0 | 0 |
| Reciprocal | Timberline 4445-6, *In* = 73 | 4748 | 60 | 57 | 3 | 0 | 0 |
| Lucerne 421746, *In* = 64 X | Athabasca 4249-1, *In* = 70 | 4751 | 57 | 45 | 12 | 0 | 0 |
| Lucerne 4217-18, 2« = 63 X | ssp. *alpigena* Lapland, 4251-12 | 4753 | 306 | 276 | 30 | 0 | 0 |
| Reciprocal | | 4754 | 60 | 59 | 1 | 0 | 0 |
| Lucerne 4217-12, 2» = 63 X | The Pines 4252-14, *In* = 56 | 4755 | 1085 | 959 | 126 | 0 | 0 |
| Reciprocal | | 4756 | 60 | 52 | 8 | 0 | 0 |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| Lucerne 4217-19, *In* = 63 | X | Mather 4253-4, *In* = 68 | 4757 | 400 | 352 | 48 | 0 | 0 |
| Reciprocal |  |  | 4758 | 60 | 60 | 0 | 0 | 0 |
| Lucerne 4217-12, *In* = 63 | X | Boiler Bay 4467-2, *In* = 84 | 4759 | 144 | 110 | 134 | 0 | 0 |
| Mather 4222-1 | x | ssp. *alpigena* Lapland 4250-1, *In* = 74 | 4567 | 444 | 380 | 64 | 1 | 0 |
| Reciprocal |  |  | 4568 | 210 | 177 | 33 | 0 | 0 |
| Paso Robies 5847410 | X | The Pines 4252-12 | 6280 | 1050 | 1045 | 0 | 5 | 0 |
| Paso Robies 5847-105 | X | Mono Lake 4453-11 | 6282 | 810 | ... | ... | 52 | 0 |
| Paso Robies 5847-109 | X | Las Vegas 4883-105 | 6284 | 630 | ... | ... | 30 | 0 |
| Reciprocal |  |  | 6285 | 90 | 87 | 3 | 0 | 0 |
| Watsonviile 4214-1 | x | Athabasca 4249-1 | 4561 | 7028 | 6948 | 65 | 15 | 2 |
| Reciprocal |  |  | 4562 | 240 | 231 | 9 | 0 | 0 |
| Watsonviile 4214-2, *In* = 82 | X | Leevining 4258-3, *In* = 68 | 4563 | 2092 | 2057 | 34 | 1 | 0 |
| Reciprocal |  |  | 4564 | 210 | 197 | 13 | 0 | 0 |
| Watsonville 4214-5 | X | Leevining 4258-2, *In* = 68 - / | 4565 | 1245 | 1178 | 67 | 0 | 0 |
| Reciprocal |  |  | 4566 | ... | 210 | 202 | 8 | 0 |
| Watsonviile 4570 | X | Athabasca 4249-1, *In* = 70 | 4745 | 334 | 301 | 33 | 0 | 0 |
| Reciprocal |  |  | 4746 | 60 | 60 | 0 | 0 | 0 |
| Watsonviile 4214-1 | X | Timberline 4445-8, *In* = 74-77 | 4749 | 1910 | 1797 | 131 | 0 | 0 |
| Reciprocal |  |  | 4750 | 60 | 58 | 2 | 0 | 0 |

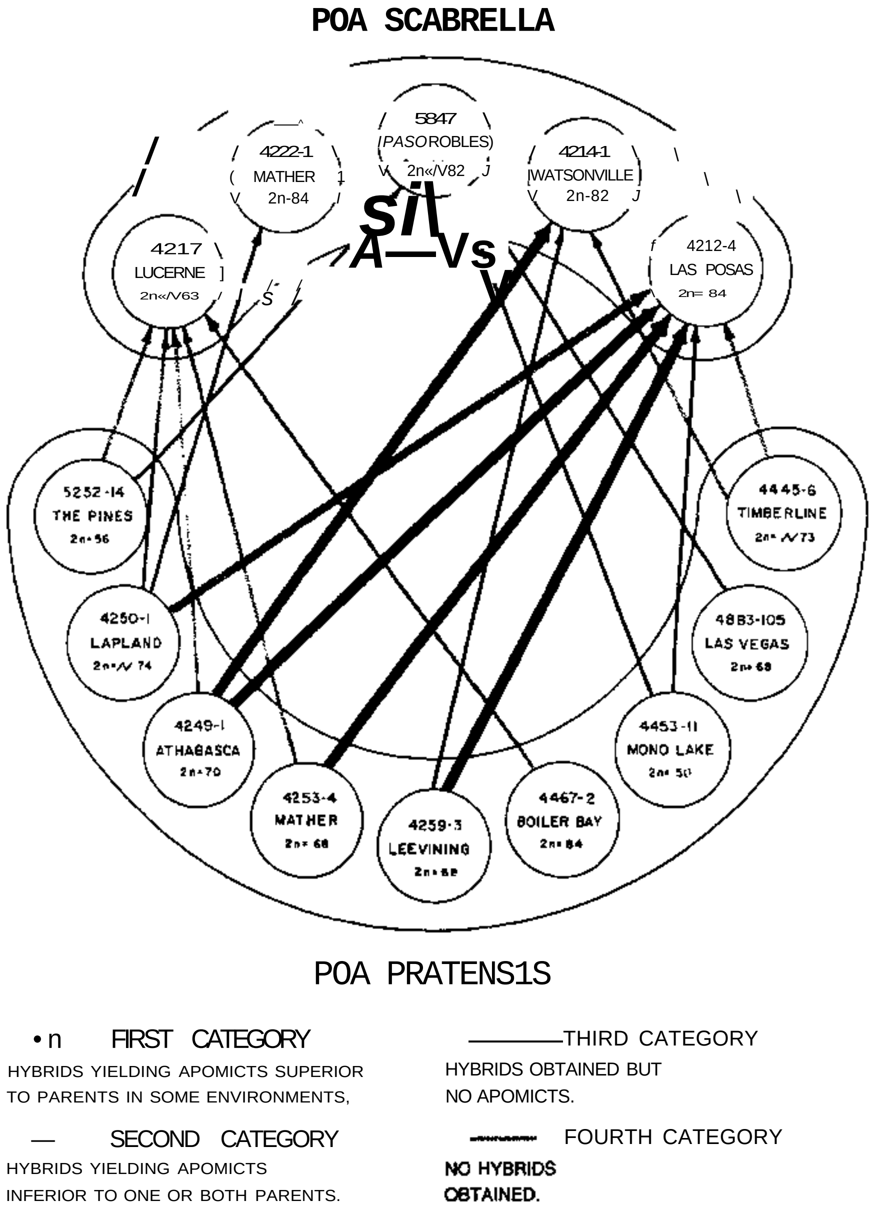


Figure 21. Summary of crosses between different forms of *Poa scabrella* (Thurb.) Benth ex Vasey (upper) and *P. pratensis* L. (lower). Arrows point to the female parent. The numbers inside the circles representing parents refer to Carnegie culture numbers (tables 2 and 15); somatic (2n) chromosome numbers of parents are also shown. Further details are given in text.

*tensis* combinations in the following pages illustrates the principal results from these studies.

POA SCABRELLA LAS POSAS 4212-7 X P. PRATENSIS ATHABASCA 4249-1. The *Poa scabrella* parent used in this cross stemmed from an original collection made by the U.S. Soil Conservation Service in the Las Posas area of Ventura County, California, one mile west and 2.5 miles north of Somis at an elevation of 190 meters. Workers of the Service maintained the collection at their nursery at Pleasanton, California. We brought to Stanford ten individuals from the collection, including plant 4212-7 used in this cross. This winter-active form flowers normally during March and April at Stanford and reaches full maturity by June, after which it passes into summer dormancy. Studies under controlled conditions by Laude (1953) and Hiesey (1953) indicate that summer dormancy in this species is triggered by high temperature, a drought-escaping mechanism enabling this species to survive in Mediterranean-type climates with warm, dry summers. Starting with the winter rains in November new rosette leaves develop, followed by the formation of culms during the moist winter and early spring periods. Figure 3 (upper left) shows a plant of *Poa scabrella* Las Posas like the individual used in this cross.

The *Poa pratensis* Athabasca parent is the same individual used as the male parent in the combination *Poa ampla* Kahlotus X *P. pratensis* Athabasca described in Chapter II, and is illustrated in figure 7. Table 16 lists the principal character differences between the two parents, as expressed at Stanford.

TABLE 16

CHARACTERISTICS DISTINGUISHING *Poa scabrella* LAS POSAS (4212-7) AND *Poa pratensis* ATHABASCA (4249-1) AS SEEN AT STANFORD

| *Poa scabrella* 4212-7 | *Poa pratensis* 4249-1 |
|---|---|
| Strict, tufted bunchgrass | Spreading rhizome grass |
| Herbage light green | Herbage dark green |
| Culms to 90 cm tall | Culms to 60 cm tall |
| Lemmas curly, pubescent | Lemmas floccose |
| Ligules long, acute | Ligules short, band-shaped |
| Flowering in mid-March | Flowering in April |
| Winter-active, summer-dormant | Winter-dormant, summer-active |
| *2n* = -84 + / | *In* = 70 |
| Rust-susceptible | Rust-resistant |

*Results from crossing*

After mutual pollination of the parents in the pollen-tight cage at Stanford during April 1944 when both were in active flower, the resulting seeds from both parents were harvested when mature.

## TABLE 17

CHARACTERISTICS OF F, HYBRIDS BETWEEN *Poa scabiella* LAS POSAS 4212-7 AND P. *pratensis* ATHABASCA 4249-1

| Plant Number | Chromosome Number, 2« | % Seed Fertility | Vigor at Stanford | Sexual or Apomictic | No. of Apomictic Derivatives | Comments |
|---|---|---|---|---|---|---|
| 45534 | 74 | 10 | Vigorous | Sexual | 0 | Variable $F_2$ |
| 4553-2 | 70 | 25 | Strong | Sexual | 2 | $F_3$ apomicts |
| 4553=3 | -69 | 6 | Weak | Apomictic | 1 | *scabrella-like* |
| 4553-4 | 69 | 4 | Strong | Apomictic | 1 | *sea brella-like* |
| 4553-5 | 71 | 55 | Strong | Sexual | 0 | Weak $F_2$'s |
| 4553-6 | ... | ... | Weak | Sexual | 0 | Non-survivor |
| 4553-7 | 82 | 5 | Strong | Sexual | 0 | Variable $F_2$'s |
| 4553-8* | -73 | 19 | Vigorous | Sexual | 0 | Variable $F_2$'s |
| 4553-9 | 72 | Sterile | Strong | ... | 0 | ... |
| 455340 | 126 | 19 | Vigorous | Sexual | 0 | Variable $F_2$'s |

•Outcrossed with *Poa ampla* Albion forming triple hybrids, which were all sexual.

From the seeds harvested on *Poa scabrella,* 2940 seedlings were grown the following year at the Stanford nursery. Of these, 2735 plants were readily recognized as being maternal-type individuals, having light-green, tufted leaves and erect, early-developing culms with long and tapering ligules. Also present were 195 weak or dwarf plants that were considered to be aberrants of the maternal parent, in contrast with 10 individuals recognized as Fj hybrids. The hybrids, although variable among themselves, were strong-to-vigorous plants and in seedling stages were identified through their divaricate leaves and culms, dark green herbage, and short, blunt ligules. (See figure 25 for drawings illustrating details of spikelets, ligules, and lemmas in *Poa scabrella* and P. *pratensis,* and the $F_2$ derivative, 4711-3.)

None of the 210 seedlings grown at Stanford that were harvested on the *Poa pratensis* Athabasca parent proved to be Fj hybrids; all but five were of the Athabasca biotype. The five exceptions were weak aberrant forms *of Poa pratensis.* When grown to maturity at Stanford, the apomictic paternal-type plants were uniform and true to the readily recognizable Athabasca strain.

Table 17 lists the ten Fj hybrids harvested on the *Poa scabrella* parent and describes some characteristics of each. All of the F/s had characters intermediate to those of the parents. Some, including plants 4553-4, -5, -8, developed short rhizomes, while the others were strict bunchgrasses. The hybrids varied among themselves from summer-dormant to summer-active and differed in degree of pubescence on lemmas, in shape of ligules, and in size, color and growth habit of leaves. Moreover, as indicated in table 17, most of these F,*s were sexual.

Many progeny tests were made on selected $F_2$ segregants of the various F, hybrids at Stanford and Pullman. These plants, for the most part, proved to be sexual and segregating in the $F_2$ and later generations, although several were found to be weakly apomictic. This extensive screening effort yielded only one apomictic derivative that appeared to have agronomic potential, line 4694-8—an $F_3$ segregant from the F, hybrid 4553-2 that was widely field-tested. Figure 22 shows space-planted individuals of this line growing at Stanford and at Pullman. This apomict was 90% fertile and summer-active like the P. *pratensis* parent; it had short rhizomes that were freely tillering, and it produced many tall, erect culms resembling those of the P. *scabrella* parent. Another $F_3$ apomictic derivative of the same lineage, line 4694-4, proved only moderately promising and was not included in the widespread field tests. The two direct F! apomictic lines from the F, hybrids 4553-3 and -4 listed in table 17 were relatively weak forms having mostly characteristics *of Poa scabrella.*

The relative growth performance of vegetatively cloned transplants of the parental plants and their $F_3$ apomictic derivative, line 4694-8, at the altitudinal transplant stations is indicated by the histograms shown at the left of figure 23. From these, it is evident that this apomict inherited the wide tolerance of the *Poa pratensis* Athabasca parent even though the P. *scabrella* parent failed to survive at Mather and Timberline*

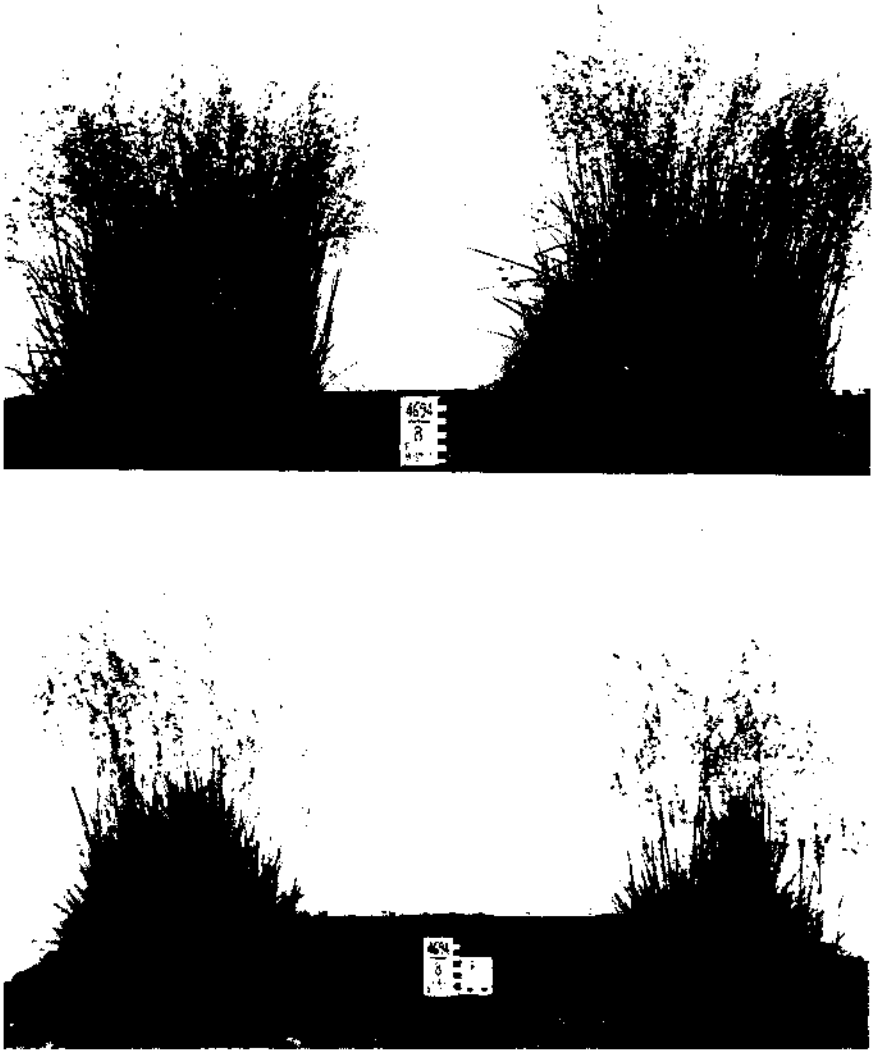


Figure 22. The apomictic line 4694-8, which originated as an $F_3$ segregant from the cross *Poa scabrelh.* Las Posas 4212-7 X *P. pratensis* Athabasca 4249-1, grown in spaced plantings at Pullman (above) and at Stanford (below). The photographs were taken on June 17, 1951, at Stanford, and on July 9, 1951, at Pullman. The black and white scale is 10 cm high. See table 17 for the origin and history of this line and figures 23 and 24 for its relative growth performance in different environments.

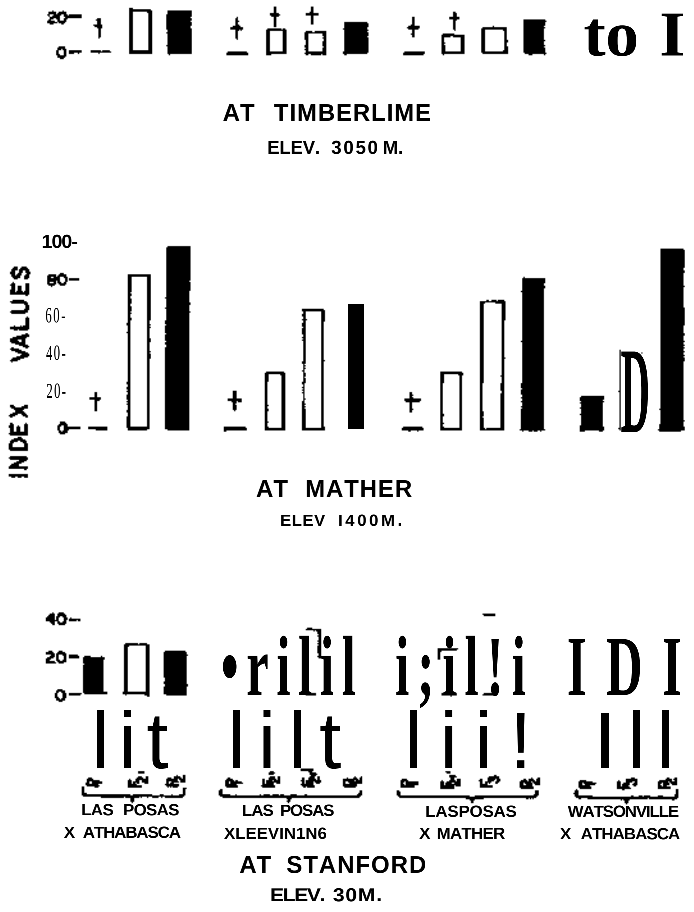


Figure 23. Histograms of response index values, indicating relative growth performance of parents (solid black columns) and hybrid derivatives (open columns) of four combinations between *Poa scabrella* and P. *pratensis* when grown as vegetatively propagated transplants at the altitudinal stations at Stanford, Mather, and Timberline. The crosses indicate nonsurvivors. See Chapter I for method of computing index values.

In the widespread field tests, this derivative likewise demonstrated its wide tolerance in climates as diverse as that of Blacksburg, Virginia; Columbia, Missouri; Purdue, Indiana; and Moccasin, Montana, as shown by the histograms in figure 24. At these stations, the P. *scabrella* parent either failed to survive or grew only poorly. At some locations, such as at Columbia and Moccasin, the apomict even surpassed the widely tolerant *P. pratensis* Athabasca parent in overall growth. In northern Europe, this same derivative thrived with outstanding vigor at Penlandfield, Scotland, but failed to survive at Volbu, Norway, and grew only weakly at Uppsala, Sweden.

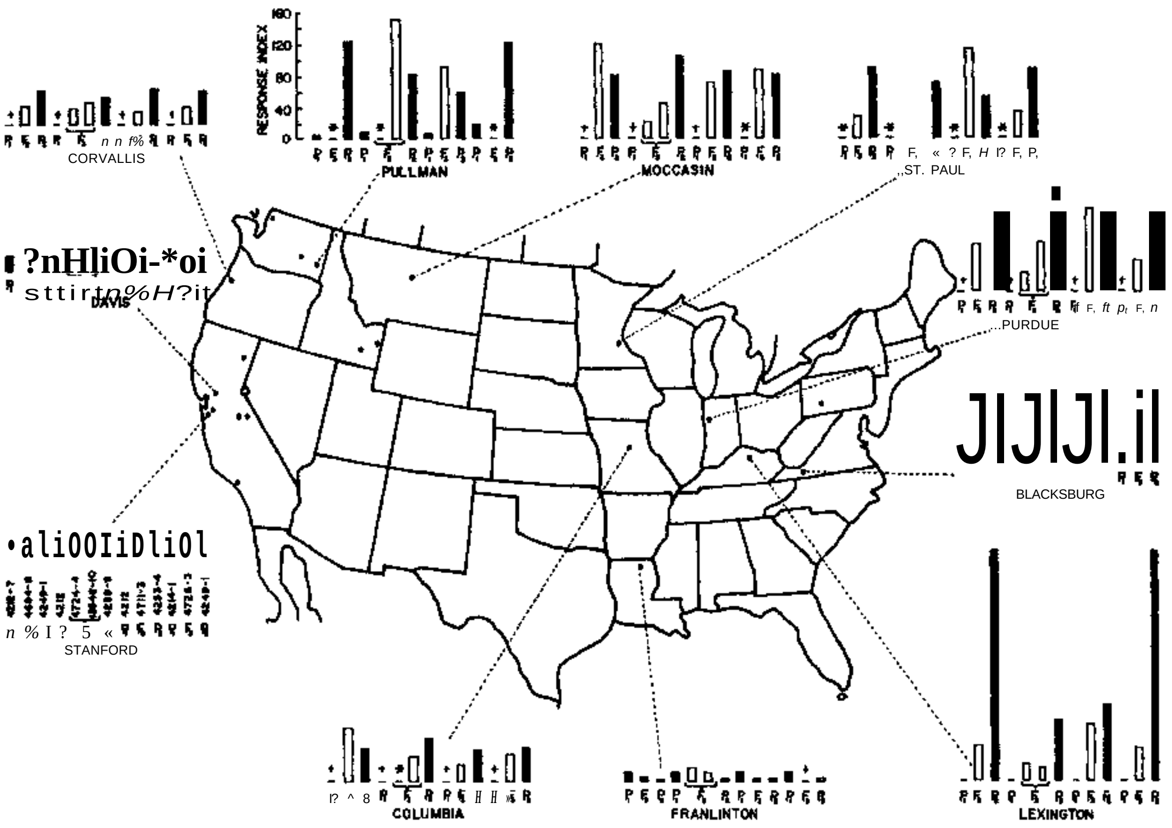


Figure 24. Histograms of response index values, indicating relative growth performance of parental and hybrid derivatives in crosses between *Poa scabrclk* and P. *pratensis* when grown in randomized seeded test plots at various stations in the United States, as indicated. Solid black columns (P,, $P_2$) represent parental lines; open columns, apomicdc hybrid derivatives. The scale of response index values, computed as explained in Chapter I, is at the left of data from Pullman. Line numbers are shown under the histogram columns for Stanford. Crosses represent nonsurvivors; stars, absence of data.

POASCABRELLA LAS POSAS 4212-4 X P. PRATENSIS LEEVINING 4259-3. This combination between a sister plant of *P. scabrella* used in the preceding cross and another form of *Poa pratensis* originally dug as a transplant in 1943 along Leevining Creek, Mono County, California, at an elevation of 2040 meters, is parallel to the cross described above. The Leevining form of *Poa pratensis* differed from the Athabasca form in having longer stems and leaves when grown in most environments, but was similar in having a wide tolerance to contrasting climates. A listing of the principal character differences distinguishing the parents would be almost identical to those shown in table 16 for the combination *P. scabrella* Las Posas 4212-7 X *P. pratensis* Athabasca 4249-1, except that *P. pratensis* Leevining had divaricate, rather than erect, stems and the chromosome number $2n = 67'$, instead of 70.

*Results from crossing*

Following mutual pollination in a pollen-tight cage at Stanford in April 1944, seeds from both parents were harvested at maturity. Among 1307 seedlings grown from the *Poa scabrella* parent, 8 proved to be Fj hybrids with *P. pratensis,* 1097 were maternal-like apomicts, and 202 were weak aberrants of maternal-type plants. The hybrids varied among themselves, but on the whole were more vigorous than the maternal-type offspring and were readily distinguishable from them in seedling stages. Most of the hybrids were more summer-active than the *P. scabrella* parent, and several were somewhat rhizomatous, characters inherited from *P. pratensis.* One of the weaker F/s failed to survive at Stanford.

Table 18 lists the hybrids individually and indicates those giving rise to apomictic lines. As shown in this table, the F, plants 4555-1 and -2 were both directly apomictic. The fertility of the line derived from the former was, however, less than 2%; moreover, the line was a relatively weak form having *scabrella*-like characteristics. Although the line derived from the F, plant 4559-2 was more fertile and more vigorous, it was not considered sufficiently promising for agronomic potential.

The sexual F} hybrids yielded widely segregating offspring in the $F_2$ generation, ranging from weak to vigorous recombinations of the parental types. Many progeny tests were made at Stanford and Pullman of the most promising $F_2$ segregants, but most proved to be sexual. Three $F_3$ derivatives, however, proved to be apomictic, two of which stemmed from the Fj plant 4559-3 (lines 13548-6 and 13548-10 selected at Pullman) and one from the F, plant 4559-7 (line 4724-4 selected at Stanford). The line 13548-6 was only weakly apomictic and proved to be disappointing in field tests, but lines 13548-10 and 4724-4 performed better.

In figure 23 the histograms (left of center) indicate the relative growth performance of cloned transplants of the parental lines and their apomictic derivatives, lines 4724-4 and 13548-10, at the altitudinal transplant stations.

TABLE 18

F, HYBRIDS BETWEEN *Poa scabrella* LAS POSAS 4214-4 X *P. pratensis* LEEVINING 4259-3

| Plant Number | Chromosome Number, *2n* | %> Seed Fertility | Vigor at Stanford | Sexual or Apomictic | No. of Apomictic Derivatives | Comments |
|---|---|---|---|---|---|---|
| 45594 | ***71*** | <2 | Fairly strong | Apomictic | 1 | Nearly sterile apomict |
| 4559-2 | -79 | 20 | Fairly vigorous | Apomictic | 1 | *scabrcHa-Wks.* |
| 4559-3 | ~80 | 90 | Vigorous | Sexual | 2 | $F_3$ apomicts |
| 4559-4 | 79 | 20 | Weak | Sexual | 0 | Weak, variable $F_2$ |
| 4559-5 | 96 | 24 | Strong | Sexual | 0 | Variable $F_2$ |
| 4559-6 | 76 | ... | Vigorous | Non-flowering | 0 | ... |
| 4559-7 | 75 | 22 | Vigorous | Sexual | 1 | $F_3$ apomict |
| 4559-8 | **~68** | <1 | Vigorous | Sexual | 0 | Nearly sterile |

The parental P. *scabrella* Las Posas line survived only at Stanford, whereas the P. *pratensis* Leevining parent grew at all three altitudes. The apomictic line 13548-10 almost equalled the performance of the *P. pratensis* parent at all three altitudes. The other apomict, 4724-4, was able to make a considerably better showing at Mather and Timberline than the *P. scabrella* parent, but fell short of the growth of *P. pratensis* Leevining at all three stations.

The apomictic lines 4724-4 and 13548-10 were also included in the widespread field tests in the United States, and their performance relative to the parental lines is indicated by the histograms shown in figure 24. A feature of interest is that the growth of both of these apomicts was slightly better than that of either parent at the southernmost station at Franklinton, Louisiana, although none were successful there. At Blacksburg, Virginia, the line 13548-10 considerably exceeded the performance of both parents, but at Lexington, Kentucky, P. *pratensis* Leevining well exceeded the apomicts, a pattern also evident at Purdue, Indiana. In the highly continental climate at St. Paul, Minnesota, where the *scabrella* parent was a strict nonsurvivor, the apomict 13548 managed to live, but was considerably outperformed by the *P. pratensis* Leevining parent. In the Mediterranean-type climates at Stanford, Davis, and Pleasanton, all in California, the lines 4729-4 and 13548-10 were comparable in production with the P. *pratensis* parent.

At Edinburgh, Scotland, and 0toftogaard, Denmark, the apomicts 4559-2 and 13548-10 thrived moderately well, but they failed at Uppsala, Sweden, and at Volbu, Norway.

POA SCABRELLA LAS POSAS 4212-3 X P. PRATENSIS MATHER 4253-4. The *Poa scabrella* parent in this combination was another sister plant of the same Las Posas strain used in the two preceding crossings. The *Poa pratensis* Mather parent was the same individual that entered into the cross *Poa ampla* Albion X P. *pratensis* Mather described in Chapter II.

Drawings showing details of spikelets, lemmas, and ligules of the parent plants and an apomictic hybrid derivative, 4711-3, obtained in the $F_2$ generation from the $F_1$ plant 4557-10 (cf. table 18) are shown in figure 25. A view of this same apomictic line grown at Stanford is shown in figure 26.

### *Results from crossing*

Following mutual pollination between the parental individual at Stanford in April 1944, approximately 2000 viable seeds were harvested on the *Poa scabrella* parent. From these, 1416 plants were germinated, 1226 of which were of the apomictic maternal type, while 170 were aberrant forms of the maternal *Poa scabrella* and 20 were $F_1$ hybrids with P. *pratensis.* The maternal types were of normal vigor and uniform in both morphological and growth characteristics, in contrast with the aberrants, which were mostly weak and included lethal subdwarfs and some variegated plants.

The 20 Fj plants were distinguishable from the maternal-like apomicts in early seedling stages by their darker green herbage, their more spreading, divaricate leaves and stems, and their shorter, band-shaped ligules. Some of the F/s were somewhat rhizomatous, and all were intermediate between the parents in most characters. As in the other Fj populations, there was a considerable range of variability. All were early flowering at Stanford; mature culms became dormant in June, showing the strong influence of the *scabrella* parent. The rosette-leaves, however, like those of the *pratensis* parent, mostly remained green and active through the summer growing period.

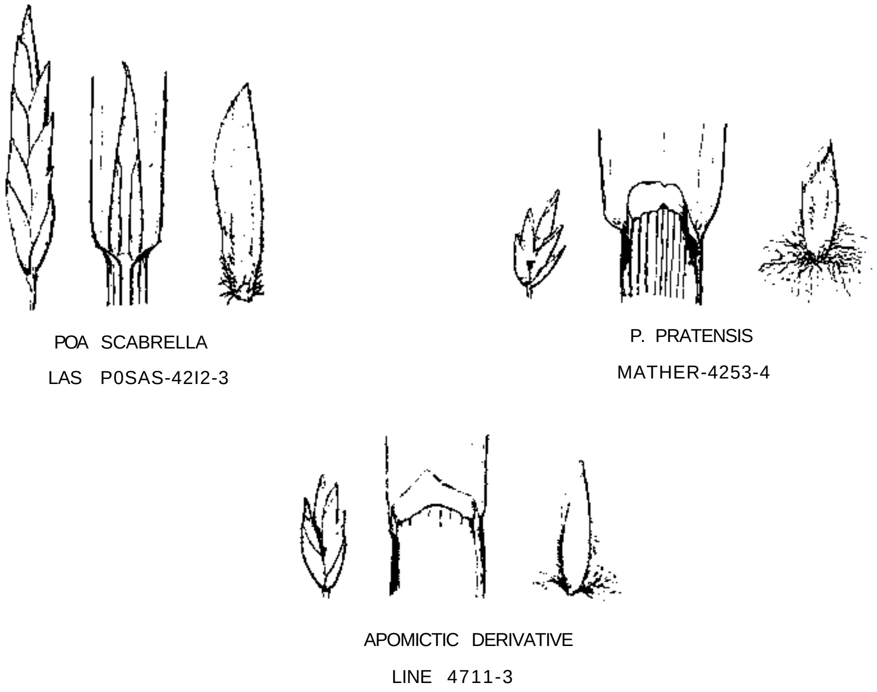


Figure 25. Drawings of spikelets, lemmas, and ligules of *Poa scabrella* Las Posas, *P. pratensis* Mather, and an $F_3$ apomictic derivative, line 4711-3, all shown to the same scale. All plants were grown at Stanford.

Table 19 lists the $F_s$ hybrids individually with their major reproductive characteristics. All except one of the hybrids proved to be sexual, and many were weak. We performed numerous progeny tests both at Stanford and at Pullman on individuals of F{ and $F_2$ plants, and also on later generations to screen promising apomicts. This effort finally netted several self-reproducing lines. Table 20 lists these apomicts and some of their characteristics. One of the most promising was line 4711-3 (cf. figures 25 and 26), which was derived from an $F_2$ segregant of the vigorous $F_t$ hybrid 4557-10.

The growth responses at the altitudinal transplant stations of vegetatively cloned transplants of the apomictic derivatives, lines 4706-1 and 4711-3, in comparison with the parents is indicated by the histograms in figure 23 (right of center). The line 4711-3, while having many of the characteristics of the *Poa scabrella* parent, inherited much of the tolerance to extreme climates possessed by the *P. pratensis* parent. In the widespread field tests in the United States, the much greater tolerance of the apomictic line 4711-3 compared with that of the *scabrella* parent is clearly shown by comparison of the patterns of growth performance of this apomict and those of the parents, shown in the histograms of figure 24. A feature of special interest is the superior performance of this apomict as compared with the *pratensis* parent in the Mediterranean-like climates at Stanford and Davis, as well as at San Fernando, Sunol, and Pleasanton, all in California (not shown in figure 24)—illustrating a capability doubtless inherited from *scabrella*. This feature is in contrast with the responses of the *ampla-pratensis* combinations described in Chapter II, which mostly performed poorly at these test stations. The outstanding performance of the apomict 4711-3 in comparison with both parents in such contrasting climates as those of Pullman, St. Paul, and Blacksburg, is of particular interest, since the *scabrella* parent is a nonsurvivor in climates with

Figure 26- The apomictic line 4711-3, an $F_3$ derivative of the cross *Poa scabrella* Las Posas 4212-3 X *P. pratensis* Mather 4253-4, grown in a spaced planting at Stanford. The photograph was taken on May 14, 1951. The black and white scale is 10 cm high. See tables 19- and 20 relating to the origin of this line, figure 25 for drawings of spikelets, lemmas, and ligules of the original parents and this apomict, and figures 23 and 24 for their relative growth responses in different climates.

TABLE 19

CHARACTERISTICS OF F, HYBRIDS BETWEEN *Poa scabrella* LAS POSAS 4212-3 AND P. *pratensis* MATHER 4253-4

| Plant Number | Chromosome Number, *In* | $^{c}$,$y_0$ Seed Fertility | Vigor at Stanford | Sexual or Apomictic | No. of Apomictic Derivatives |
|---|---|---|---|---|---|
| 4557-1 | 74 | 48 | Strong | Sexual | 0 |
| -2 | 71 | 66 | Vigorous | Sexual | 0 |
| -3 | 75 | 59 | Strong | Apomictic | 1 |
| -4 | 64-66 | 42 | Strong | Sexual | 2($F_3$) |
| -5 | -68-69 | 61 | Vigorous | Sexual | 0 |
| -6 | -71 | 42 | Weak | Sexual | 1 ($F_3$) |
| -7 | 67 | 49 | Weak | Sexual | 0 |
| -8 | 70 | ... | Weak | Sexual | 0 |
| -9 | 68 | 66 | Moderate | Sexual | 0 |
| -10 | 75 | 84 | Vigorous | Sexual | 2($F_3$) |
| -11 | 70 | 17 | Weak | Sexual | 0 |
| -12 | 71 | 21 | Moderate | Sexual | 0 |
| -13 | ... | ... | Weak | ... | 0 |
| -14 | ... | 11 | Weak | Sexual | 0 |
| -15 | -66-70 | 50 | Vigorous | Sexual | 0 |
| -16 | ... | 71 | Moderate | Sexual | 0 |
| -17 | -76-80 | 20 | Weak | Sexual | 1 ($F_3$) |
| -18 | ... | 17 | Weak | ... | 0 |
| -19 | ... | ... | Weak | ... | 0 |
| -20 | ... | ... | Weak | ... | 0 |

winters of such severity. At Lexington, Kentucky, and Purdue, Indiana, where *pratensis* thrives and *scabrella* fails, the apomict 4711-3 performed as well as the *pratensis* parent.

At the northern European test stations, the apomictic derivatives of this combination that were tested were not very successful. At Penlandfield, Scotland, the line 4557-3 grew more vigorously than the *scabrella* parent, but lagged considerably behind the *pratensis* parent. At Uppsala, Sweden, and Volbu, Norway, this line barely survived. Unfortunately the line 4711-3 was not included in the European tests.

POA SCABRELLA WATSONVILLE 4214-1 X P. PRATENSIS ATHABASCA 4249-1. In this combination, the maternal *Poa scabrella* Watsonville parent differed from the Las Posas strain used in the preceding three crosses in being more robust, with taller and more numerous culms and longer leaves, but it was similar in being a winter-active, summer-dormant bunchgrass typical of the California foothill region. This strain was collected by the Soil Conservation Service at Watsonville, Santa Cruz County, California, at a low elevation and maintained at their Pleasanton, California, nursery. Ten uniform individuals were dug from this collection and brought to Stanford in December 1943, one of which, plant 4212-1 with *In* = 82 chromosomes, was used in the above cross.

The *Poa pratensis* parent was the same individual used in the cross *Poa ampk* Kahlotus X P. *pratensis* Athabasca described in Chapter IL The major

TABLE 20

APOMICTIC LINES DERIVED FROM *Poa scabrella* LAS POSAS 4212-3 X *P. pratensis* MATHER 4253-4

| Line Number | Chromosome Number, *2n* | Lineage | Characteristics |
|---|---|---|---|
| 4557-3 | ***75*** | Direct Fi apomict | Bunchgrass type, weak |
| 4706-1 | 64 | $F_3$ from 4557-4 | Tall, *pratensis*-\xk.z leaves |
| 4706-3 | ... | $F_3$ from 4557-4 | Strict bunchgrass, not vigorous |
| 4708-4 | ... | $F_3$ from 4557-6 | Rather weak bunchgrass |
| 4711-2 | ... | $F_3$ from 4557-10 | Semi-bunchgrass, moderate vigor |
| 4711-3 | -66-68 | $F_3$ from 4557-10 | Tall, many culms, rhizomes |
| 4717-7 | ... | $F_3$ from 4557-17 | *scabrella*-like, weak bunchgrass |

morphological differences distinguishing these parental species were essentially the same as those listed in table 16 in the preceding *scabrella-pratensis* crosses.

*Results from crossing*

Among a population of 8048 seedlings grown at Stanford in 1944 from seeds harvested on the *Poa scabrella* Watsonville parent after mutual pollination in a pollen-tight cage with *Poa pratensis* Athabasca, a total of 15 F} hybrids, representing a frequency of approximately 0.17%, were obtained. These displayed the usual range of variation from weak to vigorous, with different recombinations of the characters of the parental plants. The 7968 maternal-type offspring were uniform, and in addition there were 65 weak aberrants.

The Fj hybrids were extensively progeny-tested, and most were found to be sexual in both $F_2$ and later generations; widely segregating progeny ranged from *scabrella-like* individuals to others approaching the *P. pratensis* parent. The *2n* chromosome numbers of the Fj plants varied from 71 to —123, and seed fertilities from less than 1% to 55%.

Altogether, four apomictic lines were obtained from this combination, two of which were direct *F*: apomicts (lines 4561-13 and 4561-19). The first of these was approximately 60% apomictic but of unpromising vigor when grown at Stanford, and the latter was nearly sterile. Two other apomictic lines, 4726-1 and 4726-3, were derived as $F_3$ segregants from the sexual and moderately vigorous Fj plant 4561-1 having $2n = 71$ chromosomes. Of these, only line 4726-3 was selected for wide field tests, the line 4726-1 having a very low seed fertility.

RELATIVE GROWTH PERFORMANCE. The histograms in figure 23 (extreme right) indicate the relative growth performance of cloned transplants of the parental plants and their $F_3$ apomictic derivative, line 4726-3, at the altitudinal transplant stations. It is of interest that P. *scabrella* Watsonville survived at Mather, the mid-altitude station, unlike the Las Posas strain of this species used in the previous crosses. The apomict made a creditable showing at the three transplant stations as a whole, but was not better than the hybrid apomicts derived from the Las Posas strain.

In the widespread field tests the Watsonville strain of *Poa scabrella* unfortunately was not included at many of the sites because of lack of seed. The apomictic line 4726-3, as shown by the histograms in figure 24, was consistently outperformed by the *P. pratensis* Athabasca parent, but was comparable with other *scabrella-pratensis* apomicts of the preceding combinations of these two species. Data on the performance of this apomict from the northern European test stations are too fragmentary to evaluate.

SUMMARY OF RESULTS FROM THE POA SCABRELLA X P. PRATENSIS CROSSINGS. The tests amply demonstrated the feasibility of obtaining hybrids between these two species but except in rare instances failed to obtain self-replicating apomictic hybrid derivatives showing promise of agronomic value. $F_s$ hybrids were obtained only with *Poa scabrella* as the female parent, never with the highly apomictic strains of *Poa pratensis* used as male parents. Most $F_s$ hybrids were sexual, but in a few instances apomictic F/s were obtained. Most of the apomicts were derived in the $F_3$ generation from selected $F_2$ segregants from sexual $F_t$ hybrids.

The apomictic derivatives inherited various recombinations of the characteristics of the parental strains and most possessed a greater range of tolerance *to* contrasting environments than their parental *Poa scabrella* strains. Only rarely, however, did they outperform both parents when subjected to widespread field tests.

## OTHER INTERSPECIFIC COMBINATIONS INVOLVING POA SCABRELLA

Table 2! lists attempts to cross *Poa scabrella* with species of *Poa* other than P. *pratensis.* The failure to secure $F_t$ hybrids in many instances indicates genetic incompatibility between *Poa scabrella* and the other species. It is of interest to review briefly some of the results of these crossings, especially as they throw light on biosystematic relationships.

CROSSES WITH Pn.\ AMPLA. An F, apomictic derivative from the cross *Poa scabrelta* Las Posas 42124 *(2n* = 84) X P. *ampla* Kahlotus 4173-1 (2/2 = 64) appeared at one time to have agronomic potential. This line, 4569-1 *(In* = ^7^1 was approximateK 7ilT apomictic, but had a rather low seed fertility of approximate!) 4u'*. In milder climates in California and at Edinburgh, it grew vigorously as a hunchgrass with numerous long rosette leaves, was fairly prolific in producing culms with open panicles, and outperformed its parents. It was *wukh* field-tested and did relatively poorly in climates with more severe winters, as at St. Paul, Purdue, Volbu in Norway, and Uppsala, Sweden. At the latter two stations it was subject to winter-kill.

A sister apomictic line of the same origin, 4569-2 *{In* = ~73), had similar morphological characteristics and growth responses at stations where it was tested, but was consistently less vigorous in growth even under the most favorable conditions.

The combination *Poa scabrella* Watsonviile 4175-1 *(In* = 63) X *Poa ampla* Wenatchee 4175-1 *(In* = 63) yielded an $F_3$ apomictic derivative (line 13843) which was also widely field-tested. This proved to be considerably weaker than lines 4569-1 and -2.

CROSSES WITH POA GRACILLIMA. From the cross *Poa scabrella* Watsonviile (4214-4, *In* = 62) X *P. gracillima* Timberline (4226-4, *In* = ~84), altitudinally contrasting members of the *P. scabrella* complex, we obtained five Fj hybrids. All of these proved to be sexually segregating in the $F_2$, and progeny tests in $F_3$ generations failed to disclose any apomicts. As a typical example, the F, hybrid 4571-4 *(In* = — 113) had a low seed fertility, and its few offspring segregated widely in morphological characters. For the most part, the $F_2$ progeny were weak and failed to survive at Stanford. Similar results were obtained when the Yager Creek form of *P. scabrella (In* = 84) was used with the same form of *P. gracillima* (cf. table 20).

CROSSES WITH POA COMPRESSA. The three F, hybrids derived from the cross *P. scabrella* Las Posas 4212-7 *{In* = 84 + *f)* X *P. compressa* Chorsum (4260-1, *In* = 50) listed in table 20 varied widely among themselves; *In* values were 65, 105, and 115 chromosomes, respectively. In these hybrids the characteristics of P. *scabrella* were more dominant than those of P. *compressa:* all three F/s were bunchgrasses without rhizomes. The $F_l$ hybrid 4761-3 *{In* = — 115) was approximately 17% fertile, and some of its $F_2$ offspring were progeny-tested at various stations. These segregated widely, and a few individuals appeared to have some promise as new recombinations, but none proved to be apomicts. Most of the $F_2$'s were weak plants and clearly nonsurvivors.

In another combination between the same form of *P. scabrella* with a California form of *P. compressa* from Crescent Mills, two Fj hybrids having 2/2 = 63 and *In* = 101 chromosomes, respectively, were obtained. These hybrids also were bunchgrasses indicating the predominant influence of P. *scabrella* characters, and both proved to be sexual.

CROSSES WITH POA ARIDA. TWO FJ hybrids from the cross P. *scabrella* Las Posas 4553 *(In* = 84 + / j X P. *arida* North Platte 426241 *(In* = 63) had characteristics intermediate between the parents, both having *In* = 76 chromosomes. The stronger of the two, plant 4766-1, had a seed fertility of approximately 30% and was sexual, yielding widely segregating offspring. Prog-

## TABLE 21

ATTEMPTED HYBRIDIZATIONS BETWEEN *Poa scabrella* AND SPECIES OTHER THAN P. *pratensis*

| Parental Combinations | | CIW Culture No. | Maternal Progeny Grown | No. of Maternal Apomicts | No. of Aberrant Plants | No. of F, Hybrids | No. of Apomictic Lines |
|---|---|---|---|---|---|---|---|
| *Poa scabrella* Las Posas 4212-1, *In* » -82 | X P. *atnpla* Kahlotus 4178-1, *In* = 64 | 4569 | 1101 | 1101 | 88 | 2 | 2 |
| *Poa scahrella* Watsonville 4214-6, *In* = 63 | X P. *ampla* Wenatchee 4175-1, *In* = -63 | 4570 | 1222 | 1068 | 48 | 6 | 1 |
| *Poa scabrella* Watsonville 4214-4, *In* = 62 | X P.*giacillima* Timberline 4226-5, *In* = ~84 | 4571 | 237 | 213 | 19 | 5 | 0 |
| *Poascabrella* YagerCk. 4220-1, *In* * 84 | X P. *gracillima* Timberline 4226-4, *In* = 84 | 4572 | 1023 | 175 | 844 | 4 | 0 |
| Reciprocal | | 4573 | 472 | 408 | 61 | 3 | 0 |
| P«? *nerwsa* Timberline 4257-3, *In* = 63 | X P. *scabrella* Las Posas 4212-4, *In* = -82 | 4576 | 464 | 439 | 25 | 0 | 0 |
| Poa *nervosa* Timberline 4257-6, *2n* = 63 | X P. *scabrella* Las Posas 4212-2 | 4577 | 288 | 276 | 12 | 0 | 0 |
| *Poa nervosa* Timberline 4557-8, *In* = 63 | X P, *scabrella* Las Posas 4212-2, 2« = -82 | 4578 | 384 | 365 | 19 | 0 | 0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Pm H-alnella* Las Posas 4553-18, *hi* H4 + / | X P. *compressa* Chorsum 4260-1, 2/i = 50 | 4761 | 25 | 15 | 7 | 3 | 0 |
| Reciprocal | | 4762 | 57 | 57 | 0 | 0 | 0 |
| ***Poa*** *siafaetta* Las Posas 4555, *2tt* -84 | *X P. compressa* Crescent Mills 4532-6, *In* = 42 | 4763 | 57 | 45 | 10 | 2 | 0 |
| Reciprocal | | 4764 | 15 | 15 | 0 | 0 | 0 |
| *Pm scabrelk* Watsonvillc 4571 | X *P, arida* N. Platte 4263-13, *In* = 63 | 4767 | 63 | 54 | 9 | 0 | 0 |
| *Poa scabrelk* Las Posas 4553 | x *P, arachnifera* Stillwater 4248-12 (male) | 4769 | 967 | 893 | 74 | 0 | 0 |
| Reciprocal | | 4776 | 932 | 840 | 92 | 0 | 0 |
| *Pm scabrelk* Watsonvillc 4561-5, *2n* = -82 | X *P.amchnifaa* Woodward 4435-12, *In* = ~63 | 4771 | 133 | 121 | 12 | 0 | 0 |
| *Poa scabrelk* Lucerne 4217-17, *In* = 63 | X *P. arachnifera* Stillwater 4248-12 (male) | 4772 | 1117 | 1070 | 46 | 1 | 0 |
| *Poa caespitosa* Canberra 5164-23 | X *P. scabrelk* Watsonville 4214-1 | 6240 | 43 | 36 | 7 | 0 | 0 |
| Reciprocal | | 6241 | 1128 | 1102 | 2.6 | 0 | 0 |
| *Poa scabrelk* Watsonville 5160-2, 2*i = 63 | X P. *arachnifera* Stillwater 4248-12, *In* = 63 (male) | 6271 | 210 | 32 | 12.9 | 49 | 0 |
| *Pm smbrdk* Paso Roblcs 5847-120 | X P. *arida* N. Platte 4766-2 | 6286 | 870 | ? | ? | 17 | 0 |

eny tests on six of the more promising $F_2$ individuals failed to uncover any apomictic derivatives in the $F_3$ generation.

The reciprocal combination, with *Poa arida* as the female parent (see table 20), also yielded two $F_l$ individuals. One of these, 4766-1 *(2n* = 90), was approximately 10% fertile; the other, 4766-2 *(2n* = 105), had a fertility of approximately 36%. Both were reasonably vigorous plants with rhizomes. The $F_2$ progeny of both were variable, but the offspring of 4766-2 consisted of many individuals (~66%) strongly resembling the $F_x$ parent, suggesting that it may have been an unstabilized amphiploid—a conclusion supported by the chromosome number, the sum of both parents. Progeny tests on four promising $F_2$ segregants from this individual failed to reveal any apomicts.

CROSSES WITH POA ARACHNIFERA. A single $F_:$ hybrid from *P. scabrella* Lucerne 4217 *(2n* = 63) X a male plant of P. *arachnifera* Stillwater 4248-12 *{In* = 63) proved to be weakly bisexual and completely sterile, and had *2n* = 57 chromosomes. This hybrid developed rhizomes, a character inherited from *P. arachnifera,* and had leaves and stems intermediate in character between the parents.

In contrast, the combination between a male-sterile strain of *P. scabrella* Watsonville 5160-2 *(2n* = 63) with a male plant of P. *arachnifera* Stillwater 4248-12 yielded 49 $F_{(}$ plants with chromosome numbers *(2n)* ranging from 69 to 113. These were highly variable morphologically, and included strictly female individuals, female plants with aborted anthers, and fully bisexual plants. All these hybrids were consistently sterile and yielded very few $F_2$ progeny. The few that were obtained were weak, nonsurviving individuals at Stanford.

OTHER CROSSES. The attempts to cross *Poa scabrella* with female plants of *Poa nervosa* listed in table 21 all failed to produce any F, hybrids. The seeds harvested in P. *nervosa* yielded only maternal-type replicas together with a relatively few maternal-type aberrants (cf. Grun, 1955b). Similar results were obtained in crossing *Poa caespitosa* with P. *scabrella.*

In conclusion, the likelihood of obtaining self-perpetuating apomictic hybrid derivatives of agronomic value between *Poa scabrella* and the other species listed in table 21 is rather remote, but since some recombinations of promise were realized, this possibility cannot be entirely ruled out.

# IV
# MISCELLANEOUS ATTEMPTED COMBINATIONS, INCLUDING QUADRUPLE HYBRIDIZATIONS

## IV

# MISCELLANEOUS ATTEMPTED COMBINATIONS, INCLUDING QUADRUPLE HYBRIDIZATIONS

We attempted to intercross other species of *Poa* in combinations other than those described in the previous chapters. These are listed in table 22 with a summary of results. Most of the attempts were unsuccessful, indicating genetic incompatibilities. It is nevertheless interesting to review some of the more significant data that suggest biosystematic relationships between the various species involved. Of special importance are the attempts to cross interspecific hybrids in an effort to produce quadruple apomictic hybrid derivatives, listed near the end of the table.

The comments below are intended to supplement the information in table 22 for some of the crossings listed.

POA CANBYI BLUE MOUNTAINS X P. PRATENSIS OTTAWA (CIW NO. 4263). The single Fj hybrid, 4263-1, *2n = 11* chromosomes, was approximately 50% fertile. It was moderately vigorous and developed rhizomes, a characteristic inherited from *Poa pratensis*, and displayed other features intermediate between the parents. Cloned propagules of this hybrid displayed a wide tolerance when grown at the altitudinal transplant stations at Stanford, Mather, and Timberline. It proved to be sexual; $F_2$ progenies grown at both Stanford and Pullman segregated widely. One $F_3$ line selected at Stanford (4692-6) was weakly apomictic but definitely inferior to the parents in growth performance.

POA AMPLA ALBION X P. COMPRESSA CHORSUM AND RECIPROCAL (CIW Nos. 4273-3, 4275). The four F, hybrids, 4274-1 *(In = -50)*, 4274-2 *{In* = 62), 4264-3 *{In* = 86), and 4274-6 *(2n* =- 70), were mostly sterile, with weak, segregating $F_2$ progenies. Likewise, the two reciprocal ¥$_x$ hybrids with *In* = 56 and *In* = 59 chromosomes, respectively, were sterile, and no apomictic derivatives were obtained.

POA AMPLA ALBION X P. ARIDA N. PLATTE AND RECIPROCAL (CIW Nos. 4543, 4544). An F, hybrid, 4543-2 *{In* = 59), proved to be entirely sexual. Cloned transplants at Timberline barely survived a single winter, but those at Stanford and Mather were reasonably vigorous. An $F_{\}}$ from the reciprocal combination 4544-2 *(In* = 98) was fairly fertile but sexual. It displayed wide tolerance when cloned and grown at the three altitudinal stations. Several of its $F_2$ derivatives were progeny-tested, but none proved to be apomictic. This $F_1$

## TABLE 22

### MrSC3ELLANF.OUS INTERSPECIFIC CROSSING ATTEMPTS

| Parental Combinations | | CIW Culture No. | No. of Plants Grown | No. of F, Hybrids |
|---|---|---|---|---|
| *Pm canbyi* Blue **Mts.** 42064, *In* = -84 | X P. *pratensis* Athabasca 4249-1, *In* = 70 | 4263 | 49 | 1 |
| Reciprocal | | 4264 | 115 | 0 |
| Pew *pratensis alpigena* Lapland 4250-1, *2n* = 74 | X P. *canbyi* Mt. Misery 4207, *In* = 82 | 4265 | 178 | 0 |
| Reciprocal | | 4266 | 14 | 0 |
| Pew *ampk Albion* **4183-1, 2« = 63** | X P. *compressa* Chorsum 4260-1, *In* = 52 | 4274 | 1181 | 4 |
| Reciprocal | | 4275 | 809 | 2 |
| *Poa mrtda* N. Platte 4262-1, *In* = 63 | X P. *ampla* Albion 4183-2, 2» = 63 | 4543 | 748 | 1 |
| Reciprocal | | 4544 | 960 | 1 |
| *Pm nevadensis* Hart Mt. Pass 4192-1, 2» = 62 | *X P. compressa* Chorsum 4260-1, *In* = 50 | 4545 | 340 | 4 |
| Reciprocal | | 4546 | 480 | 0 |
| *Poa netmdensis* Winchester 4200-1, *In* = 70 | X P. *longifolia* Armenia 42454, *In* = 43 | 4547 | 480 | 1 |
| Reciprocal | | 4548 | 300 | 0 |
| *Poa canbyi* Goldendale 4204-1, *In* = -86 | X P. *longifolia* Armenia 4245-1, *2n* = 43 | 4549 | 39 | 0 |
| Reciprocal | | 4550 | 15 | 0 |
| *Poa canbyi* Blue Mts. 42064, *In* = 84 | X P. *pratensis* Leevining 4258-2, *In* = 68 | 4551 | 1080 | 0 |
| Reciprocal | | 4552 | 210 | 0 |
| *Poa ncrvosa* Timberline 4257-5, *2n* = 62 | X P, *canbyi* Emmett 4233-1, *In* = 84 | 4574 | 480 | 0 |
| *Poa nervosa* Timberline 4257-8, *2n* = 63 | X P. *canbyi* Goldendale 4203-1, *In* = *97* | 4574 | 768 | 0 |
| *Pm canbyi* Goldendale 4204-1, *In* = ~-88 | X P. *pratensis* Mather 4253-12 | 4733 | 121 | 0 |
| Reciprocal | | 4734 | 30 | 0 |
| *Poa ampk* Spokane 4180-12, *In* = 63 | X P. *compressa* Crescent Mills 4532-2, *In* = 42 | 4735 | 354 | 4 |
| *Poa nevadensis* Hart Mtn. Pass 4192-1, *In* = *63* | X P. *compressa* Crescent Mills 4532-2, *In* = 42 | 4742 | 2 | 0 |
| Reciprocal | | 4743 | 30 | 0 |
| *Pm caespitosa* Canberra 516447 | X P. *ampla* Albion 5155-2, *In* = 63 | 6236 | 351 | 0 |
| Reciprocal | | 6237 | 120 | 0 |
| *Poa caespitosa* Canberra 5164-17 | X P. *ampla* Albion 5156-20, *In* = 56 | 6238 | 210 | 0 |
| Reciprocal | | 6239 | 501 | 0 |
| *Pm caespitosa* Canberra 5164-3 | X P. *scabrella* Watsonville 4214-1 | 6240 | 43 | 0 |
| Reciprocal | | 6241 | 1128 | 0 |
| *Pm caespitosa* Canberra 5164 | X P. *pratensis* Mather 5168-23 | 6242 | 45 | 0 |
| Reciprocal | | 6243 | 90 | 0 |
| *Pm pratensis* Mather 5168-23 | X P. *caespitosa* Canberra 5164-24 | 6244 | 120 | 2 |

| | | | | |
|---|---|---|---|---|
| *Pm caespilosa* Canberra 5164-24 | X *P. compressa* Crescent Mills 4532-1 | 6247 | 330 | 0 |
| Reciprocal | | 6248 | 330 | 3 |
| *Poa cacspitosa* Canberra 5164-23 | X P. *arachnifera* Stillwater 5165-16 (male) | 6249 | 111 | 6 |
| *Pm amchnifem* Stillwatcr 5165-29 (female) | X *P. ampk* Spokane 418042 | 6264 | 30 | 0 |
| *Pm ampk* Spokane 418042 | X *P. amchnifem* 4284-12 (male) | 6265 | 600 | 0 |
| *Pm ampk* Albion 5156, 2« = 56 | X *P. amchnifem* Stillwater 4248-12 (male) | 6266 | 360 | 0 |
| *Pm amchnifem* Stillwater 5165-23 (female) | X P. *pratensis* Mather 5168-25 | 6272 | 32 | 0 |
| *Pm ampk* Albion 5156-20, *In* = 56 | X P. *compressa* Crescent Mills 4532-1 | 6290 | 203 | 0 |
| *Pm ampk* Albion 5164-24, *In* = 56 | X P. *compressa* Crescent Mills 4532-1 | 6291 | 300 | 1 |
| *Pm ampk* Albion 5155-27, *In* = 63 | X P. *compressa* Crescent Mills 5174-24, *In* = 42 | 6294 | 718 | 1 |
| Reciprocal | | 6295 | 240 | 0 |
| *Pm arida* N. Platte 426243 | X P. *ampk* Wenatchee 5153-23 | 6296 | 324 | 25 |
| Reciprocal | | 6297 | 210 | 0 |
| *Pm arida* N. Platte 4262, *In* = 63 | X P. *ampk* Albion 5156-23, *In* = 56 | 6298 | 540 | 48 |
| *Poa arida* N. Platte 4262-11, *In* = 63 | X P. *ampk* Albion 5156-23, *In* = 56 | 6299 | 90 | 37 |
| Reciprocal | | 6300 | 513 | 0 |
| *Quadruple Combinations* | | | | |
| *Pm ampk-arida* N. Piatte- Albion 4784-109 | X P, *ampk-alpigena* Albion-Lapland 4222-130 | 6301 | 510 | 2 |
| Reciprocal | | 6302 | 870 | 5 |
| *Pm orida^mpk* N. Platte-Albion 4787407 | X P. *ampk'pratensis* Albion-Mather 4794-414 | 6303 | 390 | 3 |
| Reciprocal | | 6304 | 120 | 3 |
| *Poa arida^mpk* N. Platte-Albion 4787410 | X P. *ampk-pratensis* Albion-Mather 4799-518 | 6305 | 480 | 6 |
| Reciprocal | | 6306 | 37 | 0 |
| *Pm arida-ampk* N, Platte-Albion 4787-112 | X P. *ampk-pratensis* Condon 4818-304 | 6307 | 180 | 0 |
| Reciprocal | | 6308 | 120 | 0 |
| *Pm ampk-pratensis* Albion-Lapland 4683-1 | X P. *scabrelk-pratensis* Las Posas Mather 4711-3 | 6309 | 540 | 0 |
| Reciprocal | | 6310 | 450 | 32 |
| *Pm ampk-pmtensis* Albion-Lapland 4825-322 | X P. *ampk-pmtensis* Condon 4817-227 | 6311 | 44 | 0 |
| Reciprocal | | 6312 | 630 | 0 |
| *Pm ampk-pratensis* Heise-Newport 4804-503 | X P, *ampk-alpigena* Albion-Lapland 4916-228 | 6313 | 6 | 0 |
| Reciprocal | | 6314 | 180 | 7 |
| *Pm ampk-pratensis* Heise-Newport 4804-523 | XP. *ampk-alpigena* Albion-Lapland 4916-209 | 6315 | 90 | 0 |
| Reciprocal | | 6316 | 300 | 5 |

hybrid was used in crosses with other Fj combinations in an attempt to obtain quadruple combinations (cf. CIW 6391, 6303).

POA NEVADENSIS HART MOUNTAIN PASS X P. COMPRESSA CHORSUM (CIW No. 4545). The four $F_l$ hybrids varied among themselves, showing recombinations of the characteristics of the parents. All four were weak, nonflowering plants when grown at Stanford and failed to survive more than a single season.

POA NEVADENSIS WINCHESTER X P. LONGIFOLIA ARMENIA (CIW No. 4547). The single weak, nonflowering $F_}$ hybrid survived only a single year at Stanford.

POA AMPLA SPOKANE X P. COMPRESSA CRESCENT MILLS (CIW No. 4735). Four F, hybrids were obtained: 4735-1 *(2n* = 51), 4735-2 *{In* = ?), 4735-3 *{In* = 84), and 4735-4 *(In* = 81). All varied among themselves with different recombinations of the parental characters (see figure 27), with seed fertilities ranging from about 12 to 48%. All four were progeny-tested and found to be sexual, with mostly very weak offspring; no apomictic derivatives were obtained. Cloned transplants of the four F/s were most vigorous at Mather and managed to survive at Timberline for several years.

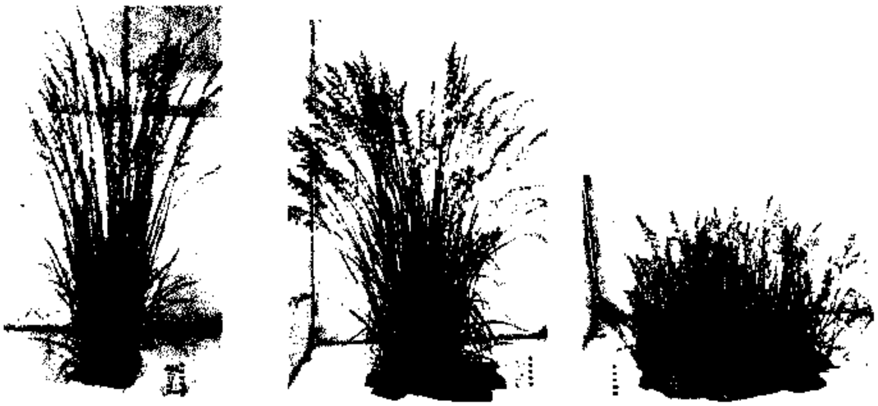


Figure *27. Poa ampla* Spokane 4180-12 (left), *P. compressa* Crescent Mills 4532-5 (right), and one of their sterile F, hybrids, 4735-4 (center), all grown at the mid-altitude station at Mather, Tuolumne County, California, at an elevation of 1400 meters. The photographs were taken on July 10, 1951. The black and white scale is 10 cm high. See table 22 for further details.

POA PRATENSIS MATHER X P. CAESPITOSA CANBERRA (CIW No. 6244). Both F, hybrids that were obtained were sterile; 6244-1 had *In* = 67 chromosomes. Cloned transplants of the hybrids were moderately strong at Stanford and Mather but weak at Timberline.

POA COMPRESSA CRESCENT MILLS X P. CAESPITOSA CANBERRA (CIW No. 6248). Three individuals were obtained that were considered to be $F_\}$ hybrids. The plant 6248-1 was completely sterile, whereas 6248-2 *(In* = ~52), the most vigorous of the three, yielded an $F_2$ population of 120 individuals that were weak and highly segregating when grown at Stanford. The third plant, 6248-3 *(In* = ~54), was approximately 10% fertile but was a weak nonsurvivor. Cloned transplants of the three hybrids brought to Timberline barely survived two winters.

POA CAESPITOSA CANBERRA X P. ARACHNIFERA STILLWATER (CIW No. 6249). Six plants proved to be Fj hybrids of this combination between bisexual P. *caespitosa* and dioecious P. *arachnifera,* 6249-1, -2, -105, -113, -120, and -129. All of these were bisexual and moderately vigorous at Stanford, but varied in morphology among themselves. All were nonsurvivors when transplanted as clones to Timberline. Their seed fertilities ranged from sterile to ~-50%.

$F_2$ progeny from 6249-2 *(2n* = ~52) segregated widely, and ranged from weak to moderately vigorous. Included were bisexual, male, and female plants; most were male with low fertility. Sixteen of the $F_2$ individuals were progeny-tested, but most proved to be of low fertility, having only from 2 to 48 surviving seedlings. The progenies displayed wide segregation and all $F_3$ derivatives were weak nonsurvivors at Stanford. Progeny tests of the F, plant 6249-113 yielded similar results in the $F_2$ and $F_3$ generations. See Clausen (1961) for further discussion of this cross.

POA AMPLA ALBION X P. COMPRESSA CRESCENT MILLS (CIW No. 6291). The single $F_Y$ hybrid derived from this combination was a weak, nonflowering, rhizome-producing individual.

POA AMPLA ALBION X P. COMPRESSA CRESCENT MILLS (CIW No. 6294). The Fj hybrid 6294-2 *(2n* = ~53) was a plant with short rhizomes and mostly cauline leaves with few flowering stems, and was approximately 17% fertile. In its morphology it reflected the strong influence of P. *compressa* in its wiry stems, which were erect with short inflorescences. No apomictic derivatives were obtained from progeny tests made on it. The reciprocal combination failed to yield any $F_?$ hybrids.

POA ARIDA N. PLATTE X P. AMPLA WENATCHEE (CIW No. 6296). Among the 324 progeny harvested from the P. *arida* female parent grown at Stanford, 25 appeared to be valid $F_1$ hybrids with *Poa ampla,* as fudged both by morphological and cytological characters. The hybrids varied in chromosome number *(2n)* from 86 to 96 in 18 F, individuals that were counted and considered to be triploids, both parents having *In* = 63 chromosomes. Seed fertilities among the $F_t$ hybrids ranged between 0 and ~!2$^{r}$T; the plants \aricd morphologically among themselves, but all were consistently weak in growth at Stanford. None were considered to be of sufficient promise to warrant progeny testing for apomictic derivatives. Of interest is that no F, hybrids were obtained in the reciprocal combination.

POA ARIDA N. PLATTE X P. AMPLA ALBION (CIW NO. 6298). The surprisingly large number of 48 F, hybrids were obtained among the 540 progeny of the *Poa arida* female parent after cross-pollination at Stanford. These varied widely among themselves in morphological characteristics and in vigor of growth at Stanford. Seventeen of the ¥$_x$ plants that were studied cytologically ranged in chromosome number *(In)* from 64 to *97,* and in seed fertilities from less than 5% to approximately 50%. Although none of the hybrids were outstandingly vigorous when grown at Stanford, some seed was harvested from most of them for progeny testing. Among 24 of the F, plants that were progeny-tested at either Stanford or Pullman, 16 proved to be sexual and widely segregating with mostly weak offspring, 6 proved to be partially apomictic (13-57%), and 2 were classed as only "slightly apomictic." None of the partially apomictic lines was considered to be sufficiently promising to warrant field testing.

Twenty of the Fj's grown as cloned transplants at Stanford, Mather, and Timberline varied considerably among themselves when grown at Stanford and Mather, and most failed to survive a second winter at Timberline.

POA ARIDA N. PLATTE X P. AMPLA ALBION (CIW No. 6299). This cross was nearly a repetition of the combination described above, except that a different individual was used as the female parent line *Poa arida* N. Platte.

As in the preceding combination, a surprising number of F! hybrids (37) were obtained. Of these, 21 individuals were studied cytologically, one of which had *2n* = 63 chromosomes (plant 6299-213) whereas the remainder ranged within the relatively narrow margin of *2n* = 88-97, suggesting that most of the hybrids were triploids (the parents having *In* = 63 and 2/2 = 56 chromosomes, respectively). Seed fertilities of the hybrids ranged from — 10% to 80%, and the hybrids were highly variable among themselves. None were truly vigorous in growth at Stanford. Of 32 Fj individuals that were progeny-tested in the $F_2$ generation, 23 were sexual with mostly weak, non-surviving offspring, while nine were weakly apomictic (**—12-40%).** None of the apomictic lines were considered to be of sufficient promise to warrant field testing. Among seven F, hybrids grown as clones at the altitudinal transplant stations, only two managed to survive a second winter at Timberline. As in the previous combination, the reciprocal of this cross with *Poa ampk* Albion as the female parent failed to yield any F, hybrids.

## QUADRUPLE COMBINATIONS

As listed at the bottom of table 22, we attempted to make quadruple hybrids with the thought that recombinations among their progeny might give rise to outstanding self-reproducing apomictic lines of agronomic value. These crossings were made mostly during 1951 and 1953 at Stanford. We review the results, below, as a matter of record.

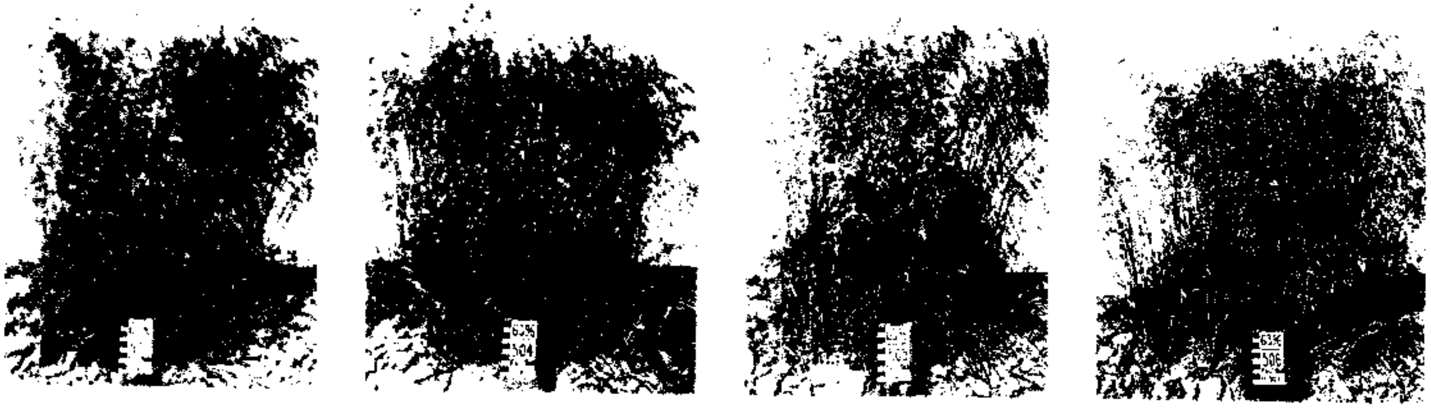
POA AMPLA-ARIDA N. PLATTE-ALBION X P. AMPLA-PRATENSIS ALBION-LAPLAND (CIW No. 6301). Among the variable progeny of 510 individuals grown from the female parent of the above cage-pollinated cross made at Stanford, the recognition of true F} quadruple hybrids proved difficult because of evident recombinations of the *ampla-arida* parent that were also present. Two plants, 6301-13 and 6301-16, considered to be true quadruple hybrids, were progeny-tested at Stanford and found to be sexual, producing highly variable and mostly weak offspring. Clone-members of the F\ hybrids grown at the three altitudinal stations proved to be quite tolerant to the severe winter at Timberline.

Among 870 progeny grown from the reciprocal cross (CIW No. 6302), five individuals were thought to be true Fj hybrids: 6302-1 ($2n$ = 91), 6302-2, and -3, -4, and -5, all of which were weak. Plant 6302-1 yielded some seed and was progeny-tested in the $F_2$ at Stanford, but the offspring were variable and mostly weak nonsurvivors.

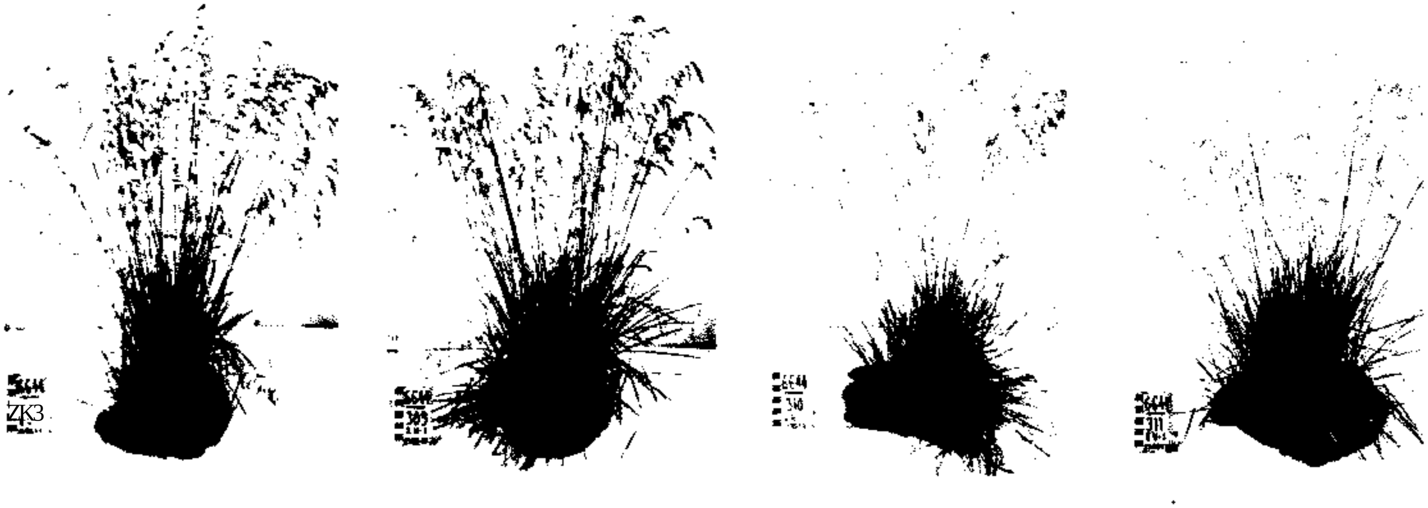
POA ARIDA-AMPLA N. PLATTE-ALBION X P. AMPLA-PRATENSIS ALBION-MATHER (CIW No. 6303). Among 390 seedlings harvested on the *Poa arida-ampla* parent following cross-pollination in a cage at Stanford, were three individuals considered to be valid quadruple hybrids (6303-1, *In* = 89, 6303-4, and -5). In progeny testing, their $F_2$ progenies segregated widely and most offspring were weak. The F} hybrids were only of moderate vigor when grown at Stanford, and seed fertilities ranged from 16% to 17%. Many of the $F_2$ individuals of the three *F{* plants failed to produce flowering stems at Stanford and were nonsurvivors. No apomictic lines were derived from this combination. Most cloned transplants of the F,'s grown at the altitudinal field stations survived only a single winter at Timberline.

The reciprocal cross (CIW No. 6304) yielded several plants that were regarded as quadruple hybrids (6304-2, -4, -6). These were all weak and of low fertility, and were not considered to be of sufficient promise to be progeny-tested.

POA ARIDA-AMPLA N. PLATTE-ALBION X P. AMPLA-PRATENSIS ALBION-MATHER (CIW No. 6305). Among six plants considered to be quadruple *F{* hybrids, two (6304-8 and -9) were progeny-tested and found to be highly variable in the $F_2$ with weak offspring. No apomictic lines were derived. Cloned trans-



AT PULLMAN, WASHINGTON



AT STANFORD, CALIFORNIA

Figure 28. An apomictic quadruple hybrid *(In = —99)*, as seen in two environments. Above: Sample of four space-planted individuals among a uniform population grown at the U.S. Soil Conservation Service nursery at Pullman, Washington, from seedlings germinated during the spring of 1952. The black and white scale is 10 cm high; the photograph was taken on June 16, 1953. Below: A similar sample of space-planted individuals at Stanford on June 23, 1955, from seedlings germinated in the spring of 1954. This apomict originated as an $F_2$ derivative of a cross between an F, hybrid of *Poa scabrelk* Las Posas 4242-3 *{In = —84)* X *Poa pratensis* Mather 4253-4 *(In = 68)* and presumably another F, of *Poa ampla* Albion 4183-I *(2n = —70)* X P. *pratensis* ssp. *alpigena* Lapland 4250-1 *(In = —74)*. The hybrid of this quadruple combination (plant no. 13838-305) was first recognized among a segregating population grown in 1949 at Pullman, where it survived the severe winter of 1951. $F_3$-generation progeny of this apomictic line were widely field-tested.

plants of the hybrids proved to be widely tolerant at the three altitudinal stations, and survived over three winters at Timberline. In the reciprocal cross (CIW 6303) no quadruple F/s were obtained.

POA AMPLA-PRATENSIS ALBION-LAPLAND X P. SCABRELLA-PRATENSIS LAS POSAS-MATHER (CIW No. 6309). No quadruple F, hybrids were obtained from this combination; all of the 540 offspring from the female parent were of the apomictic maternal type.

In contrast, the reciprocal combination (CIW No. 6310) with the facultative apomictic *Poa scabrella-pratensis* Las Posas-Mather (line 4711-3) as the female parent, 32 among 450 progeny grown at Stanford were considered to be valid quadruple hybrids. Among 21 of these studied cytologically, chromosome numbers *{In)* varied between 56 and 80, the highest frequency being between *In* = 66-74. Seed fertilities among the hybrids varied between 0% and approximately 70%, the range 7-33% being the most frequent. Morphologically, the quadruple hybrids varied greatly among themselves and displayed various recombinations of the four original parental plants. They ranged from weak to moderately vigorous when grown at Stanford. All 32 of the hybrids were grown as cloned transplants at Stanford, Mather, and Timberline between 1953 and 1958. Most proved to be remarkably tolerant at all three altitudes, even at Timberline.

Seven of the hybrids were progeny-tested (6310-1, -2, -8, -10, -45, -300, and -313). The F, 6310-1 *(2n* = 61) was approximately 27% fertile, and from it 120 $F_2$ offspring were grown at Stanford. It was itself approximately 67% apomictic and moderately vigorous and was included in the field tests as line 6310-1. Another F,, 6310-2 *{In* = 71), proved to be approximately 90% apomictic and was a tall, leafy, vigorous form with promise of agronomic potential; this hybrid was as widely field-tested as line 6310-2. A third hybrid, 6310-45, was approximately 40% fertile and proved approximately 53% apomictic. This was a moderately vigorous, early-flowering strain, referred to as line 6310-45. Another apomictic derivation from a similar quadruple combination is illustrated in figure 28. This line, No. 13838-305, was collected at Pullman and grown at Stanford as CIW No. 6644. It was widely field-tested and appeared to have agronomic potential.

POA AMPLA-PRATENSIS HEISE-NEWPORT X P. AMPLA-ALPIGENA ALBION-L,APLAND (CIW No. 6313). Among the few plants grown from the female parent following pollination, none proved to be quadruple hybrids. In the reciprocal combination (CIW No. 6314), 180 plants were grown at Stanford, 7 of which appeared to be quadruple hybrids. These were all weak and of such low fertility that no $F_2$ progeny could be obtained.

## DISCUSSION

It is evident from the above data that most of the attempted interspecific crossings listed in table 22 were disappointing in terms of obtaining new, self-perpetuating hybrid derivatives having agronomic potential. The importance of the genetic barriers to intercrossing among the various species provides evidence of the general overall validity of the taxonomic treatment of the species of *Poa,* as presented by Hitchcock (1950). In the relatively rare instances where interspecific hybrids were obtained, their genetic instability became evident when quadruple combinations were attempted. The resulting $F_2$ progeny, if any, proved to be highly segregating sexual recombinations that were often weak nonsurvivors.

An exception, however, is the combination between *Poa scabrella-pratensis* (line 4711-3) crossed with *P. ampla-pratensis* (line 4683-1), listed in table 22 under CIW No. 6310. In this instance, quadruple hybrids were obtained which, although varying widely among themselves, included some individuals classed as "moderately vigorous." Moreover, $F_2$ derivatives yielded several moderately apomictic lines that appeared to have some promise as agronomic material. The contrast between the results of this cross and the reciprocal combination is of considerable interest in demonstrating the marked differential responses of the two hybrid parents to each other's pollen. These results underscore the unpredictability of the outcome of such methods.

The fact that at least some quadruple hybrids were, in fact, realized, is itself of interest and underscores the genetic flexibility existing in a complex genus like *Poa,* with its polyploidy and facultatively apomictic capacity to reproduce new recombinations, some of which may be particularly well suited to survive in certain environments.

# V
# CONCLUSIONS

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The data from the crossing experiments in *Poa* support the deductions made by Stebbins (1950) in his classic review *Variation and Evolution ofPlants*. From earlier studies in *Crepis* by Stebbins and Babcock (1939), these authors coined the term "agamic complex" to describe groups of species characterized by polyploidy, apomixis, and hybridization at different genome levels. With reference to *Poa*$_t$ Stebbins (1950, p. 405) speculated that when this genus is better known, it may have to be regarded as a single, high-polyploid complex. The data reviewed in this volume are too incomplete to either confirm or refute this hypothesis, inasmuch as only a few key species-groups, representing several sections of this huge genus, have been involved; neither have we studied their possible relationship to such neighboring genera as *Puccinellia* and *Glyceria*. Nevertheless, the fact that hybridizations between such divergent species as *Poa scabrella, P. pratensis, P. ampla, P. compressa,* and *P. caespitosa* have yielded viable $V_x$ progeny and in some instances self-perpetuating derivatives featuring facultative apomixis indicates the enormous potential for genetic recombination that exists in this group.

In all these instances, the basic limitation on the range of variability obtained confirms Stebbins's deduction that "agamic complexes are destined to produce only new variations on an old theme, … and are limited to recombination of the genes present in the original sexual ancestors." This limitation is seen to apply to quadruple interspecific hybrid combinations as well as to derivatives from crosses between two species.

SYNTHESIS OF HYBRID DERIVATIVES. That new self-reproducing apomictic hybrid products of potential agronomic value may be realized through interspecific crossings between facultatively apomictic species of *Poa* is demonstrated by the reasonably promising lines obtained from crosses between *Poa ampla, P. pratensis, P. scabrella,* and P. *compressa.* In table 23 are listed those apomictic derivatives described in the previous chapters and considered the most promising lines obtained.

We must acknowledge that the overall results from the present studies have fallen short of initial expectations. None of the synthesized hybrid derivatives have been clearly superior in growth performance to both parental lines when tested in all the different environments. In retrospect, this result is perhaps not surprising in view of the multitude of exacting requirements needed to produce a truly outstanding agronomic product. One cannot help but be impressed with the effectiveness of the natural evolutionary processes, which have produced the various end-products of the species-complex now growing in the wild and so well fitted to their native environments.

We emphasize that despite our extensive effort in crossing *Poa* species, only a very small fraction of the recombinations possible in this large agamic complex have actually been attempted. From this point of view, the fairly promising new derivatives that were obtained suggest the possibility of greater success by using different parental materials.

To obtain a synthetic product that attains successful equilibrium between the disruptive effects of wide hybridization and the stabilizing effects of chromosomal balancing of the constituent genomes is a result which, from a statistical point of view, seldom occurs- We conclude, however, that the experimental evidence is clear that new synthetic combinations can be obtained through considerable effort, and that, theoretically at least, it should be possible to produce self-replicating derivatives with almost any recombination of characteristics of species that can be hybridized.

TABLE 23

THE MOST PROMISING HYBRID *Poa* LINES OBTAINED

| CIW Line Number | Species Combination | Generation Obtained |
|---|---|---|
| 4683-1 | *Poa ampla-pratensis* Albion-Lapland | $F_2$ |
| 4684-5 | *Poa ampla-pratensis* Albion-Lapland | $F_2$ |
| 13536-11 | *Poa ampla-pratensis* Albion-Lapland | $F_2$ |
| 5971-208 | *Poa ampla-pratensis* Albion-Mather | $F_2$ |
| 13775-202 | *Poa ampla-pratensis* Albion-Mather | F, |
| 13833-211 | *Poa ampla-pratensis* Albion-Mather | F] |
| 13783-33 | *Poa ampla-pratensis* Kahlotus-Athabasca | $F_2$ |
| 13783-208 | *Poa ampla-pratensis* Kahlotus-Athabasca | $F_2$ |
| 13783-301 | *Poa ampla-pratensis* Kahlotus-Athabasca | $F_2$ |
| 13783-507 | *Poa ampla-pratensis* Kahlotus-Athabasca | $F_2$ |
| 4694-8 | *Poa scabrella-pratensis* Las Posas-Athabasca | $F_3$ |
| 4711-3 | *Poa scabrella-pratensis* Las Posas-Mather | $F_3$ |
| 13548-10 | *Poa scabrella-pratensis* Las Posas-Leevining | $F_3$ |
| 4569-1 | *Poa scabrella-ampla* Las Posas-Kahlotus | F, |
| 6644 | *Poa ampla-pratensis* X *P. scabrella-pratensis* (quadruple hybrid) | F, |

TRANSGRESSIVE SEGREGATION. Earlier studies on diploid plant species-complexes composed of a wide range of ecotypes have demonstrated transgressive segregation in $F_2$ and later generations from crosses between contrasting forms. In *Potentilh glandulosa,* for example, with $2n = 14$ chromosomes, Fj hybrids between tall lowland and dwarf alpine and subalpine ecotypes yielded widely segregating $F_2$ and $F_3$ plants having characters transcending the differences between the parents. Not only morphological characters, such as length of leaves and stems, but also physiological responses, such as earliness of flowering and the capacity of cloned transplants to survive at the altitudinal field stations at Stanford, Mather, and Timberline, exceeded the limits of the parents (Clausen and Hiesey, 1958). Another diploid species-complex in the *Erythranthe* section of the genus *Mimulus* ($2n = 16$) includes ecological races differing strikingly both in morphological characters and in their responses when grown in different environments. When members of this species-complex, a scarlet-flowered lowland form of *Mimulus cardinalis* DougL, were crossed with a pale pink flowered subalpine form of *M. lewisii* Pursh., highly fertile $F_1$ hybrids were obtained whose $F_2$ and later-generation progeny displayed marked transgressive segregation (Hiesey, Nobs, and Björkman, 1971; Vickery, 1978).

In polyploid species-complexes composed of morphologically and ecologically diverse climatic races, transgressive segregation has also been shown. The *Achillea millefolium* complex of the *Cornpositae* consists of both tetraploid {*In* = 36) and hexaploid (*In* = 54) forms, which occur in widely divergent climates and are also clearly differentiated morphologically. A cross between a tetraploid dwarf subalpine form and a tall coastal ecotype yielded fully fertile Fj hybrids, which in the $F_2$ generation produced a striking array of segregants surpassing the expression of the parents in vigor and plant dimensions. Another cross on the hexaploid level between a subalpine dwarf originally from Kiska Island, Alaska, and a giant form from the San Joaquin Valley in central California yielded a fertile Fj hybrid whose progeny likewise transcended both parents. Cloned transplants of the parents and a sample of 300 $F_2$ progeny from this cross grown over a four-year period at Stanford, Mather, and Timberline displayed especially striking effects of transgression at the mid-altitude station at Mather, where neither of the parents were successful survivors whereas many of their $F_2$ offspring were outstandingly vigorous (Hiesey and Nobs, 1970).

In view of these results, the question arises whether transgressive segregation was expressed in the progeny of the highly polyploid forms of *Poa* used in the present investigations, a matter kindly brought to our attention by Professor Ledyard Stebbins. We feel that the available data do not provide a clear answer, although one might consider the performance of some of the apomictic lines at some of the test stations to support the suggestion. The sterility barriers between the parental lines preclude a satisfactory analysis, while the interaction of multiple sets of genomes coupled with a high degree of meiotic irregularity characteristic of the F, hybrids obtained further complicates the question. Under these circumstances, transgressive segregation could have been a factor but cannot be demonstrated.

RELEVANT EXAMPLES FROM THE LITERATURE. The reviews by Gustafsson (1946, 1947a, 1947b), Stebbins (1950, 1971), Grant (1971, 1975), and Dobzhansky, Ayala, Stebbins, and Valentine (1977), cover adequately the extensive literature relating to the biological structure of polyploid or agamic complexes, as known to date.

In the complex and polymorphic genus *Rubus,* Gustafsson (1943) concluded: "The blackberries have formed a special system of equilibrium characterized by two features: the disappearance of apomixis in hybridization and the recovery of apomixis in segregation." A parallel situation seems to have evolved in *Poa* except that, instead of an equilibrium at the tetraploid level, as in *Rubus,* many species of *Poa* equilibrate at a higher polyploid level. In taking issue with an early view expressed by Stebbins (1940) that apomixis is an "evolutionary dead end," Gustafsson (1942) pointed to the constant rejuvenation of cycles of sexuality alternating with apomixis, thereby maintaining a continuing process of evolution and natural selection of biotypes. A similar view was expressed by Clausen (1952, 1954, 1961) with respect to *Poa.*

In a later study by Gustafsson and Gadd (1965), reporting results from the effects on seeds of *Poa pratensis* of X-irradiation, which changed highly apomictic biotypes to partial or completely sexual forms, these authors suggested that such radiation experiments and also treatment with chemical mutagens open the possibility of producing new biotypes by such means. These methods may well be used in conjunction with crossing experiments in the development of agronomically useful plants. Sprague, Alexander, and Dudley (1980) mention the possible role of "genetic engineering" (including gene-splicing techniques) in crop improvement, but conclude that these newer developments can best be applied as an adjunct rather than a replacement for conventional plant breeding.

A remarkable example of biotypic differentiation in the polyploid grass species *Saccharum spontaneum* L., a tropical species whose center of distribution is in India, has been described by Panje (1970). When forms of this native polymorphic weed whose chromosome numbers (2M) range from 40 to 128 were crossed with commercial varieties of the cultivated sugar cane, *Saccharum officianarum,* success was obtained in synthesizing disease-resistant commercial varieties. Panje found the extreme and highly varied range of the numerous biotypes of *Saccharum spontaneum* at various levels of ploidy to be closely associated with a wide range of differences in natural local habitats, making this plant a highly successful and troublesome weed in tropical agriculture.

The extensive long-term cytogenetic and breeding studies conducted by Dr. fack Harlan and his associates in Oklahoma on members of the grass tribe *Andropogoncac* are of special interest in connection with our studies on *Poa.* Members of the *Andropogoneae* are naturally distributed in warm-tropical climates (Cclaricr and Harlan, 1955, 1957, 1958), whereas the species *Poa* are primarily confined to cool-temperature and cold climates (Harley, 1961). Both groups include species that have agronomic value as forage grasses, and both consist of widely polymorphic members whose species include polyploid agamic complexes displaying both facultative and obligate apomixis *(c(.* Celariar and Harlan, 1955; Harlan, de Wet, Richardson, and Chcda, 1961). The term "compilospecies" was proposed by Harlan and de Wet (1963) to describe the complex biosystematic relationships found in groups such as the *Bothriochloa-*

*Dichanthium* complex. The major objective of these investigations by the Oklahoma group was to develop new agronomic strains suitable for use in the southern Great Plains region of the United States. Many crossings involving combinations between different species were attempted, and, as in our studies on *Poa,* many were unsuccessful. Much was learned about the biosystematic relationships within the tribe *Andropogonme* but for the objective of obtaining new superior agronomic lines the overall results of the Oklahoma group's extensive investigations appear to be disappointing.

THE FUTURE OF PLANT BREEDING TECHNIQUES. The many successes of plant breeders throughout history in improving crop plants by standard crossing methods together with newer developments is well known. An aspect that we wish to emphasize is the importance of preserving native wild species everywhere in the world in their original native habitats, as a prime basic source of plant breeding materials.

Much has been written and much is being done, in establishing "gene banks" of key varieties of agricultural plants for breeding purposes, and such collections serve a vital role in ongoing studies with particular plant groups. We have seen, however, even within our short lifetimes, how quickly such collections can become genetically contaminated and deteriorate when brought together in a given environment. Natural selection is a continuing process that goes on everywhere, even in the most carefully maintained garden collections. The maintenance of such collections, even of a relatively specialized group of key forms, is, moreover, time-consuming and costly; as usually happens, even in the best institutions, changes in personnel bring new interests and new projects, and make it virtually impossible to maintain properly such "gene banks" over appreciable lengths of time. Much as we value the importance of adequate working collections of a variety of forms for experimental breeding work in a specific project, it seems apparent to us that the only really dependable gene sources are those preserved in the wild state, in the world's innumerable environmental niches where native vegetation has been relatively undisturbed. The genetic authenticity of such plant materials is thus essentially preserved through the continuing process of natural selection.

The preservation of wild areas in all kinds of environments in the world is of prime importance for the continued success of agricultural plant breeding—an activity that can never end as long as man depends on plants for food.

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