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Variability of Factors Influencing Stand Establishment in Green Needlegrass Populations from Western South Dakota

by

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A thesis submitted
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1980

Variability of Factors Influencing Stand Establishment in Green Needlegrass Populations from Western South Dakota

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable as meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Thesis Advisor   Date

Head, Plant Science Department   Date

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INTRODUCTION

In recent years, there has been an alarming conversion of rangeland to cropland in western South Dakota. More importantly, much of this increase in cropland has resulted in the plowing of large areas of land where the soils are unsuited or only marginally suited to continuous cultivation. During the period from 1967 to 1975, the extent of this trend represented a net increase of about 200,000 acres of Class VI soils and a net increase of about 300,000 acres of Class IV soils, which are used for the production of annual crops.[1]

Historically, such unwise expansions of cropland to land areas that are susceptable to severe wind and water erosion have ultimately resulted in costly and time consuming revegetation of these areas to perennial grasses. After the severe drought of the 1930's, crested wheatgrass *Agropyron desertorum* (Fisch.) Shult. was used almost exclusively to revegetate the eroded croplands in western South Dakota. Although crested wheatgrass is an introduced species with wide acceptance for use in early spring pastures, it was used for this purpose primarily because of its distinct ability to establish a stand quickly in a harsh environment. Attempts to use native species for revegetation of cropland in the 1930's met with very little success. Seed of native species was not readily available, and the seedling vigor of widely distributed natives such as green needlegrass (*Stipa viridula* Trin.) and western wheatgrass (*Agropyron smithii* Rydp.) was found to be

[1] Soil Conservation Service, U.S. Department of Agriculture. 1975. 1975 update of South Dakota conservation needs inventory. SCS Technical Service Center. Lincoln, Neb.

greatly inferior to that of crested wheatgrass.

The native grasses present an attractive solution to the prospective problem of having to convert large areas of eroding cropland to a perennial cover. Native grasses in rangeland offer versatility of use and stability of vegetative production over long periods of time. There appears to be a genuine need to explore the potential of some native species of grass, which are adapted to arid and semi-arid portions of the northern Great Plains states.

Green needlegrass (Stipa viridula Trin.) is a cool season native species, which is well adapted to semi-arid regions of the northern Great Plains. Where range condition is good or excellent in western South Dakota, green needlegrass is a dominant species on medium to fine-textured soils. As a mid-height species of grass, it is an important contributor to the total forage production of rangeland in western South Dakota.

As a highly self-pollinated species, green needlegrass has some advantages over cross-pollinated species for improvement through selection. Selection for superior characteristics is more rapid in selfed than in cross-pollinated species. Therefore, it is possible that natural selection within specific populations may occur at a relatively rapid rate (Iman and Allard, 1965).

The objective of this study was to evaluate the variability of factors influencing stand establishment of green needlegrass and to determine the potential for selecting an improved variety from collections made at seven sites (representing 6 ecotypes) in western South Dakota. Variation of mature plant characteristics was also studied to determine if seed and forage production could be improved through selection.

REVIEW OF LITERATURE

Agronomic Evaluations

Harlan (1962) and Keim and Newell (1962) have described the historical uses of the native grasses for revegetation in the Great Plains. Rogler (1960) and Schaaf and Rogler (1960) reported that green needlegrass (Stipa viridula Trin.) formed an important cool-season component of native ranges in the semi-arid regions of central North America, and emphasizsed that it had a number of valuable characteristics including good seedling vigor, high forage yield, good forage quality, and ability to recover after use. Kinch and Wiesner (1964) and Frank and Larson (1970) reported similar qualities for green needlegrass, and pointed out that it had good potential for the renovation of abused rangeland.

Newell (1968) pointed out that strains of native grasses have evolved in the natural vegetation and have persisted through recent fluctuations of climatic conditions attesting to their adaptability to stresses such as drought, heat, and cold and to their resistance of insect and disease damage. He also emphasized the importance of preserving the best of these germ pools of variation and gathering more information about their characteristics.

In semi-arid regions of central North America, climatic conditions favorable for seedling establishment are frequently of short duration. Plummer (1943) studied the germination and early seedling development of 12 range grasses and emphasized that these characteristics of range grasses were critical to successful establishment of reseeded stands. MeKell (1972) reported that grass species consistently showing a rapid germination rate, fast rates of root and top growth, and resistance to stress were often referred to as having seedling vigor. He also pointed out that under unfavorable environmental conditions, only those plants with a high degree of seedling vigor would survive and that most grass species did not have large seeds with the attendant advantages of extensive food reserves.

The relationship between seed size or weight to seedling vigor in grasses has been studied extensively. Kittoch and Patterson (1962) studied the emergence and growth rate of 10 species of dryland grasses and concluded that seed weight was more closely related to seedling vigor within species than between species or genera. They also concluded that the benefits of heavier seeds were largely confined to better emergence and were relatively short lived. They suggested that the spread of germination over a broad period could have little value for seedling survival, inferring that a rapid germination rate was particularly important to stand establishment. Major et al. (1960) pointed out that rapid germination was often a characteristic of weedy grasses that invade grass communities when a short period of favorable conditions occured. Rapid germination and emergence rates of larger seeds have been associated with superior stand establishment in switchgrass (Panicum virgatum L.) by Kneebone and Cremer (1955) and in Schismus grass (Schismus arabicus Nees) by Whalley et al.(1966). Plummer (1943) pointed out that the slow germination and emergence rates of western wheatgrass (Agropyron smithii Rydb.) and Stipa arida Jones were distinct disadvantages, and he suggestd that this was a primary cause of their reputation for difficult stand establishments. He also studied several other range grasses and concluded that early development of roots was directly related to success or failure of stand establishment in western ranges, and he pointed out that seed weight was generally correlated with early root growth. Davies (1967) compared strains of commonly used British grasses and reported that the heaviest seeded strains generally gave the best seedling establishment. Kneebone and Cremer (1955) reported the effect of seed size on seedling vigor in several warm season native grasses and concluded that the larger seeds of a species produced more vigorous seedlings and better assurance of a stand than the smaller seeds. Whalley et al. (1966) studied the early nonphotosynthetic stage of seedling growth in grasses and concluded that the heavier seeds of a species not only produced faster growing seedlings than did smaller seeds but the heavier seeds kept growing longer. Rogler (1954) found that seed size in crested wheatgrass (Standard, Agropyron desertorum (Fisch.) Schult.) was positively associated with the size of seedlings and the rate of emergence at planting depths greater than 1 inch and suggested that the major causes of establishment failures of crested wheatgrass could be attributed to the inability of seedlings to penetrate the soil surface. Lawrence (1963) compared lines of Russian wild ryegrass (Elymus junceus Fisch.) and reported that seed weight was positively associated with emergence from planting depths greater than 1 inch. Kalton et al. (1959) studied the effect of seed size on emergence in smooth bromegrass (Bromus inermis Leyss.) and other forage species and concluded that the difference in seedling emergence between large and small seeds increased with an increase in seeding depth.

In some range grasses, seed dormancy remains high for a number of years after seed harvest and can have a significant effect on stand establishment. McAlister (1943), McWilliams (1950), Schaaf and Rogler (1960), and Rogler (1960) reported prolonged dormancy in seeds of green needlegrass (*Stipa viridula* Trin). Dawson and Heinrichs (1952) and Frank and Larson (1970) reported that two types of dormancy were evident in green needlegrass: physiological, which was largely overcome by prechilling moistened seeds before germination; and mechanical, which was largely overcome by removal of the lemma and palea and scarification of the seed coat. Rogler (1960) studied the effect of age on seed dormancy in green needlegrass and concluded that dormancy gradually decreased over a period of seven years. He also pointed out that seedling emergence from newly harvested seed was generally poor, unless planting was done in late fall and seed was allowed to overwinter in the soil before germination. Schaaf and Rogler (1960) reported that much of the seed dormancy in green needlegrass was the result of an indeterminate development of inflorescences accompanied by shattering of mature seeds before harvest and that the immature seeds from the lower panicle branches exhibited a high degree of dormancy and poor seedling emergence in greenhouse tests. Kinch and Wiesner (1964) found the average germination percentage of freshly harvested seed was 15.5% compared to an average viabilty of 82.1% for 15 hand-harvested samples of green needlegrass seed. Kinch and Wiesner (1963) reported that the immature seeds of green needlegrass were lower in viability than mature seeds and exhibited an average viability of only 22% for 31 commercial lots of seed.

They also pointed out that seed lots containing many immature seeds were generally of low seed weight, purity, and viability.

Breeding for Increased Seedling Vigor

Johnson and Rogler (1943) found that green needlegrass was highly self-pollinated and suggested that reproduction was sexual and essentially cleistogamous. Schaaf and Rogler (1960) studied variation among individual green needlegrass plants for germination of freshly harvested seeds from 1950 to 1959. They concluded that low dormancy in green needlegrass was a heritable trait and that varieties with low post-harvest dormancy could be developed. Schaaf and Rogler (1970) indicated that 'Lodorm' green needlegrass, released in 1969, had been selected for low post-harvest dormancy and that it was characterized by quicker seed germination than 'Green Stipagrass', a variety of green needlegrass released in 1946. They also indicated that Lodorm seed was slightly smaller than that of 'Green Stipagrass', but the varieties were otherwise indistinguishable on the basis of morphological characteristics.

Although there was no indication in the literature that green needlegrass had been selected for increased seed weight, several authors suggested that selection for larger or heavier seeds in many grass species would result in increased seedling vigor (Kneebone and Cremer, 1955; Rogler, 1954; Tossell, 1960; Trupp and Carlson, 1971; and Kneebone, 1972). Seed size was found to be highly heritable in many grass species. Wherever progenies have been tested, combinations of high seed weight parents have given progency with higher seed weights than combinations of low seed weight parents (Kneebone, 1972).

Seed size was not only correlated with seedling vigor in many grass species but it was positively correlated with some other desirable mature plant traits (Kneebone, 1972). Christie and Kalton (1960) found significant positive correlations between seed weight and seed yield per plant, leaf width, and vigor in smooth bromegrass (Bromus inermis Leyss.) Kneebone (1956) found that sand bluestem (Andropogon hallii Hack.) progenies grown from large seeds tended to be more vigorous throughout the first season of growth, as well as in the early seedling stages. Lawrence (1963) found highly significant correlations between seed size and seed yield in Russian wildrye (Elymus junceus Fisch.).

MATERIALS AND METHODS

Germ Plasm Collections

In the summer of 1976, seed was collected from at least six distinctively different environments in western South Dakota. These environments or ecosystems are characterized by the range site descriptions given in Table 1. Figure 1 gives the locations of all sites, as well as a range site designation for each. Sites 1, 3, 5, 6, and 7 had never been disturbed by cultivation and were subject to very low grazing pressure because of their isolation from grazing animals. Sites 2 and 4 were areas that had been cropland in the distant past, but they had returned to a complex of native species at the time of collection. Both sites appeared to be subject to low grazing pressure and infrequent clipping of forage.

At each of the seven sites, seed from 50 randomly selected individual plants, as well as bulk seed, was collected. Individual plants were selected by walking an approximate transect across the site and taking seed from the nearest plant at every second step. If the stand density at the site was not sufficient to collect seed from 50 individual plants with one transect, a second approximate transect was made across the site perpendicular to the first. Stand densities varied to some extent, but all sites produced heavy yields of seeds. Sites varied in size from 30 to 50 square meters, but each site appeared quite uniform for plant height, seed production, and plant vigor. Table 2 presents measurements made at each site including the percent of slope, the

Table 1. Brief descriptions of range sites.†

Range Site	Description
Thin Upland	This site includes steep uplands having thin soils developed in calcareous materials. The principal plants in the original vegetation were: needleandthread, western wheatgrass, blue grama, plains muhly, and threadleaf sedge. Dotted gayfeather is an important forb on this site.
Clayey	This site includes deep soils that have a silt loam to clay surface and silty clay to clay subsoil. Permeability is moderate to slow. The principal plants in the original vegetation were: green needlegrass, western wheatgrass, and an understory of shortgrasses.
Overflow	This site regularly receives additional moisture from adjacent slopes or stream overflow. The principal plants in the original vegetation were: western wheatgrass, green needlegrass, Canada wildrye, big bluestem, and perennial forbs. In a few places trees or shrubs are significant.
Silty	This site includes deep or moderately deep soils that have a very fine sandy loam to silty clay loam surface and subsoil. The principal plants in the original vegetation were: western wheatgrass, green needlegrass, needleandthread, and blue grama.
Shallow	This site includes soils underlain at depths of 10-20 inches by impervious materials which reduce the water-holding capacity. Principal plants in the original vegetation were: little bluestem, sideoats grama and needleandthread. Forbs, such as black samson, and woody plants, such as leadplant and rose, are of common occurrence.
Sandy	This site includes deep, well drained soils that have a sandy loam or fine sandy loam surface that grades into sandy loam or sand in the subsoil. Principal plants in the original vegetation were: little bluestem, prairie sandreed, sand bluestem, western wheatgrass, and needleandthread.

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†Soil Conservation Service, U.S. Department of Agriculture. 1967. Technical guide for western South Dakota, land resource areas 58 and 60. SCS Technical Service Center. Lincoln, Neb.

Legend:

Site	Range site
1	thin upland
2	clayey
3, 5	overflow
4	silty
6	shallow
7	sandy

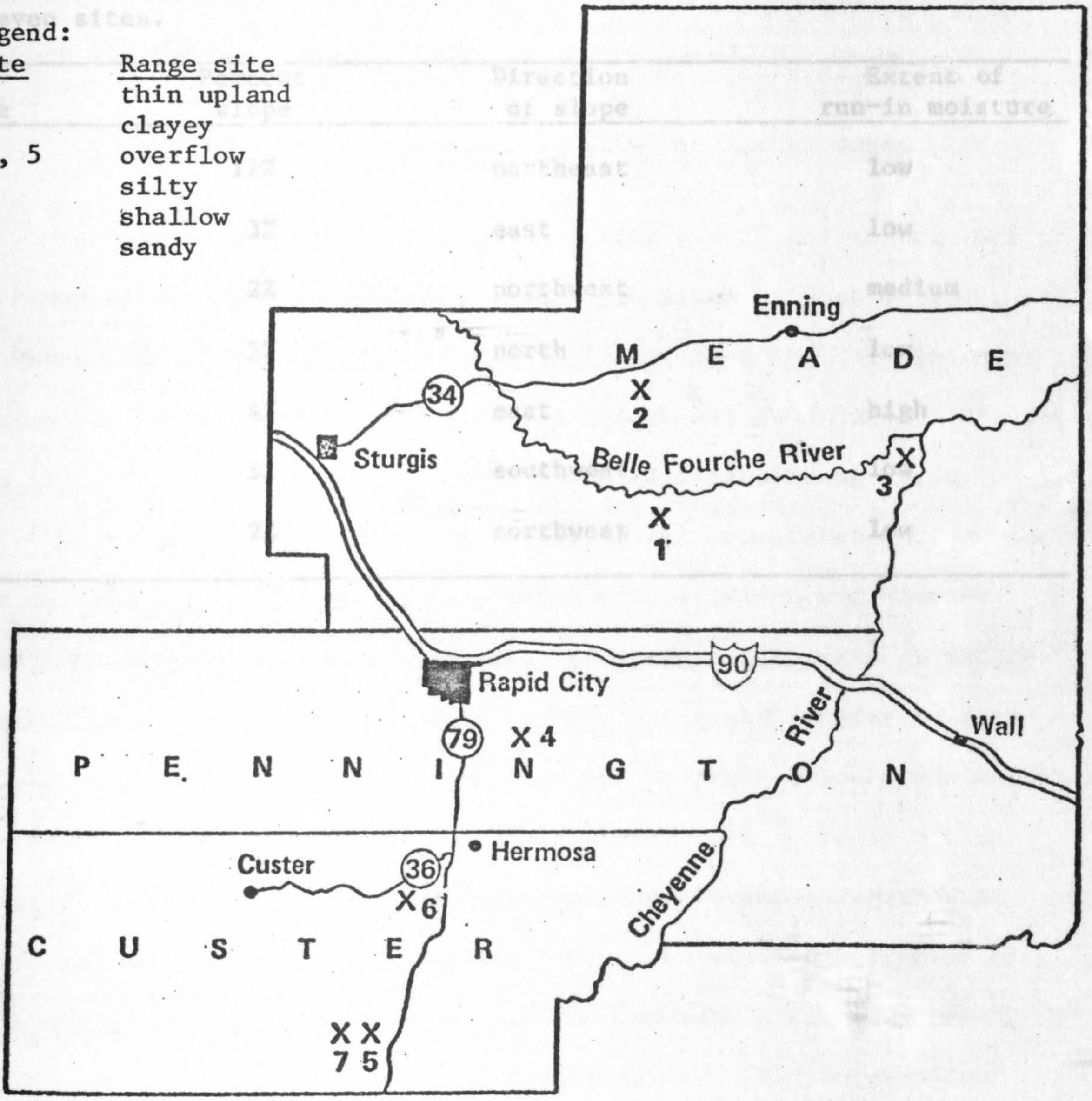

Figure 1. Locations and range site designations of the seven sites, where green needlegrass seed was collected for this study.

Table 2. Measurements of environmental conditions made at each of the seven sites.

Site	Percent slope	Direction of slope	Extent of run-in moisture
1	17%	northeast	low
2	3%	east	low
3	2%	northwest	medium
4	2%	north	low
5	4%	east	high
6	5%	southwest	low
7	2%	northwest	low

direction of slope, and a subjective estimate of the extent of run-in moisture available to the plants.

Seed and Seedling Growth Measurements on Mature Seeds

Laboratory studies of seed and seedling growth characteristics of the seven sites of green needlegrass were conducted between October, 1976 and March, 1977. The objectives were to investigate the relationship between seed weight and initial seedling growth and to determine if there were significant differences in these characteristics among sites.

In these laboratory studies, measurements were taken only on the dark colored seeds from each of the seven sites. Kinch and Wiesner (1963) described the dark colored seeds of green needlegrass as mature seeds. Subsequently, in this study, mature seeds shall refer to dark colored seeds and immature seeds shall refer to light colored seeds. An indeterminate maturation of inflorescences was found to cause a high degree of dormancy, and poor seedling emergence in immature seeds of green needlegrass (Schaaf and Rogler, 1966). In addition, studies by Kinch and Wiesner (1963) suggestd that the immature seeds of green needlegrass contained less than 25% viable seeds. This information indicated that the immature seeds from the seven sites would contribute very little to stand establishment in the field, and therefore, were omitted from the laboratory studies. Characteristics measured included the weight of individual seeds, their speed of germination, and the rates of growth of the resulting seedlings within one week after germination.

Two seeds were taken from each of 30 randomly selected individual plant collections within each of the seven sites. One of these two seeds was left intact with lemma and palea attached, while the lemma and palea were removed with forceps from the other seed. Subsequently, in this study, intact seeds shall refer to those with lemmas and paleas attached, and dehulled seeds shall refer to those with lemmas and paleas removed. The removal of lemmas and paleas from half of the seeds assisted in breaking dormancy so that a larger number of seedling growth measurements could be obtained.

Dehulled seeds were weighed individually on an analytical balance to the nearest ten-thousandth of a gram, treated with a fungicide, and placed on blotters moistened with distilled water inside plastic germination boxes. The seeds were placed in a randomized design within the boxes, and identification was maintained by a numbering system along the side of several plastic dividers within each box. Opaque boxes were used in the experiment to prevent the influence of light. All seeds were subjected to a 2-week prechill of 2-4 C constant temperature in order to assist breaking dormancy. Next, the seeds were placed in a germination chamber with alternating temperatures of 16 hours at 15 C and 8 hours at 30 C. Germinations of seeds were recorded every day in each of the boxes from October 18 to November 17, 1976. Seven days after germination of each seed, the root and shoot lengths of the resulting seedling were measured to the nearest millimeter. Seedlings were removed from the germination boxes prior to measurement to prevent prolonged light exposure to the remaining seedlings and evaporation of moisture from the boxes. To prevent moisture differences within boxes, blotters were moistened with distilled water every 3 to 4 days. Intact seeds were treated exactly the same as dehulled seeds, but because of space limitations, they were germinated at different times. Differences among site means in the number of days to germination, shoot length, and root length were tested at the 5% probability level by Duncan's Multiple Range Test. Correlations between characters measured and significance levels of correlations were obtained with the use of an electronic computer.

Field Tests of Stand Establishment Capability

Another part of this study involved field testing for potential stand establishment differences among sites. For this purpose, field collected seed was increased under uniform environmental conditions; bulked seed collected from each site was planted with three standard varieties in a randomized complete block design at Brookings, South Dakota, in April, 1977. All plots were irrigated three times in the summer of 1977 and 1978 with applications of 1 inch of water per irrigation. In July, 1978, seed was harvested from the increase planting, and the seed from five replications was bulked for each entry before testing. Bulking of seed for each entry was done in order to facilitate laboratory and field testing. Four to five subsamples of 100 seeds were taken at random from each entry and tested for percentage germination, germination rate, and ratio of mature to immature seeds. Differences among site means for each of these measurements were tested at the 5% probability level by Duncan's Multiple Range Test.

Field establishment tests were planted at three locations: Brookings, South Dakota; Bismark, North Dakota; and Highmore, South

Dakota. All tests were seeded with a four-row plot seeder equipped with double disk furrow openers and depth bands. Plots at all three locations were arranged in a randomized complete block design. Every plot was planted with 10 grams germinable seed. All plots were 4 feet by 21 feet in size.

The Brookings and Bismarck tests were planted on fallowed land in late August, 1978, and irrigated twice within the next 3 weeks with applications of 1/2 inch of water. This was intended only to simulate normal rainfall during the germination period. In late October, 1978, stand density and seedling height were measured at both Brookings and Bismarck. Measurements were taken on three randomly selected subsamples of 1 linear foot from the two center rows of each plot. All measurements were taken the same day on all plots within each test.

In August of 1979, the total forage 3 inches above the ground was harvested from the two center rows of all plots in the test at Brookings. A flail-type harvester was used to collect the forage. The total wet-weight of forage from each plot was measured in the field, and a sample of 200-300 grams was taken into the laboratory to determine the moisture content. Tons of dry matter per acre were calculated for each plot.

In August of 1979, plant height measurements were made in the test at Bismarck. Single-plant measurements were made at 2 foot intervals along the two center rows of each plot. Stand density was not measured, because it was impossible to distinguish between individual plants.

The field test at Highmore was planted in small grain stubble during the first few days in November, 1978. No seedbed preparation was made, and no water or fertilizer were applied to this test, either after seeding or during 1979. In August, 1979, stand density was measured by counting the live seedlings in two randomly selected subsamples of 2 linear feet from the two center rows of each plot. Seedling height measurements were not taken, because the entire test had been clipped off at a height of 4 inches above the ground in July, 1979, to control a very dense population of annual weeds.

Differences among site means in seedling counts, seedling heights, forage yield, and plant heights were tested at the 5% probability level by Duncan's Multiple Range Test.

Variation and Heritability of Mature Plant Characteristics

Variation of mature plant characteristics within and among sites were studied in order to determine if selection for improved forage and seed production would be possible. During February, 1977, seeds from the individual plant collections within each of the seven sites were planted in plant bands in the greenhouse. Five progeny from each of the 350 individual plant collections were transplanted into a space-planted nursery at Brookings in May, 1977. The five progeny of each individual plant collection were considered a family. Each site was assigned at random to an experimental unit; families were nested within sites, and the progeny of each family were randomized in five replications. All plants were spaced 40 inches apart in all directions in order to facilitate cultivation.

Plant mortality within the nursery was extensive during the summer of 1977, due to a combination of rabbit damage and dry weather conditions soon after transplanting. Only enough plants remained alive through 1978 and 1979 to take measurements on three progeny per family and a range of 8-22 families per site.

A total of 333 individual plants were used for analysis. Subjective measurements that were made on each plant included vigor, leafiness, inflorescence production, and seed retention. A rating scale of one to five was used, giving superior plants the lowest number ratings and inferior plants the highest number ratings (Ross et al., 1975). Objective measurements made on each plant included plant height at anthesis, total clean seed weight from 10 heads, and the weight of 100 mature seeds.

Variance components used in calculating proportions of the total phenotypic variation associated with sites, families within sites, and progeny within families within sites were obtained from a hierarchal analysis of variance (Kempthorne, 1957) as follows:

Source	Degrees of freedom	Parameters estimated
Total	sfp-1	
Sites	s-1	$\sigma_e^2 + p\sigma_f^2 + pf\sigma_s^2$
Families within sites	s(f-1)	$\sigma_e^2 + p\sigma_f^2$
Progeny within families within sites	sf(p-1)	σ_e^2

The letter s denotes the number of sites; f, the number of families within sites; p, the number of progeny in each family.

Between and within family variance components were obtained from the analysis of variance of individual sites as follows:

Source	Degrees of freedom	Parameters estimated
Total	fr-1	
Replicates (R)	r-1	
Families (F)	f-1	$\sigma_e^2 + \sigma_f^2$
F * R	(f-1) (r-1)	σ_e^2

The letter f denots the number of families; r, the number of replicates.

Broad sense heritability estimates for each character were calculated using between and within family variance components as follows:

$$H = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_e^2}$$

The standard error of the broad sense heritability estimate was determined after Becker (1975) as follows: $\text{S.E. (H)} = \sqrt{\frac{2(1-H)^2\ [1 + (K-1)H]^2}{K(K-1)\ (F-1)}}$

where, K = number of measurements/family and F = number of families.

RESULTS AND DISCUSSION

Seed and Seedling Growth Measurements on Mature Seeds

Tables 3 and 4 present the means and ranges of measurements made on intact and dehulled seeds respectively. Analysis of variance tables 3A and 4A are presented in the appendix for measurements shown in Tables 3 and 4 respectively. Differences in seed weight among sites were significant for both intact and dehulled seeds. Although there were some differences in the ranking of sites between the two types of seeds, sites 1, 4, and 5 consistently had the three highest seed weights. Site 4 had the highest seed weight for both seed types and was significantly different from all other sites, except site 5 for intact seeds. Site 5 had the second highest seed weight for both seed types and was significantly different from sites 2 and 3 for intact seeds and from site 2 for dehulled seeds. Site 1 had the third highest seed weight for both seed types and was significantly different from sites 2 and 3 for intact seeds. Differences in the ranking of sites by seed weight between intact and dehulled seeds indicated that the proportion of seed weight due to lemma and palea was larger for some sites than others.

Differences in the number of days to germination among sites were significant for dehulled but not for intact seeds. For dehulled seeds, site 4 had the lowest number of days to germination and was significantly different from sites 1, 2, and 5. There were considerable differences in the ranking of sites between the two seed types, because of large differences in germination percentage and rate between them. Within the 21-day germination period 57% of all intact seeds germinated with a mean

Table 3. Means and ranges of seed and seedling measurements on intact†, mature seeds from the seven sites.

Entry	Number of observations	Seed weight		Days to germination		Shoot length at 7 days growth		Root length at 7 days growth	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
		mg/seed		days/germination		mm/shoot		mm/root	
Site 1	15	4.19 b*	22-58	4.87 a*	2-17	46.80 a*	13-65	40.00 a*	16-64
Site 2	15	3.47 c	19-51	9.33 a	2-18	40.07 a	24-54	22.60 bc	7-40
Site 3	15	3.51 c	24-48	5.27 a	2-10	47.80 a	21-68	28.47 abc	13-57
Site 4	15	4.97 a	36-62	6.87 a	2-18	44.13 a	31-58	30.47 ab	5-58
Site 5	15	4.47 ab	34-54	6.53 a	1-19	49.40 a	16-68	35.60 a	12-61
Site 6	15	3.82 bc	20-50	4.73 a	2-12	44.27 a	26-61	18.13 c	8-38
Site 7	15	3.83 bc	25-51	6.60 a	2-16	40.67 a	17-61	19.80 bc	9-52

*Means within a column of the table not followed by the same letter or letters are significantly different at P = 0.05 probability level by Duncan's Multiple Range Test.

†Lemmas and paleas were attached.

Table 4. Means and ranges of seed and seedling measurements on dehulled†, mature seeds from the seven sites.

Entry	Number of observations	Seed weight		Days to germination		Shoot length at 7 days growth		Root length at 7 days growth	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
		mg/seed		days/germination		mm/shoot		mm/root	
Site 1	28	3.04 bc*	16-43	1.89 a*	1-2	37.71 ab*	10-61	27.57 bc*	12-53
Site 2	26	2.67 c	16-42	1.89 a	1-2	38.35 ab	3-57	23.50 c	11-39
Site 3	28	2.92 bc	17-41	1.43 ab	1-2	42.86 ab	12-55	26.46 bc	20-43
Site 4	29	3.68 a	24-48	1.24 b	1-2	35.79 b	12-51	31.00 ab	7-50
Site 5	25	3.11 b	21-39	1.88 a	1-2	38.60 ab	7-62	34.76 a	21-58
Site 6	28	2.88 bc	18-38	1.68 ab	1-2	45.75 a	17-68	27.68 bc	12-45
Site 7	29	2.85 bc	12-38	1.38 ab	1-2	38.03 ab	10-59	26.55 bc	8-42

*Means within a column of the table not followed by the same letter or letters are significantly different at P = 0.05 probability level by Duncan's Multiple Range Test.

†Lemmas and paleas were removed.

of 6.3 days to germination, while 90% of all dehulled seeds germinated with a mean of 1.6 days to germination. Results indicated that a major portion of seed dormancy was removed with the removal of lemmas and paleas.

Differences in shoot length at 7 days growth among sites were also significant for dehulled but not for intact seeds. For dehulled seeds, site 6 had the longest shoot length and was significantly different from site 4. There were considerable differences in the ranking of sites between seed types. Results seemed to indicate that some sites were affected more than others by the removal of the lemmas and paleas.

Differences in root length measured at 7 days growth among sites were significant for both intact and dehulled seeds. Although there were some changes in the ranking of sites between seed types, sites 4 and 5 had root lengths among the three longest for both seed types. Site 1 had the longest root length for intact seeds and was significantly different from sites 2, 6, and 7. Site 5 had the longest root length for dehulled seeds and was significantly different from all other sites, except site 4.

It was noted that both seed types showed significant differences among sites only in seed weight and root length. Significant differences among sites in days to germination and shoot length were found only in dehulled seeds. Although this may have resulted partially from a larger number of observations taken on dehulled seeds, there was some evidence that it resulted from physiological changes within seeds after the removal of lemmas and paleas. Not only were sites affected differently, as shown by the differences in ranking of sites between seed types, but the removal of lemmas and paleas had an undesirable effect on shoot and root lengths of seedlings. Site means for shoot and root lengths were generally lower for dehulled seeds than for intact seeds.

Linear correlations between all measurements for both seed types are shown combined across sites in Table 5 and within sites in Table 6. For both seed types, combined across sites, there was a significant correlation of -0.25 between seed weight and days to germination. This indicated that heavier seeds of both types tended to germinate more rapidly than lighter weight seeds. The same relationship was fairly consistent within sites as well, since only sites 6 and 7 failed to show a significant negative correlation for either seed type.

For intact and dehulled seeds, combined across sites, significant correlations of 0.203 and 0.218 respectively were found between seed weight and root length. This indicated that heavier seeds of both types tended to produce longer roots. However, correlations within sites were not consistently positive for either seed type, and significance was found only in site 6 for dehulled seeds. This and previous correlations seemed to indicate that seed weight was not as closely associated with root length as it was with germination rate within most sites.

For intact and dehulled seeds, combined across sites, correlations of 0.409 and 0.108 respectively were found between seed weight and shoot length. The correlation for intact seeds was highly significant but was not significant for dehulled seeds. Therefore, heavier intact seeds tended to produce longer shoots than lighter weight intact seeds. Correlations within sites were fairly consistent and showed the same

Table 5. Correlations between seed and seedling measurements for intact† and dehulled‡ seeds, combined over all seven sites.

Character	Mature Seed weight	Number of days to germination	Shoot length at 7 days growth	Root length at 7 days growth
			Intact seeds	
Mature seed weight		− 0.250*	0.409**	0.203*
Number of days to germination	− 0.254*		− 0.431**	− 0.086
Shoot length at 7 days growth	0.108	0.053		0.244*
Root length at 7 days growth	0.218*	− 0.011	0.022	
		Dehulled seeds		

*P<.05. **P<.01.

†Lemmas and paleas attached.

‡Lemmas and paleas removed.

Table 6. Correlations between seed and seedling measurements on intact† and dehulled‡ seeds within each of the seven sites.

Measurement		# days to germination				Shoot length at 7 days growth				Root length at 7 days growth			
		Intact		Dehulled		Intact		Dehulled		Intact		Dehulled	
	Site	# Obs.	Corr.	# Obs.	Corr.	# Obs.	Corr.	# Obs.	Corr.	# Obs.	Corr.	# Obs.	Corr.
Seed weight	1	15	- 0.597*	28	- 0.420*	15	0.451	28	- 0.064	15	0.249	28	0.086
	2	15	- 0.717**	26	- 0.367*	15	0.559*	26	0.340	15	- 0.073	26	- 0.245
	3	15	- 0.575*	28	- 0.129	15	0.651**	28	0.368*	15	0.227	28	0.183
	4	15	- 0.529*	29	0.120	15	0.597*	29	0.425*	15	- 0.119	29	0.048
	5	15	0.214	25	- 0.564**	15	- 0.035	25	- 0.410*	15	- 0.099	25	0.271
	6	5	- 0.127	28	0.190	15	0.525*	28	0.555**	15	0.263	28	0.486**
	7	15	0.021	29	- 0.062	15	0.536*	29	0.098	15	0.155	29	0.268
# days to germination	1					15	- 0.699**	28	0.148	15	- 0.511*	28	0.101
	2					15	- 0.493*	26	- 0.140	15	0.279	26	0.024
	3					15	- 0.411	28	- 0.377*	15	0.108	28	0.031
	4					15	- 0.351	29	0.087	15	- 0.092	29	- 0.063
	5					15	- 0.580*	25	0.302	15	- 0.462	25	- 0.238
	6					15	- 0.301	28	0.101	15	0.102	28	- 0.012
	7					15	- 0.085	29	- 0.185	15	0.612**	29	0.205
Shoot length at 7 days	1									15	0.432	28	0.321
	2									15	0.003	26	- 0.336
	3									15	0.185	28	- 0.245
	4									15	0.199	29	- 0.033
	5									15	0.380	25	- 0.170
	6									15	0.090	28	0.498**
	7									15	0.189	29	0.120

*P<.05. **P<.01.

†Lemmas and paleas attached.

‡Lemmas and paleas removed.

relationship between measurements; only sites 1 and 5 failed to show a significant positive correlation between seed weight and shoot length for either seed type. The removal of lemmas and paleas had the effect of reducing the overall correlation between seed weight and shoot length. The negative correlation within site 5 for dehulled seeds was also responsible for this low correlation.

For intact seeds, combined across sites, a correlation of -0.431 between days to germination and shoot length was highly significant. This indicated that faster germinating intact seeds also tended to have longer shoots. For dehulled seeds, combined across sites, the correlation between these two measurements was near zero. Correlations within sites were consistently negative for intact seeds, but they were very inconsistent for dehulled seeds, in which case four sites showed positive correlations. The removal of lemmas and paleas had the effect of decreasing initial growth of shoots within most sites.

Although none of the correlations found in this study were particularly high, the results indicated that seed weight was positively associated with germination rate, initial shoot growth, and initial root growth. Since these characteristics have been associated with seedling vigor (McKell, 1972), it seemed likely that their combined effects on stand establishment would give heavier seeds of this species a better chance of producing a stand under most environmental conditions.

The effect of removing lemmas and paleas from seeds was considerable. Correlations between measurements were reduced significantly in some instances, and in others the sign of the correlation was changed. Frank and Larson (1960) pointed out that part of seed dormancy in green needlegrass was caused by the mechanical barrier of the lemmas and paleas to water and part was caused by a physiological condition of the seeds. In this study, the removal of lemmas and paleas had the effect of increasing germination rate but decreasing the growth rates of shoots and roots. This may have resulted from an injury to the embryos and possibly a subsequent release of growth inhibitors. From these results, it was apparent that measurements on dehulled seeds were less reliable than those on intact seeds as indicators of the potential for improvement of seedling vigor. Therefore, measurements on intact seeds were used exclusively for comparisons of laboratory data with field test results.

It is important to note that laboratory studies on mature seeds from the seven sites were made on seeds collected in the field and that the influence of environment on seed development, seed weight, and seedling growth may have been greater in some sites than in others. If results were biased by this, correlations between measurements should have been biased downward by greater variability in the physiological condition of seeds. However a comparison of site means should take into consideration the possibility that some sites may have benefited from better environmental conditions. Before proceeding with field tests it seemed appropriate to produce seed for all seven sites under uniform environmental conditions.

Measurements on Bulk Seed, After Increase Under Uniform Conditions

Laboratory and field measurements made on seed of the seven sites and three standard varieties grown under uniform environmental conditions are shown in Tables 7-9. Analysis of variance tables 7A-9A are presented in the appendix for these measurements.

The three standard varieties Lodorm, Green Stipagrass, and SD 93 were included in order to determine if any of the seven sites had potential advantages for stand establishment over commonly used varieties.

Seed yields and ratios of mature to immature seed are given in Table 7. Differences among entries for seed yield, were not significant. Although the immature seeds of green needlegrass were found to be largely dormant (Schaaf and Rogler, 1960) and to contain very few viable seeds (Kinch and Wiesner, 1963), a measure of proportion of immature seeds was taken in order to determine if it had any effect on field establishment. Site 6 and Green Stipagrass had the highest ratios and were significantly different from all other entries, except site 3. Lodorm had the lowest ratio and was significantly different from all other entries, except sites 1, 4, and 5. Site 3 had a ratio significantly higher than sites 1, 4, and 5. An attempt was made to remove the immature seeds from mature seeds before field testing, but mechanical separation proved impractical, because immature seeds often could not be distinguished by weight or size.

Differences among entries in germination percentage, which is a measure of dormancy, are shown in Table 8. Lodorm had the highest germination and was significantly different from all other entries, except Green Stipagrass. Green Stipagrass had the second highest germination and was significantly different from sites 1, 2, and 5. Among sites, no

Table 7. Means and ranges of seed yield and the ratio of mature to immature seeds for all entries of green needlegrass in a seed increase planting at Brookings, South Dakota.

Entry	Seed yield		Ratio of mature to immature seeds	
	Mean	Range	Mean	Range
	grams/plot		# mature seeds/# immature seeds	
Site 1	258a*	121-141	0.89 cd*	0.53-1.25
Site 2	209a	160-279	1.12 bc	1.03-1.58
Site 3	234a	95-403	1.43ab	0.95-2.23
Site 4	208a	125-280	0.94 cd	0.61-1.52
Site 5	203a	100-355	0.87 cd	0.61-1.03
Site 6	193a	146-245	1.68a	1.16-2.00
Site 7	189a	111-239	1.18 bc	0.92-1.35
Lodorm	199a	109-288	0.67 d	0.53-0.83
G. Stipa†	246a	130-382	1.66a	1.10-2.39
SD93	173a	121-231	1.10 bc	0.98-1.33

*Means within a column of the table not followed by the same letter or letters are significantly different at P = .05 probability level by Duncan's Multiple Range Test.

†Green Stipagrass, a variety released in 1946.

Table 8. Means and ranges of percent germination and germination rate for all entries of green needlegrass in a seed increase planting at Brookings, South Dakota.

Entry	Percent germination		Germination rate	
	Mean	Range	Mean	Range
	# germinations/100 seeds		# germinations/day	
Site 1	15.25 c*	10-26	6.41a*	5.56-7.14
Site 2	17.00 c	5-26	6.86a	6.32-7.71
Site 3	28.00 bc	16-41	7.12a	6.10-8.06
Site 4	21.75 bc	6.37	7.08a	6.40-7.94
Site 5	14.50 c	4-33	6.95a	5.84-8.93
Site 6	26.75 bc	15-44	7.11a	6.51-7.48
Site 7	24.50 bc	9-40	7.27a	6.25-7.86
Lodorm	55.75a	37-71	7.74a	6.63-8.75
G. Stipa†	41.75ab	14-70	7.52a	6.12-8.72
SD93	32.50 bc	22-47	7.45a	6.71-8.21

*Means within a column of the table not followed by the same letter or letters are significantly different at P = .05 probabilty level by Duncan's Multiple Range Test.

†Green Stipagrass, a variety released in 1946.

significant differences were found. The results of germination percentage tests were used to adjust the total germinable seed for each entry in field tests to ten grams per plot.

Germination rate (Table 8) of entries was calculated for non-dormant seeds only. Dormant seeds of green needlegrass become germinable only gradually over a period of several years (Rogler, 1960) and therefore, they were not expected to contribute significantly to field establishment during the relatively short period of this study. A modification of the formula proposed by Maguire (1968) for germination rate (G. R.) was used as follows:

$$\text{G.R.} = \frac{\begin{array}{c}\text{\% of Total}\\ \text{Normal Seedlings}\\ \underline{\text{from start to 1st}}\end{array}}{\text{Days to 1st Count}} + \frac{\begin{array}{c}\text{\% of Total}\\ \text{Normal Seedlings}\\ \underline{\text{from 1st to 2nd}}\end{array}}{\text{Days to 2nd Count}} + \frac{\begin{array}{c}\text{\% of Total}\\ \text{Normal Seedlings}\\ \underline{\text{from 2nd to final}}\end{array}}{\text{Days to Final Count}}$$

No significant differences in germination rate among entries were found.

Mature and bulk seed weights for entries are shown in Table 9. Sites 1 and 4 had significantly higher mature seed weights than all other entries. Sites 2, 3, and 5, as well as SD 93, had significantly higher mature seed weights than sites 6 and 7, Lodorm, and Green Stipagrass. Site 7 had a significantly higher mature seed weight than site 6, Lodorm, and Green Stipagrass. Differences in bulk seed weights among entries were also significant. Sites 3 and 4 had the highest bulk seed weights and were significantly different from site 7, Lodorm, and Green Stipagrass.

Results of seed weight measurements indicated that fewer differeces among entries could be found for bulk seed compared to mature seed. Some differences occurred in the ranking of entries between

Table 9. Means and ranges of mature seed† weight and bulk seed‡ weight for all entries of green needlegrass in a seed increase planting at Brookings, South Dakota.

Entry	Mature seed weight		Bulk seed weight	
	Mean	Range	Mean	Range
	grams/100 seeds		grams/100 seeds	
Site 1	0.418a*	0.41-0.43	0.302abc*	0.25-0.31
Site 2	0.375 b	0.37-0.38	0.302abc	0.27-0.32
Site 3	0.385 b	0.38-0.40	0.316ab	0.29-0.37
Site 4	0.423a	0.42-0.43	0.328a	0.31-0.35
Site 5	0.383 b	0.38-0.39	0.294abc	0.28-0.31
Site 6	0.338 d	0.33-0.34	0.294abc	0.26-0.32
Site 7	0.358 c	0.35-0.36	0.270 c	0.24-0.30
Lodorm	0.338 d	0.33-0.34	0.278 c	0.26-0.30
G. Stipa§	0.338 d	0.32-0.35	0.272 c	0.25-0.30
SD93	0.378 b	0.37-0.38	0.292 bc	0.25-0.31

*Means within a column of the table not followed by the same letter or letters are significantly different at P = .05 probability level by Duncan's Multiple Range Test.

†Dark colored seeds only.

‡Including both mature and immature seeds.

§Green Stipagrass, a variety released in 1946.

the two seed weight measurements, resulting mainly from the influence of immature seeds on bulk seed weights. Differences in mature seed weight among sites were very much like those found in field collected seeds (Table 3), indicating that seed weight could be a highly heritable trait.

Field Tests of Stand Establishment Capability

Field tests were planted at three locations in 1978: Brookings, South Dakota; Bismarck, North Dakota; and Highmore, South Dakota. The Brookings and Bismarck tests were planted on fallowed land in late August, 1978 for fall establishment, and the Highmore test was planted into small grain stubble in early November, 1978 for spring establishment. Tables 10-15 present the results obtained from these tests. Analysis of variance Tables 10A-14A are presented in the appendix for the measurements presented in Tables 10-14 respectively.

Seedling counts and seedling heights were measured in the Brookings test on October 25, 1978 (Table 10). No significant differences among entries were found, indicating that the advantages of heavier seeds found in laboratory tests (Tables 5 and 6) had no effect on initial estblishment in this field test.

Forage yield measured in the Brookings test on July 2, 1979 is shown in Table 11. Lodorm had the highest yield and was significantly different from all other entries, except site 6. Site 6 had the second highest yield and was significantly different from sites 3 and 4 and Green Stipagrass. Previous measurements in the Brookings test (Table 10) indicated that a dense stand had been established for all entries by

Table 10. Means and ranges of seedling counts and seedling heights measured in the Brookings field test on October 25, 1978.

	Seedling Numbers		Seedling Heights	
Entry	Mean	Range	Mean	Range
	seedlings/ft. of row		cm/seedling	
Site 1	28a*	12-47	5.34a*	4.69-6.36
Site 2	21a	7-33	5.05a	4.50-6.00
Site 3	27a	17-40	5.54a	4.25-6.50
Site 4	29a	20-44	5.62a	4.76-6.39
Site 5	30a	12-45	5.41a	4.30-6.56
Site 6	21a	9-27	5.10a	4.00-6.09
Site 7	28a	17-38	5.48a	4.29-6.48
Lodorm	23a	14-34	5.82a	4.50-6.75
G. Stipa†	27a	9-37	5.41a	4.05-6.50
SD93	26a	15-34	5.42a	4.42-6.50

*Means within a column of the table not followed by the same letter or letters are significantly different at P = .05 probability level by Duncan's Multiple Range Test.

†Green Stipagrass, a variety released in 1946.

Table 11. Means and ranges of forage yield measured in the Brookings field test on July 2, 1979.

Entry	Forage yield	
	Mean	Range
	tons/acre	
Site 1	1.07 bc*	0.93-1.30
Site 2	1.10 bc	0.55-1.72
Site 3	0.99 c	0.58-1.40
Site 4	0.97 c	0.74-1.25
Site 5	1.02 bc	0.73-1.30
Site 6	1.21ab	0.86-1.47
Site 7	1.08 bc	0.71-1.42
Lodorm	1.49a	1.25-1.67
G. Stipa†	0.99 c	0.78-1.25
SD93	1.10 bc	0.77-1.38

*Means within a column of the table not followed by the same letter or letters are significantly different at P = .05 probability level by Duncan's Multiple Range Test.

†Green Stipagrass, a variety released in 1946.

October 25, 1978. Therefore, it appeared that differences in forage yield resulted from post-establishment growth rather than from initial growth of seedlings.

Table 12 shows seedling counts and seedling heights measured in the Bismarck test on October 27, 1978. Lodorm had the highest seedling count and was significantly different from all other entries, except SD 93. No significant differences in seedling heights among entries were found. Seedling counts for all entries were much lower in this test than in the Brookings test, indicating that the environment was less favorable for establishment. A large part of the difference in environment was probably due to a coarser soil texture at Bismarck, where water percolation was faster and moisture available to seedlings was lower. It appeared that, even under the less favorable environment in the Bismarck test, seed weight had no effect on establishment. The reason for this was not clear, nor was the reason why Lodorm had a significantly higher seedling count. The germination rate of Lodorm measured just prior to seeding was higher but not significantly different from other entries (Table 8). Perhaps, the adjustment of total germinable seed to ten grams per plot for all entries gave Lodorm and other small seeded entries (Table 9) some advantges, because they contained more seeds per gram. Another possible cause of the higher seedling count of Lodorm was the selection of this variety for low post-harvest dormancy (Schaaf and Rogler, 1969). The 21-day germination tests used in this study may not have been long enough to accurately estimate the germination potential of this variety.

Plant heights were measured in the Bismarck test on August 7,

Table 12. Means and ranges of seedling counts and seedling heights measured in the Bismarck field test on October 27, 1978.

	Seedling numbers		Seedling heights	
Entry	Mean	Range	Mean	Range
	seedlings/ft. of row		--- cm/seedling ---	
Site 1	9.16 b*	2-24	4.85a*	3.50-6.16
Site 2	9.75 b	4-14	4.42a	3.73-6.25
Site 3	8.00 b	3-14	4.93a	4.16-7.50
Site 4	6.08 b	2-12	5.24a	3.70-7.50
Site 5	9.25 b	3-16	5.24a	4.25-6.16
Site 6	8.00 b	3-20	5.06a	3.75-7.42
Site 7	9.50 b	1-19	5.44a	4.33-7.50
Lodorm	16.25a	9-25	4.22a	3.50-4.92
G. Stipa†	6.42 b	-10	4.33a	3.61-6.16
SD93	10.50ab	5-20	4.80a	4.03-6.00

*Means within a column of the table not followed by the same letter or letters are significantly different at P = .05 probability level by Duncan's Multiple Range Test.

†Green Stipagrass, a variety released in 1946.

1979 (Table 13). Lodorm was significantly taller than all other entries. Site 3 and Green Stipagrass were also significantly taller than all the other entries, except Lodorm, site 4, and SD 93. In this test, there was a clear contrast between the sparse stand found in October 1978, and the dense stand found in August 1979. This may have resulted from an intense production of tillers by plants established in 1978 or from newly emerging seedlings in the spring of 1979. Plant counts could not be taken in August of 1979, because individual plants were indistinguishable from tillers of plants. Without this information, it was impossible to determine the effect of spring emergence on plant height measurements. The greater height of Lodorm may have been due to the larger proportion of Lodorm plants, which had been established the previous fall, or it may have been due to a genetic advantage of Lodorm in growth rate, since Lodorm also showed a higher forage yield at Brookings.

Seedling counts measured in the Highmore test on August 8, 1979 are shown in Table 14. Sites 1 and 5 had the highest seedling counts and were significantly different from all other entries, except site 2 and Green Stipagrass. Lodorm had the lowest seedling count and was significantly different from all other entries, except sites 3, 4, and 7. More significant differences were found at Highmore than at Brookings or Bismarck. This may have been due to the greater environmental stress on seedlings at Highmore. There was little or no weed competition in the Brookings and Bismarck tests, while a dense cover of annual weeds occurred at Highmore. Seedbed preparation in the Brookings and Bismarck tests had assured a relatively uniform planting depth,

Table 13. Means and ranges of plant heights measured in the Bismarck field test on August 7, 1979.

Entry	Plant heights Mean	 Range
	---------- cm/plant	----------
Site 1	45.74 d*	30-66
Site 2	46.64 cd	30-65
Site 3	52.06 b	37-67
Site 4	48.56 bcd	32-70
Site 5	46.43 cd	35-65
Site 6	46.98 cd	29-65
Site 7	47.47 cd	29-65
Lodorm	57.98a	33-74
G. Stipa†	52.63 b	33-76
SD93	50.65 bc	37-70

*Means within a column of the table not followed by the same letter or letters are significantly different at P = .05 probability level by Duncan's Multiple Range Test.

†Green Stipagrass, a variety released in 1946.

Table 14. Means and ranges of seedling counts measured in the Highmore field test on August 8, 1979.

Entry	Seedling numbers	
	Mean	Range
	# seedlings/2 ft. of row	
Site 1	30.00a*	13-46
Site 2	22.75ab	10-31
Site 3	18.63 bc	7-32
Site 4	18.25 bc	9-33
Site 5	30.25a	17-42
Site 6	20.00 b	8-33
Site 7	15.38 bc	10-24
Lodorm	11.38 c	6-16
G. Stipa†	22.13ab	8-39
SD93	21.13 b	11-32

*Means within a column of the table not followed by the same letter or letters are significantly different at P = .05 probability level by Duncan's Multiple Range Test.

†Green Stipagrass, a variety released in 1946.

while the small grain stubble prevented this in the Highmore test. The Brookings and Bismarck tests were irrigated after planting, while the Highmore test was not.

Table 15 shows some simple linear regressions of site means for seedling counts made in the Highmore field test on site means for seed and seedling measurements made in the laboratory. The first three independent variables represent site means for measurements made on bulk seed (Tables 7, 8 & 9). Germination rate appeared to have a significant negative effect on seedling counts. Data presented in Table 8 indicated that there were no significant differences in germination rate among sites, but very slight differences in germination rate may have become critical under very harsh environmental conditions. A few sites with low seed weights had slightly higher germination rates; these sites may have germinated more rapidly but lacked the seedling vigor to survive. The effects of mature seed weight and the ratio of mature to immature seeds on seedling counts appeared to be small and nonsignificant, as indicated by their small coefficients of determination (r^2). The high standard error of the regression coefficient for mature seed weight indicated that there was considerable variation in the ability of heavy seeded sites to produce higher seedling counts. This was particularly true of site 4, which had the heaviest seed weight but ranked low in seedling counts.

The last three independent variables presented in Table 15 represent site means for measurements made on seedlings produced by mature seeds (Tables 3 and 4). Although these measurements were made on seedlings from field collected seeds, it was felt that differences in

Table 15. Simple linear regressions of site means for seedling counts made in the Highmore field test on site means for seed and seedling measurements made in the laboratory.

Dependent variable	Independent variable	Regression coefficient	Standard error	F	r^2
Seedling numbers	Germination rate of bulk seed	- 16.827	5.552	*	0.648
	Mature seed weight of bulk seed	67.283	80.714	NS	0.122
	Mature to immature seed ratio of bulk seed	- 10.508	7.253	NS	0.296
	Shoot length of individual mature seeds at 7 days growth	0.960	0.608	NS	0.333
	Root length of individual mature seeds at 7 days growth	0.543	0.209	*	0.575
	Combined shoot & root length of individual mature seeds at 7 days growth	0.400	0.158	NS	0.563

* $P<.05$.

seedling root and shoot lengths among sites were large enough and that the relationship between them and seed weight was strong enough to warrant their use in regression analysis. Seedling vigor, as indicated by root length at 7 days growth in the laboratory, had a significant positive effect on seedling counts in the Highmore test. The effect of total seedling length was nearly as great as that of root length, but was not significant. The effect of shoot length was smaller than either root length or total seedling length and was not significant.

Although the regression of seedling counts, in the Highmore test, on seed weight of sites was not significant, a trend was observed indicating that heavier seeded entries tended to produce higher seedling counts. Figure 2 shows a comparison between two seed weight classes (Little in the and Hills, 1978) for the number of seedlings produced. Class I was composed of all entries with mean seed weights greater than the overall mean, and class II was composed of all entries with mean seed weights less than the overall mean (Table 9). The entries in class I produced approximately 25% more seedlings and differed highly significantly from the entries in class II (Table 14A). This was not shown in the regressions in Table 15, because of the limited number of means available for comparison. The genetic diversity, the range of seed sizes, and the range of seed maturity within entries were undoubtedly contributing factors to deviation from the regression line. Considering this diversity within entries, the comparison of seed weight classes was probably a better indicator of the effect of seed weight on stand establishment in the Highmore test.

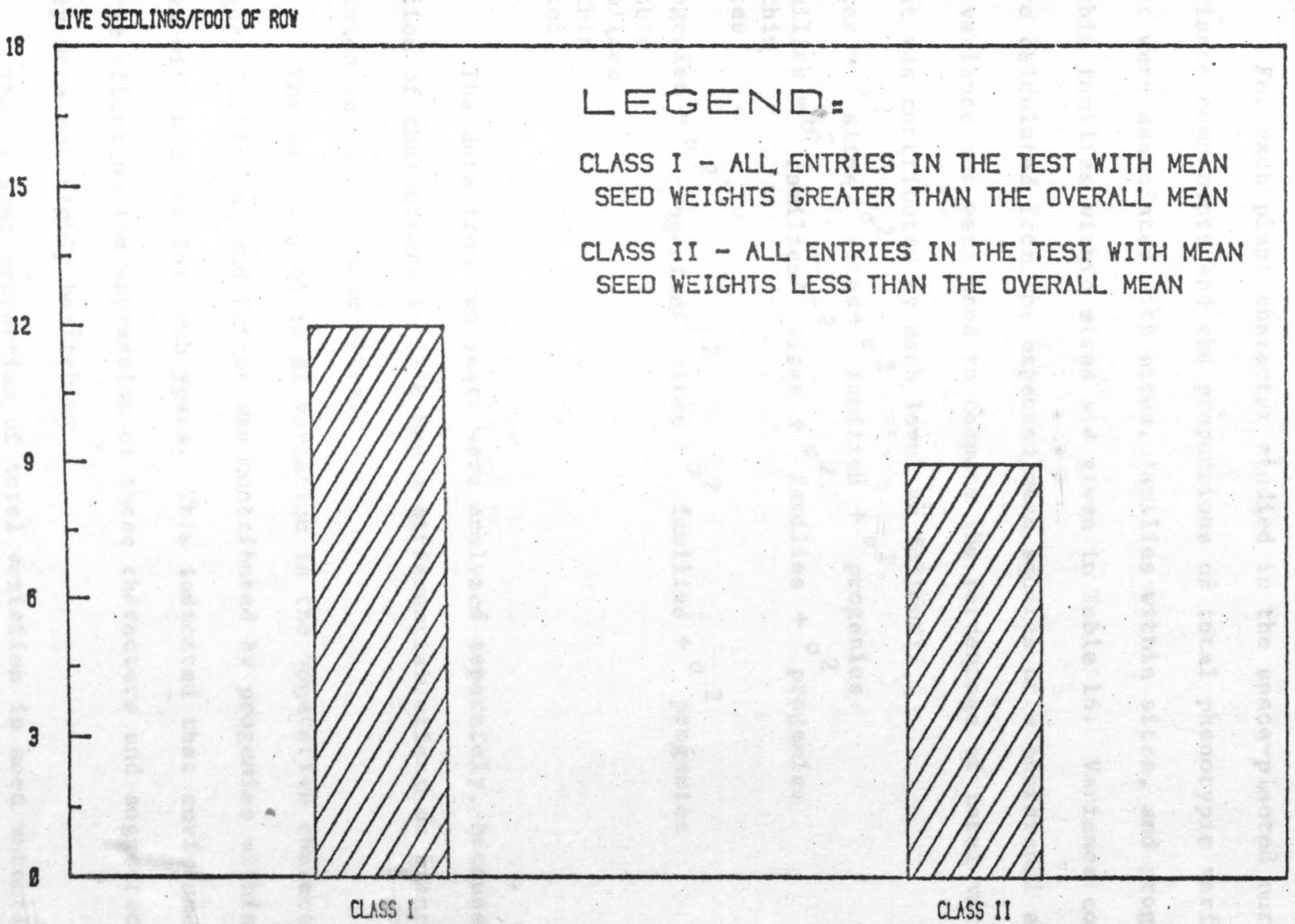

FIGURE 2. A COMPARISON BETWEEN CLASSES OF SEED WEIGHT IN THE NUMBER OF LIVE SEEDLINGS PRODUCED AT THE HIGHMORE FIELD EXPERIMENT TEST. THE DIFFERENCE BETWEEN CLASSES WAS SIGNIFICANT AT THE 1% LEVEL.

Variation and Heritability of Mature Plant Characteristics

For each plant character studied in the space-planted nursery, variance components and the proportions of total phenotypic variation that were associated with sites, families within sites, and progenies within families within sites are given in Table 16. Variance components were calculated from the expected mean squares of a hierarchal analysis of variance and were used to compute the percentage of total variation that was contributed by each level as follows:

Sites = $\sigma^2_{\text{sites}} / \sigma^2_{\text{sites}} + \sigma^2_{\text{families}} + \sigma^2_{\text{progenies}}$

Families within sites = $\sigma^2_{\text{families}} / \sigma^2_{\text{sites}} + \sigma^2_{\text{families}} + \sigma^2_{\text{progenies}}$

Progenies within families within sites = $\sigma^2_{\text{progenies}} / \sigma^2_{\text{sites}} + \sigma^2_{\text{families}} + \sigma^2_{\text{progenies}}$

The data from two years were analyzed separately, because inundation of the nursery in 1978 had a differential effect on plant growth between and within some sites.

The majority of total variation in the vegetative characters of vigor, leafiness, and height was contributed by progenies within families within sites for both years. This indicated that environment had a large effect on the expression of these characters and suggested that they were not highly heritable.

The largest proportion of total variation in seed retention was contributed by sites in both years. However, the proportion contributed by progenies within families within sites was also quite large in both

Table 16. Variance components and proportions of total phenotypic variation for each plant character that were associated with sites, families within sites, and progenies within families within sites.

Class	Year	Vigor		Leafiness		Height		Seed retention		Inflorescence production		10-head seed weight		100-mature-seed weight	
		Var. Comp.	%	Var. Comp.	%	Var. Comp.	%	Var. Comp.	%	Var. Comp.	%	Var. Comp.	%	Var Comp.	%
Sites	1978	0.22097	25	0.24640	29	124.680	32	0.48259	46	0.11503	13	0.41733	15	0.00025	52
	1979	0.03257	4	0.01786	4	36.377	28	0.29748	42	0.12893	17	0.53529	42	0.00027	52
Families within sites	1978	0.03868	5	0.06009	7	18.165	5	0.16283	16	0.08300	9	0.49534	17	0.00012	24
	1979	0.00000	0	0.09092	18	23.633	18	0.13943	19	0.11808	15	0.39008	30	0.00014	28
Progenies within families within sites	1978	0.60807	70	0.55327	64	245.110	63	0.39574	38	0.69635	78	1.96913	68	0.00012	24
	1979	0.83333	96	0.39193	78	71.290	54	0.28234	39	0.53106	68	0.35851	28	0.00010	20

years. Results suggested that seed retention was moderately heritable and that there was more variation among than within sites.

For inflorescence production, the majority of total variation was contributed by progenies within families within sites for both years. Inflorescence production appeared to be strongly influenced by environment, suggesting that it was not highly heritable.

For 10-head seed weight, 1978 data showed that the majority of total variation was contributed by progenies within families within sites, while 1979 data showed that the largest proportion was contributed by sites and the second largest proportion was contributed by families within sites. The discrepancy between years was mainly the result of greater seed shattering prior to harvest in 1979. Since seed shattering during inflorescence maturation has been recognized as a common occurrence in green needlegrass (Schaaf and Rogler, 1960; Kinch and Wiesner, 1963), 1979 data were considered a more accurate estimate of variation. Therefore, 10-head seed weight appeared to be a moderately heritable trait. More variation occurred among than within sites.

The majority of total variation in 100-seed weight was contributed by sites in both years. The remaining proportions were about equally contributed by families with sites and progenies within families within sites. Results suggested that 100-mature-seed weight was the most highly heritable of the characters studied.

It was interesting to note that the proportion of total variation contributed by sites was larger than that contributed by families within sites for every plant character. This indicated that there was more genetic diversity among than within sites and that selection progress for these characters would be most rapid through selection within superior sites.

The large proportions of total variation contributed by progenies within families within sites for most characters was somewhat surprising, because green needlegrass was reported to be highly self-pollinated (Johnson and Rogler, 1943). However, the design of the nursery was such that the three progeny of each family within a site were separated from one another by as much as 120 feet. Thus the potential for strong differential effects of environment on the progeny of a family was great. In addition, the use of subjective ratings for some plant characters and the necessary time difference between rating the first and last progeny of a family may have introduced even more variation among progenies.

Estimates of within site variability and heritability for vegetative plant characters are given in Table 17. For plant vigor, within family variability was much greater than between family variability in all sites. Only one site showed a significant difference between families, and estimates of heritability were very low.

Within family variability for leafiness was larger than between family variability in all sites. Significant differences between families were found within sites 2 and 3 at the 1% level and within site 6 at the 5% level. Estimates of heritability were quite low, but progress

Table 17. Estimates of between (σ_f^2) and within family (σ_e^2) variability and estimates of heritability (H) for vegetative plant characters within each of the seven sites.

Character	Site	Range of family means	Grand mean	σ_f^2	d.f.	σ_e^2	d.f.	H	S.E. (H)
Plant Vigor	1	1.33 - 2.67	2.13	0.000	17	1.528	34	0.00	± 0.00
A subject rating	2	1.33 - 3.00	2.19	0.014	15	0.839	30	0.00	± 0.00
on a scale of 1 to	3	1.00 - 2.67	1.68	0.194*	18	0.473	36	0.29	± 0.15
5, giving the low-	4	1.00 - 2.67	1.84	0.000	14	0.841	28	0.00	± 0.00
est numbers to	5	1.00 - 3.00	1.97	0.236	10	0.721	20	0.25	± 0.20
superior plants.	6	1.00 - 3.00	1.80	0.020	22	0.749	44	0.03	± 0.13
	7	1.00 - 2.00	1.56	0.000	8	0.653	16	0.00	± 0.00
Leafiness	1	1.67 - 3.33	2.35	0.061	17	0.463	34	0.12	± 0.15
A subjective rating	2	1.67 - 4.00	2.50	0.249**	15	0.321	30	0.44	± 0.16
on a scale of 1 to	3	1.33 - 3.00	2.42	0.125**	18	0.250	36	0.33	± 0.15
5, giving the low-	4	1.67 - 3.00	2.29	0.013	14	0.289	28	0.04	± 0.16
est numbers to	5	2.00 - 2.67	2.48	0.427	10	0.294	20	0.00	± 0.00
superior plants.	6	1.33 - 3.00	2.07	0.125*	22	0.472	44	0.21	± 0.14
	7	1.33 - 2.67	2.07	0.051	8	0.495	16	0.09	± 0.22
Plant Height	1	116.67 - 141.67	131.85	23.73*	17	49.81	34	0.33	± 0.16
An objective	2	120.00 - 138.33	128.54	5.59	15	58.65	30	0.09	± 0.16
measurement of	3	126.67 - 155.00	140.18	34.16**	18	52.05	36	0.40	± 0.15
height (cm) at	4	131.67 - 151.67	142.00	41.43**	14	43.81	28	0.49	± 0.16
the top of the	5	128.33 - 150.00	137.88	19.55	10	58.18	20	0.25	± 0.21
tallest inflor-	6	130.00 - 156.67	144.13	22.15	22	131.18	44	0.15	± 0.14
escence	7	130.00 - 151.67	144.63	30.09*	8	38.43	16	0.44	± 0.21

*P<.05. Family mean squares were significantly different.

**P<.01. Family mean squares were significantly different.

from selection might have been made within at least two sites.

For plant height, within family variability was larger than between family variability in all sites, but significant differences between families were found in sites 1 and 7 at the 5% level and in sites 3 and 4 at the 1% level. Estimates of heritability were generally higher for plant height than for vigor or leafiness but they were still quite low within most sites. Some selection progress for taller plants would have been possible within a few sites.

Table 18 presents estimates of between and within family variability and estimates of heritability for seed and seed production characters within sites.

Within family variability for seed retention was larger than between family variability, except in site 7. Significant differences between families were found in all sites, except site 3, and estimates of heritability were generally larger for seed retention than for any of the vegetative characters. Selection progress for seed retention would have been possible within most of the sites.

For inflorescence production, within family variability was considerably larger than between family variability for all sites. Significant differences between families were found only in sites 2 and 3, and estimates of heritability were low for most sites. Very little selection progress for inflorescence production would have been possible within any of the sites.

For 10-head seed weight, within family variability was larger than between family variability, except in sites 3, 4, and 5. Significant differences were found between families in all seven sites,

Table 18. Estimates of between (σ_f^2) and within family (σ_e^2) variability and estimates of heritability (H) for seed production characters within each of the seven sites.

Character	Site	Range of family means	Grand mean	σ_f^2	d.f.	σ_e^2	d.f.	H	S.E. (H)
Seed Retention A subjective rating on a scale of to 5, giving the lowest numbers to superior plants.	1	1.33 - 3.33	2.46	0.153**	17	0.293	34	0.34	± 0.16
	2	1.67 - 3.33	2.40	0.124*	15	0.350	30	0.26	± 0.17
	3	2.33 - 3.67	2.98	0.062	18	0.238	36	0.21	± 0.15
	4	1.33 - 3.00	2.22	0.165*	14	0.298	28	0.36	± 0.17
	5	2.00 - 3.67	3.06	0.170**	10	0.212	20	0.45	± 0.19
	6	2.67 - 4.33	3.65	0.117**	22	0.210	44	0.36	± 0.14
	7	2.00 - 4.00	3.33	0.421**	8	0.069	16	0.86	± 0.08
Inflorescence production A subjective rating on a scale of 1 to 5, giving the lowest numbers to superior plants.	1	1.67 - 3.67	2.69	0.126	17	0.502	34	0.20	± 0.16
	2	1.33 - 4.00	2.88	0.233*	15	0.583	30	0.29	± 0.17
	3	2.00 - 4.67	3.46	0.227**	18	0.438	36	0.34	± 0.15
	4	2.67 - 4.00	3.49	0.000	14	0.556	28	0.00	± 0.00
	5	2.33 - 4.67	3.64	0.185	10	0.609	20	0.23	± 0.21
	6	2.67 - 4.33	3.59	0.049	22	0.547	44	0.08	± 0.13
	7	2.67 - 3.67	3.15	0.019	8	0.454	16	0.04	± 0.21
10-Head Seed Wt. An objective measurement of total seed weight (grams) from 10 seed heads randomly selected.	1	1.71 - 4.22	2.77	0.279**	17	0.449	34	0.38	± 0.15
	2	1.37 - 3.49	2.35	0.278**	15	0.461	30	0.38	± 0.16
	3	0.56 - 3.34	1.43	0.326**	18	0.204	36	0.62	± 0.12
	4	1.02 - 4.81	2.93	1.221**	14	0.625	28	0.66	± 0.12
	5	0.77 - 3.25	1.67	0.379**	10	0.302	20	0.56	± 0.17
	6	0.43 - 2.02	1.04	0.132**	22	0.175	44	0.43	± 0.13
	7	1.07 - 3.02	1.85	0.254*	8	0.400	16	0.39	± 0.22
100-Mature-Seed Wt. An objective measurement of the mean weight (grams) of two 100-seed samples.	1	0.172 - 0.218	0.197	0.00024**	17	0.00006	34	0.80	± 0.07
	2	0.157 - 0.202	0.172	0.00014	18	0.00005	30	0.72	± 0.10
	3	0.145 - 0.202	0.172	0.00021**	18	0.00011	36	0.65	± 0.11
	4	0.185 - 0.220	0.203	0.00005	14	0.00015	28	0.26	± 0.17
	5	0.158 - 0.198	0.177	0.00009**	10	0.00007	20	0.57	± 0.11
	6	0.140 - 0.192	0.159	0.00001**	22	0.00009	44	0.61	± 0.11
	7	0.157 - 0.178	0.167	0.00003	8	0.00011	16	0.20	± 0.23

*P<.05. Family mean squares were significantly different.

**P<.01. Family mean squares were significantly different.

and estimates of heritability were quite high for most sites. Considerable selection progress for increased seed weight per head would have been possible within most sites.

Between family variability for 100-mature-seed weight was larger than within family variability, except in sites 4 and 7. Significant differences between families were found in all sites, except sites 4 and 7. Estimates of heritability were generally higher for this character than any of the other characters studied in the nursery. Considerable selection progress for increased seed weight would have been possible within most sites.

Correlations between characters, combined across sites in the space-planted nursery, are shown in Table 19. It was noted that vegetative characters were positively correlated with only one seed or seed production character. Plant vigor and leafiness were significantly and positively correlated with inflorescence production. However, estimates of heritability for all three of these characters were quite low (Tables 17 and 18), so correlations between them were of limited value for selection purposes. Plant height was significantly and negatively correlated with seed retention and with 10-head seed weight. Although these correlations were small, they indicated that selection for taller plants may reduce seed yield.

Perhaps the most important correlations shown in Table 19 were those between seed or seed production characters. All such characters were significantly and positively correlated, except inflorescence production and 100-mature-seed weight. This indicated that selection for any one seed or seed production character would have a positive effect

Table 19. Correlations between mature plant characters, combined over all sites for measurements taken in 1979 within the space-planted nursery.

Character	Vigor	Leafiness	Height	Seed retention	Inflorescence production	10-head seed weight	100-mature-seed weight
Vigor		0.380**	0.504**	- 0.001	0.491**	- 0.092	- 0.113
Leafiness			0.268**	- 0.040	0.293**	- 0.056	- 0.048
Plant height				- 0.142*	0.103	- 0.143*	- 0.082
Seed retention					0.236**	0.689**	0.456**
Inflorescence production						0.154*	0.054
10-head seed weight							0.517**

*P<.05. **P<.01.

on most of the others. Of particular interest were the rather high correlations between seed retention and 10-head seed weight and between seed retention and 100-mature-seed weight. Since these characters were found to be moderately to highly heritable (Table 18), increased seed production and increased seed weight would have been possible through selection for seed retention.

CONCLUSIONS

Genetic differentiation in seed weight was greater among sites than among families within sites, indicating that selecting heavy seeded genotypes from within the best sites would be the most effective method of improving seedling vigor. Site 1, in particular, appears to have superior seed weight and seedling vigor. In laboratory tests, site 1 had a significantly greater root length than most other sites, and in the field test at Highmore, it produced significantly higher seedling counts than most other sites and two standard varieties, Lodorm and SD 93. The seed weight of site 1 was also significantly higher than all three standard varieties and all other sites, except site 4.

Studies of mature plant characteristics in a space-planted nursery indicate that selection for seed weight would very probably increase seed production, and it would not adversely affect forage production. A larger proportion of variation was found among progenies within families within sites than among families within sites for all characteristics studied, except 100-seed weight. This indicated that there is a large family by environment interaction; consequently, selection for most characteristics should be based on data collected from two different years and, possibly, from two different locations.

The results of this study are important, because they show that genetic differentiation in factors related to stand establishment can be found among ecotypes, which were collected from western South Dakota. From these collections, seedling vigor and stand establishment can be improved significantly by selection for seed weight followd by selection for rapid root development in the laboratory. The materials collected for this study have good potential for selection of an improved variety.

SUMMARY

As a result of recent economic factors, native grasslands in western South Dakota, not adapted for cultivation, have been plowed. Suitable varieties of native grasses for reseeding these areas in the future are not available.

The objective of this study was to evaluate the variability of factors influencing stand establishment of green needlegrass and to determine the potential for selecting an improved variety from collections made at seven sites (representing 6 ecotypes) in western South Dakota.

Laboratory tests on both dehulled (to reduce dormancy) and intact seeds showed significant differences among sites in seed weight and root length at 7 days growth. Significant differences were also found among sites in germination rate and shoot length for dehulled, but not for intact seeds. Seed weight was positively and significantly correlated with germination rate and root length for both seed types and with shoot length for intact seeds.

Seed from the seven sites and three standard varieties, including Lodorm, Green Stipagrass, and SD 93, was increased under uniform environmental conditions. Field establishment tests were planted with this seed on fallowed land in late August of 1978 at both Brookings and Bismarck, North Dakota, and on small grain stubble in early November of 1978 at Highmore. Under the more favorable environmental conditions (Brookings and Bismarck), no significant differences among entries were found during the initial establishment period, except at Bismarck, where

sites than among families within sites, indicating that selection for a superior variety would be most rapid within superior sites. In addition, highly significant differences in seed weight, seed retention, and 10-head seed weight were found among families within most sites; consequently, selection within superior sites should improve these characteristics.

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APPENDIX

Table 3A. Analysis of variance of laboratory measurements on intact, mature seeds and the resulting seedlings from the seven sites.

Mean squares of characters

Source	d.f.	Seed weight	Days to germination	Shoot length	Root length
Total	104				
Site	6	441.75**	38.10	185.87	1004.22**
Remainder	98	60.53	18.57	148.30	223.13

*P < .05. **P < .01.

Table 4A. Analysis of variance of laboratory measurements on dehulled, mature seeds and the resulting seedlings from the seven sites.

Mean squares of characters

Source	d.f.	Seed weight	Days to germination	Shoot length	Root length
Total	192				
Site	6	300.22**	2.09**	335.47*	340.11**
Remainder	186	43.94	0.69	160.92	79.34

*P < .05. **P < .01.

APPENDIX

Table 7A. Analysis of variance of seed yield and ratio of mature to immature seeds for all entries in a seed increase planting at Brookings, South Dakota.

Mean squares of characters

Source	d.f.	Seed yield	Dark/light ratio
Total	49		
Treatment	9	4,184	0.579**
Replication	3	25,845	0.195*
Remainder	37	5,534	0.083

*P < .05. **P < .01.

Table 8A. Analysis of variance of percent germination and germination rate for all entries in a seed increase planting at Brookings, South Dakota.

Mean squares of characters

Source	d.f.	Germination percent	Germination rate
Total	39		
Treatment	9	665.56**	0.556
Replication	3	266.96	0.730
Remainder	27	186.74	0.781

*P < .05. **P < .01.

Table 9A. Analysis of variance of mature seed weight and bulk seed weight for all entries in a seed increase planting at Brookings, South Dakota.

Mean squares of characters

Source	d.f.	Mature seed weight	d.f.	Bulk seed weight
Total	39		49	
Treatment	9	0.00397**	9	0.00170**
Replication	3	0.00003	4	0.00063
Remainder	27	0.00006	36	0.00055

*p < .05. **p < .01.

Table 10A. Analysis of variance of seedling counts and seedling heights measured for all entries in the Brookings field test on October 25, 1978.

Mean squares of characters

Source	d.f.	Seedling counts	Seedling heights
Total	149		
Treatment	9	149.44	0.704
Block	4	340.75**	0.753
Block*Treatment	36	95.06	0.866
Remainder	100	35.51	0.163

*p < .05. **p < .01.

Table 11A. Analysis of variance of forage yield measured for all entries in the Brookings field test on July 2, 1979.

Mean squares of characters

Source	d.f.	Forage yield in tons per acre
Total	49	
Treatment	9	0.119*
Block	4	0.231**
Remainder	36	0.051

$*p < .05$. $**p < .01$.

Table 12A. Analysis of variance of seedling counts and seedling heights measured for all entries in the Bismarck field test on October 27, 1978.

Mean squares of characters

Source	d.f.	Seedling counts	Seedling heights
Total	119		
Treatment	9	96.11*	2.10
Block	3	136.67**	7.44**
Block*Treatment	27	37.04	1.24
Remainder	80	13.68	1.35

$*p < .05$. $**p < .01$.

Table 13A. Analysis of variance of plant heights measured for all entries in the Bismarck field test on August 7, 1979.

Mean squares of characters

Source	d.f.	Plant heights
Total	1599	
Treatment	9	2360.59**
Block	3	1166.77**
Block*Treatment	27	268.75
Remainder	1560	35.50

*P < .05. **P < .01.

Table 14A. Analysis of variance of seedling counts measured for all entries in the Highmore field test on August 8, 1979.

Mean squares of characters

Source	d.f.	Seedling counts
Total	79	
Treatment	9	277.78**
High vs. low seed weight	1	698.42**
Block	3	59.67
Block*Treatment	27	46.93
Remainder	40	76.70

*P < .05. **P < .01.