PHYTO-EDAPHIC RELATIONSHIPS AND ECOTYPIC DEVELOPMENT OF *FESTUCA IDAHOENSIS* IN EASTERN OREGON HABITAT TYPES OF *ARTEMISIA TRIDENTATA*

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The primary purpose of this research was to assess certain specific plant-soil and community interrelationships in eastern Oregon habitat types dominated by subspecies of *Artemisia tridentata*. Three evaluations were performed.

The first assessment involved characterization of vegetation and soils for the *Artemisia tridentata* ssp. *wyomingensis*/*Festuca idahoensis* habitat type. This habitat type had not previously been described for other intermountain rangeland areas. Idaho fescue was the dominant understory perennial in climax communities, with *Poa sandbergii*, *Sitanion hystrix* and *A. tridentata* ssp. *wyomingensis* increasing as range condition declined. *Bromus tectorum* was most prevalent on sites with course textured soils.

The second evaluation described plant-induced soil chemical patterns for *Artemisia tridentata* habitat types of good and poor ecological condition. Levels of total nitrogen, organic matter, potassium and phosphorus were greater in surface horizons under vegetation influenced soil than bare soil areas.

Magnesium concentrations generally increased in lower soil horizons while calcium tended to accumulate only within the surface soils under shrub canopies. Less distinct soil chemical patterns were apparent as soil depth increased. Structural rearrangement of soil chemicals occurred as range condition declined.

The final investigation assessed ecotypic development in *Festuca idahoensis* from sagebrush and pine communities. Results from a transplant garden indicated ramets from a *Pinus ponderosa* site were slower in phenological development and exhibited greater vegetative growth than collections from three lower elevation *A. tridentata* habitat types. Within collections from sagebrush sites, similar phenological timing was observed. Vegetative and floral development was reduced in plants selected from an *A. tridentata* ssp. *wyomingensis* dominated habitat type in comparison to ramets gathered from a high and low elevation *A. tridentata* spp. *vaseyana* habitat type. Evaluation of germination characteristics under conditions of controlled temperature and moisture stress revealed differences in relation to collection site. Seeds gathered from a *Pinus ponderosa* dominated community exhibited reduced germination under stress conditions. It was concluded response in *F. idahoensis* ecotypes to controlled environmental conditions reflected adaptational genetics of collection sites.

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INTRODUCTION

Over the past 100 years, land use practices have influenced the composition, diversity and successional development of plant communities in eastern Oregon. One considerable change has been the increased dominance of big sagebrush (*Artemisia tridentata* Nutt.) on approximately 10,000,000 hectares of rangeland which once supported a more floristically diverse sagebrush-grassland (Winward 1980). The reasons for this successional shift are complex, but can be attributed to alterations in allogenic processes controlling plant community development. Several of these factors can be identified. Overgrazing, wildfire suppression and farmland abandonment have apparently altered both macrosite and microsite interrelationships and enhanced the competitiveness of big sagebrush.

As a result of changes in plant community composition, alterations have undoubtedly occurred which influence site productivity and plant-soil interactions. One of the principle problems facing land managers in eastern Oregon is finding ways to improve ecological diversity on disturbed sagebrush rangelands. Although recognition of big sagebrush subspecies (Beetle 1960; Beetle and Young 1965) and assessment of their synecological patterns (Winward 1970; Hironaka and Fosberg 1979) have helped to clarify environmental factors important in their distribution, comparatively little information has been gathered which specifically examines dynamic plant, soil and environmental interrelationships. Assessment of plant communities presently in good ecological condition can provide insights into competitive processes and plant-soil interactions. This information coupled with management objectives can then aid in the rehabilitation of poor condition sites.

The primary purpose of this research was to assess certain specific soil-plant relationships existing on sites dominated by three subspecies of big sagebrush, and provide information which may be used to enhance land management activities. Further, within the time constraints of a graduate project, the assessments performed were designed to give insights into several soil, understory and plant community interactions. In order to meet the general purpose of this research, the following evaluations were performed:

1. The evaluation and determination of horizontal and vertical soil chemical patterns among plant communities dominated by three subspecies of big sagebrush on sites of good range condition versus poor condition.
2. The assessment of ecotypic development in Idaho fescue (*Festuca idahoensis* Elmer) collected from habitat types of big sagebrush and ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.).
3. The synecological description of the *Artemisia tridentata* ssp. *wyomingensis*/*Festuca idahoensis* habitat type, a plant community unique to eastern Oregon.

LITERATURE REVIEW

TAXONOMIC AND SYNECOLOGICAL CONSIDERATIONS RELATED TO *ARTEMISIA TRIDENTATA* NUTT.

Taxonomy

Taxonomic evaluations of *Artemisia tridentata* have been performed by numerous researchers. Nuttall (1841) first named *A. tridentata* from collections made during the Lewis and Clark expedition. Ryberg (1916) initially delineated subspecies, although formalized taxonomic units were finalized by Beetle (1960) and Beetle and Young (1965). The following three subspecies were recognized:

1. *A. tridentata* ssp. *tridentata* - Basin big sagebrush.
2. *A. tridentata* ssp. *wyomingensis* - Wyoming big sagebrush.
3. *A. tridentata* ssp. *vaseyana* - Mountain big sagebrush.

In addition, Beetle and Young included a variant: *A. tridentata* spp. *vaseyana* form *spiciformis* in their assessments.

Winward (1970) and Winward and Tisdale (1977) refined the taxonomy of *A. tridentata* in southern Idaho. They described another taxon of mountain big sagebrush--form *xericensis* (abv. "X"), which corresponded to populations found within relatively xeric plant communities. Winward (1980) further described the taxonomy and ecology of sagebrush species in Oregon. Leaf and stem morphology were included in his report. Brunner (1972) provided a vegetative key for sagebrush species found in Nevada.

Although, the separation of subspecies under natural conditions can often be based upon morphologic characteristics, difficulty in separating *A. tridentata* taxa is apparent (McDonough *et al.* 1975). Assessments utilizing chemical analyses of the foliage have been performed as a means to further delineate taxonomic differences (Holbo 1965; Winward 1970; Hanks *et al.* 1973).

Plant Community Relationships

The distribution of subspecies of big sagebrush has been shown to be related to environmental variability inherent in climatic, geologic and biotic factors. Fosberg and Hironaka (1964), Tisdale *et al.* (1969), Winward (1970), Winward and Tisdale (1977) and Hironaka (1979) have described elevational and soil relationships that exist for subspecies of big sagebrush. Generally, their results have indicated:

1. ssp. *tridentata* occurs on relatively deep soils at low elevations,
2. ssp. *wyomingensis* is found on shallow soils associated with xeric moisture conditions, and
3. ssp. *vaseyana* occupies mesic sites at higher elevations on relatively deep soils.

West *et al.* (1978) in an evaluation of pinyon-juniper communities in Utah and Nevada, supported these relative big sagebrush distributions.

Winward (1970) further differentiated big sagebrush dominated communities on the basis of floristic associations within subspecies for different habitats in Idaho. He found soil moisture and organic matter increased from sites supporting ssp. *wyomingensis* to ssp. *tridentata* to ssp. *vaseyana*, and soil temperatures declined in a similar manner. He also determined soil texture though unrelated to the sagebrush taxa, did affect the occurrence of dominant herbaceous species, and that understory associations with big sagebrush could distinguish between different habitat types.

Numerous articles have described habitat types and plant community relationships for big sagebrush. A summary of these reports and the regional location of the studies are given in Table 1.

FESTUCA IDAHOENSIS ELMER

Festuca idahoensis is a cool season perennial bunchgrass indigenous to a variety of environments in nine western states--Washington, Idaho, Oregon, Montana, Wyoming, Colorado, Utah, Nevada and California (Hitchcock 1951; Humphrey 1945). It has been reported to achieve maximum ecological dominance on sites in good ecological conditions and is considered an important forage constituent of many community types (Humphrey 1945). Although no comprehensive monograph has been presented regarding this species, various articles and reports have been published which discuss ecological and management characteristics of Idaho fescue.

Ecologically, *F. idahoensis* is reported to occupy sites intermediate between arid sagebrush grasslands and xeric forest communities. Humphrey (1945) determined *F. idahoensis* to be a major constituent of Palouse bunchgrass, ponderosa pine-grassland, sagebrush and bitterbrush-grass community types. Kuchler (1964) further indicated distribution in the northern Rocky Mountains to range from foothill grasslands to mountain meadows. Daubenmire (1942) distinguished between two important grassland vegetative zones: the *Agropyron spicatum-Poa sandbergii* association and the more mesic *Festuca idahoensis-Agropyron spicatum* association. Along an

Table 1. Summary of research identifying Pacific Northwest habitat types dominated by *Artemisia tridentata*.

Habitat Type	Author	Location
Artemisia tridentata		
/*Stipa comata*	Daubenmire (1970) McLean (1970)	Washington Alberta
/*Poa sandbergii*	Daubenmire (1970)	Washington
/*Agropyron spicatum*	Culver (1964)	Oregon
/*Festuca idahoensis*	Daubenmire (1970) Eckert (1957) Franklin and Dyrness (1973) McLean (1970) Mueggler and Stewart (1980;81) Tueller (1962)	Washington Oregon Oregon Alberta Montana Oregon
/*Festuca scabrella*	Mueggler and Stewart (1980)	Montana
/*Elymus cinereus*	Culver (1964)	Oregon
Artemisia tridentata ssp. *tridentata*		
/*Stipa comata*	Hironaka and Fosberg (1979) Winward (1970)	Idaho
/*Agropyron spicatum*	Erhard (1980) Hironaka and Fosberg (1979)	Oregon Idaho
/*Festuca idahoensis*	Hironaka and Fosberg (1979)	Idaho
Artemisia tridentata spp. *wyomingensis*		
/*Sitanion hystrix*	Hironaka and Fosberg (1979) Winward (1970)	Idaho
/*Poa sandbergii*	Hironaka and Fosberg (1979)	Idaho
/*Stipa thurberiana*	Hironaka and Fosberg (1979)	Idaho
/*Stipa comata*	Hironaka and Fosberg (1979) Winward (1970)	Idaho

Table 1. Continued

Habitat Type	Author	Location
Artemisia tridentata spp. *wyomingensis*		
/*Agropyron spicatum*	Hironaka and Fosberg (1979)	Idaho
	Winward (1970)	
Artemisia tridentata spp. *vaseyana*		
/*Stipa comata*	Earhard (1980)	Oregon
	Hironaka and Fosberg (1979)	Idaho
	Winward (1970)	
/*Stipa occidentalis*	Earhard (1980)	Oregon
/*Agropyron spicatum*	Earhard (1980)	Oregon
	Hironaka and Fosberg (1979)	Idaho
	Winward (1970)	
/*Festuca idahoensis*	Hironaka and Fosberg (1979)	Idaho
	Winward (1970)	
/*Purshia tridentata*/ *Festuca idahoensis*-*Agropyron spicatum*	Earhard (1980)	Oregon
/*Symphoricarpos oreophilus*/ *Festuca idahoensis*	Hironaka and Fosberg (1979)	Idaho
/*Symphoricarpos oreophilus*/ *Carex geyerii*	Hironaka and Fosberg (1979)	Idaho
Artemisia tridentata spp. *vaseyana* form *"xericensis"*/ *Agropyron spicatum*	Hironaka and Fosberg (1979)	Idaho

Table 1. Continued

Habitat Type	Author	Location
Artemisia tridentata spp. *vaseyana* form *spiciformis*/ *Bromus marginatus*	Hironaka and Fosberg (1979) Winward (1970)	Idaho
Juniperus occidentalis/ *Artemisia tridentata* ssp. *vaseyana*/ *Stipa occidentalis*	Earhard (1980)	Oregon

elevational gradient from fescue grassland to forest, the Festuca idahoensis-Symphoricarpos albus habitat type was found to be the driest community and most prone to extended summer drought (Daubenmire 1968). Within grassland communities in the Bitterroot Mountains of Montana, F. idahoensis was determined to be a major constituent of more mesic and high elevation stands (Root and Habeck 1972). This was particularly true in relation to Agropyron spicatum which was found to occupy lower elevation and drier plant communities. Soil water holding capacity was found to be greater in a Festuca idahoensis-Agropyron spicatum-Antennaria rosea habitat type than in an Agropyron spicatum-Melica bulbosa community (Mueggler and Harris 1969). In a study of habitat types of Sucia Island in Puget Sound, Washington, F. idahoensis dominated grasslands were found to occupy the drier sites on southern exposures (Fonda and Bernardi 1976).

Further evaluations of communities with F. idahoensis as an important constituent have described synecological associations. Tisdale, Hironaka and Fosberg (1965) examined an area of pristine sagebrush-grassland in east central Idaho and included in their analyses several habitat types with FEID understory. Eckert (1957), Culver (1964), Hall (1967), McClean (1970), Daubenmire (1970), Franklin and Dyrness (1973) and Hironaka and Fosberg (1979) have further delineated typal communities with dominant FEID synusiae and related these to environmental factors.

Climatic conditions which occur in fescue grasslands of mountains in the western United States were reported by Weaver (1979). He indicated climatic characteristics were sufficiently similar to those of the Pseudotsuga menziesii and Abies lasiocarpa zones to warrant the consideration that other environmental factors were important in allowing fescue grasslands to persist in coniferous climatic zones. Seasonal variation in soil nutrients among various community types were thought to play an important role in plant community distribution (Weaver and Forcella 1979).

Analyses of ecotypic development in *F. idahoensis* have indicated differences on the basis of geographic area and elevation. Tisdale (1959, 1961) collected seeds from numerous locations in the Pacific Northwest and established plants under uniform growing conditions. Differences in plant phenology and morphology were noted among collections. In a transplant study of selections from a high and low elevation steppe community, Stocker (1975) found shorter leaf length and plant height in plants collected from the high altitude site. Additionally, anther dehiscence was faster in the high elevation collection.

SOIL NUTRIENT PATTERNING

Analyses by several authors have shown strong differentiation of herbaceous vegetation along gradients from shrub centers to adjacent openings (Went 1942; Wiens 1976; Young and Evans 1975; Bratton 1976). These patterns are evidently influenced by the amelioration of environmental extremes resulting from shrub establishment. One of these modifications, autogenically induced by shrubs, is the accumulation of nutrients and organic matter under the canopy influenced soil.

Many reports have established soil fertility differences in arid-land systems between canopy and interspace soils. An initial study by

Roberts (1950) examined soil chemistry differences between canopy and bare soil zones for both *Sarcobatus vermiculatus* and *Atriplex confertifolia*. He found pH, electrical conductivity and total extractable sodium to increase under the shrub-influenced soil, with *S. vermiculatus* sites exhibiting the more pronounced differences. Also, older shrubs of *S. vermiculatus* had higher pH values than younger shrubs, indicating the degree of influence varied with age of shrub.

In a related article, Fireman and Hayward (1952) identified differences in soil pH, exchangeable sodium and soluble salts between canopy and interspace soils for *A. tridentata*, *S. vermiculatus* and *A. confertifolia*. All values were generally higher under canopy soils dominated by *S. vermiculatus* and *A. confertifolia* than interspace soils, while slight changes were found in soil chemical patterns in the *A. tridentata* community. Also, as plant size or age increased for the halophytes, more pronounced nurient patterns were evident.

Additional studies have firmly established spatially separated soil chemical patterns in halophytic shrublands of the western United States. Rickard and Keough (1968) described sodium and potassium accumulations in under shrub zones for sites dominated by *S. vermiculatus* and *Grayia spinosa*. Reuss and Wali (1980), in a report on daily fluctuations in water potential and foliar ionic concentrations of *A. canescens*, noted differences in soil pH, electrical conductivity, alkaline earth carbonates and soil cations between canopy and interspace soils. Generally, levels were greatest for soil beneath the plant canopy.

Recent reports examining semi-desert shrubland nutrient patterning in Australia (Charley and Cowling 1968; Cowling 1969) have established vertical gradients in total soil nitrogen, available phosphorus, organic carbon and nitrogen mineralization capacity. Charley (1972) emphasized the importance of stratifying the soil surface on the basis of under-shrub and bare soil area, so the errors in estimation of nutrient supply or its turnover could be avoided.

Sharma and Tongway (1973) studied soil salinity patterns in two Australian *Atriplex* communities. Both *A. vesicaria* and *A. nummulari* induced significantly higher salinity and pH values in the upper 15 cm of the soil profile when compared to interspace areas. *A. nummular* had significantly greater salt concentrations than *A. vesicaria*, possibly related to a greater litter fall per unit area under the canopy of *A. nummulari*. Soil nutrient accumulations were related to plant age.

Tiedemann and Klemmedson (1973a) examined the effects of mesquite on soil physical and chemical properties. Organic matter, total N, total sulfur (S), total soluble salts were found to be up to three times greater in the upper 4.5 cm of the canopy-influenced soil than adjacent bare soil. The difference declined with increasing depth until the levels were approximately the same as open soil. Total potassium (K) was somewhat greater under mesquite than interspace areas but increased with depth. Total P and total N did not differ between canopy and shrub soils. The authors suggested mesquite trees further improved the microsite fertility by the redistribution of nutrient ions from areas beyond the canopy to areas underneath the canopy. However, Paulsen (1953) reported opposite results for semiarid grasslands recently invaded by mesquite. He described a reduction in soil chemical concentrations and deteriorated physical properties in under-shrub canopy soils. This was attributed to a declining range condition.

In a comprehensive survey of several desert shrub communities, Charley and West (1975) examined soil chemical patterning in relation to under canopy and interspace soils. They found organic carbon (C) and total nitrogen (N) exhibited vertical and horizontal concentration gradients away from the canopy area. Differences in the degree and regularity of horizontal C and N patterning were noted between various ecosystems; the *Artimesia* community had C and N levels higher than an *Atriplex* community. In an examination of grazed and ungrazed *Atriplex* community, no effect of grazing was detected in total N, but organic carbon levels showed significantly higher values under grazed bushes. Plowing of sagebrush lands and seeding *Agropyron desertorum* apparently obliterated the horizontal N patterns. Other relationships determined include:

1. Horizontal patterning was only shown for N, C and phosphorus (P). Available P levels were usually greatest under shrubs but exceptions did occur.
2. Concentration gradients probably result from the relocation of elements through uptake from an extensive volume of soil and then incorporation into a spatially limited surface volume from which back leakage is negligible.
3. The inference that the nutrient capital of an area is redistributed under the shrub dominated space.

This last point was inferred by Charley (1972) when he suggested that under canopy soils, nutrient accumulations are at the expense of the surrounding soil areas.

In a complimentary article to their 1975 report, Charley and West (1977) further delineated N cycling differences between under canopy and interspace soils. Their analyses showed horizontal and vertical concentration gradients of soil N were accompanied by patterns of mineralization potential. Activity increased toward the soil surface and from interspace to the under canopy micro-soil. NO_3-N mineralization predominated in the upper 0-2.5 cm horizon, while NH_4-N became increasingly more important in the lower depths. This general pattern of nitrogen distribution in desert soils was supported by Nishita and Haug (1973).

Nutrient patterning has also been reported for non-arid land shrub communities. Zinke (1962) examined soil properties influenced by several forest tree species. He noted patterning was generally developed radially and symmetrically and varying with distance from the tree trunk. A systematic change in pH, N content, exchangeable bases and exchange capacity were noted and related to differences between the effect of bole litter, leaf litter and adjacent openings or neighboring tree. Soil pH was lower under the canopy soils.

The existence of more favorable nutrient regimes under canopy soils would seemingly indicate a more suitable environment for plant growth. Young and Evans (1975) reported enhanced germinability of _Bromus tectorum_ seeds collected under canopy soils when compared with seed related from interspace soils. The influence of soils collected from under shrub canopies and interspace areas on the growth of _B. tectorum_ was investigated by Rickard _et al._ (1973). Under controlled environmental conditions _B. tectorum_ grown in shrub-influenced soils produced a greater biomass than when grown in soils collected in the spaces between shrubs. Shrubs examined included *S. vermiculatus* and *G. spinosa*. Soils under the *S. vermiculatus* canopy had higher pH values and high N sodium concentrations than *G. spinosa* soils; both were higher than adjacent interspace soils. *G. spinosa* soils had higher phosphorus and potassium (K) values. Additions of nitrogen to these soils increased *B. tectorum* production for both the *S. vermiculatus* and *G. spinosa* collections, but the relative increase was greatest for the *G. spinosa* soil. This was attributed to a more favorable soil chemistry of the *G. spinosa* soils. Similar results were found by Tiedemann and Klemmedson (1973b) in a bioassay of grass from soils collected under mesquite and adjacent interspace areas.

GERMINATION

Seed germination is influenced by numerous interacting environmental and physiological factors (McDonough 1977). Germination responses under laboratory conditions may have value in predicting a species' applicability to field plantings (Eddleman 1978). As such, the screening of plants to varying germination parameters can aid the land manager in selecting suitable species and cultivars for specific range reseeding problems.

Germination characteristics of native and introduced species under varying conditions of temperature, moisture stress and light have been described by numerous authors. Results have established trends in species' response to controlled incubation environments. Some of these findings are presented below:

Germination Responses of Perennial Species to Temperature and Light

Boyce, *et al.* (1976) reported the effects alternating temperatures of varying duration have on the germination of dormant and nondormant seeds of *Festuca arundinaceae*. Their results indicated dormant seed initiated optimum germination under an eight hour 20-25°C warm period, alternated with a sixteen hour cool temperature of 10-15°C. Nondormant seeds exhibited optimum germination at constant temperatures of 20-25°C. Seed dormancy was reportedly enhanced or eliminated by various temperature pretreatments.

Eddleman (1978, 1979) reported on germination properties of species indigenous to eastern Montana mixed prairies. Response to a wide range of temperature, moisture stress, light and seed age conditions was described. Cleaning procedures for separating seeds from chaff were also outlined, and treatments to break seed dormancies discussed.

Germination requirements, as well as root development, phenology and soil moisture condition for *Agropyron spicatum* and *Aristida longiseta* have been examined (Evans and Tisdale 1972). Optimum germination for these two species was reported to be between 20-22°C for *A. spicatum*, and an alternating temperature of 41°C (day) and 20-24°C (night) for *A. longiseta*. Developmental characteristics of each species was related to resistance to grazing pressure.

Optimal germination temperatures for *Rudbeckia occidentalis* collected from an aspen range in Utah has been reported by Florez and McDonough (1974). Constant temperatures between 20° and 25°C and alternating temperatures of 30° day - 20°C night or 25° day - 15°C night when accompanied by an 8 hour photoperiod were determined to promote maximum germination. McDonough (1970, 1974) further assessed germination properties of numerous high elevation range plants in Utah. Most species were found to germinate under a wide range of alternating temperature environments and only a few species exhibited a stratification requirement.

Polymorphic differences in seeds of *Grindelia squarosa* were related to differences in germination response to temperature (McDonough 1975). Disc achenes were found to attain high final germination percentages over a wider temperature range than did seeds selected from ray achenes. Stratification was also reported to increase the range of conditions suitable for germination both in ray and disc achenes.

McDonough (1979) reported seed germination in *Populus tremuloides* maintained high percentages at temperatures between 2° and 30°C. Both percentage germination and abnormal germination (defined as hypocotyl elongation without concomitant root growth) appreciably increased at temperatures above 35°C. Factors influencing early seedling growth were also discussed.

Toole (1976) discussed the effects of varying light and temperature regimes on germination of *Agropyron smithii* seeds. He reported darkness concurrent with constant temperatures, prolonged high temperatures, continuously unfiltered incandescent illumination and intermittent far red light at 15-25°C alternating temperature, inhibited *A. smithii* germination. These results were related to phytochrome control and hormonal, enzymatic and substrate interactions. Optimum germination was found under dark conditions at favorable alternating temperatures of 15-20°C and 15-30°C on a 22 hour low and 2 hour high cycle.

Germination requirements of nineteen species of New Mexico mixed prairie plants have been reported by Sabo *et al.* (1979). Seeds were germinated under varying temperature regimes simulated on a thermogradient plate and light response patterns were also assessed.

Numerous reports on the germination characteristics of native perennial species indigenous to the Intermountain Region to a wide range of constant and alternating temperature conditions have been made by J. A. Young, R. A. Evans and associates. These include:

Poa sandbergii (Evans *et al.* 1977),

Purshia tridentata (Evans and Young 1977),

Sitanion hystrix (Young and Evans 1977),

Festuca idahoensis, *Festuca ovina* and *Poa canbyi* (Young *et al.* 1981),

Agropyron spicatum and *Agropyron inerme* (Young *et al.* 1981), and *Elymus cinereus* Scribu and Merr. (Young and Evans 1981).

McDonough and Harniss (1974a) examined effects of temperature on germination of three subspecies of *Artemisia tridentata*. Sagebrush seeds germinated within a broad range of temperature combinations, although the relative order of response indicated lowest germination amounts in ssp. *vaseyana*, followed by ssp. *wyomingensis* and finally ssp. *tridentata*. Within subspecies, germination was not significantly influenced by temperature. Stratification improved total germination percent in ssp. *vaseyana* only, and germination rate in all subspecies. Germination of unstratified ssp. *vaseyana* seeds was approximately 15.0%, but after a 50 day cold treatment, germination amount increased to 94%. A further examination of dormancy in ssp. *vaseyana* was reported by McDonough and Harniss (1974). Dormancy was partially relieved by light, gibberillic acid and acid scarification, while being almost completely relieved by pericarp removal. Yearly variation in germination indicated only ssp. tridentata showed significant fluctuations over the course of a three year trial (Harniss and McDonough 1976).

Germination Response of Annual Species

Evaluations of the germination response of annual plant species to their environment have indicated specific temperature, climatic and precipitation mechanisms which prevent premature germination during sporadic summer rainfall events. Newman (1963) discussed factors controlling the germination characteristics of winter annuals under natural conditions. Notably, he set out to determine why winter annuals do not germinate during the summer and exhibit very precise germination dates during the autumn. Reasons for the phenomena were attributed to the following explanations:

1. After-ripening or seed coat changes promote autumn germination and subsequent adaptability to a wide range of temperatures.
2. As after-ripening occurs optimum and maximum temperatures for germination rise until they overlap with those occurring naturally in the field.
3. In some species, summer tempertures are too high to promote seed germination. Autumn temperatures would be most favorable to germination.

In examining Aira praecox, adequate soil moisture was necessary but temperature fluctuations were most critical in initiating germination.

For *Teesdalia nudicaulis*, soil moisture was found to be of primary importance in promoting fall germination.

Young *et al.* (1973) reported on the effect of constant and alternating temperatures for *Bromus mollis*, *B. rigidus*, *Avena barbata*, *Vulpia megalura*, *Trifolium hirsutum* and *Phalaris tuberosa* var. *hirtiglunis*. They determined annual grasses germinated under a broader range of temperatures above a minimum high temperature of 0°C, while perennial grasses exhibited a narrow temperature regime that permitted germination. Rose clover cultivars generally germinated at low incubation temperatures.

Young *et al.* (1981) discussed community germination characteristics of California annual grasslands. They determined few germinable seeds were carried over from year to year, and dominant annual grasses had virtually no remaining viable seed present in the soil the year following development. After ripening requirements affecting seed germination were assessed and related to dormancy regulation mechanisms as affected by environmental parameters.

The influence of microsite on the germination of seeds of annual species has been stressed by Evans and Young (1970) and Young and Evans (1975, 1978). Plant litter was found to ameliorate surface moisture and temperature conditions and create microsites favorable to annual weed germination and establishment. Further, seeds collected from soils directly under shrub canopies were found to exhibit greater germinability than seeds selected from adjacent interspace soils. These differences were attributed to microsite modification of the canopy dominated areas.

Germination Response to Moisture Stress

The influence of various simulated water stress regimes upon native seed germination have been well documented. Excluding specific ion effects and/or temperature interaction, a decreasing osmotic potential (ψs) will reduce percent germination and/or delay germination rate (Eddleman and Doescher 1977; Frelich *et al*. 1973; Hyder and Yasmin 1972; Macke and Ungar 1971; Springfield 1968). Hadas and Russo (1974) reported as long as a critical solution ψs was not reached, total germination was not significantly reduced. However, germination rate and water uptake as a function of time were reduced as a function of declining ψs. Choudhuri (1968) discussed soil salinity effects on the germination and survival of *Agropyron spicatum*, *Artemisia tridentata*, *Lepidium perfoliatum* and *Typha latifolia*. Percent germination declined with increasing salinity and all species were less tolerant of salinity at germination than they were at the seedling stage. Dewey (1960) reported on the salt tolerance of 25 strains of *Agropyron*. His results indicated differences in salt tolerance among species. Response of *Bouteloua gracilis* and *Hilaria jamesii* to low osmotic potentials was determined to be more favorable than that exhibited by *Sporobalus airoides* (Knipe 1968). Reimold and Queen (1974) described germination and response physiology to salinity gradients for species in the Great Basin. Germination of *Atriplex canescens* at various osmotic levels was reported on by Springfield (1966).

Germination in Response to Temperature-Water Stress Environments

Apparently, there exists a temperature-water stress interaction, such that at ideal germinating temperatures seeds are better able to tolerate low osmotic potentials (Kaufmann and Ross 1970; Sharma 1976). Such a relationship has been reported for *Agropyron smithii* (Knipe 1973) and *Ceratoides lanata* (Springfield 1968; Workman and West 1967).

Bokhari *et al.* (1975) discussed the interaction between temperature and water stress on the germination of *Bouteloua gracilie*, *Buchloe dactyloides* and *Aropyron smithii*. Examination of the ψs/temperature interaction indicated that:

1. Increased water stress decreased germination rate particularly at lower temperatures.
2. Increased water stress decreased total germination under all temperatures examined.
3. Water stress greater than -11 bars inhibited germination under all temperature regimes.
4. The interactions between species and temperature and temperature and water stress were significant, while the interaction between species and water stress was not significant.

McGinnies (1960) examined the interaction of moisture stress and temperature on the germination of six range grasses. He reported moisture stress delayed germination rate and reduced total germination amount. Optimum germination for all species was found at 20°C and that under high moisture stress all species germinated better at 20°C than at 10° or 30°C. Tadmor *et al.* (1969) discussed germination of different range plant species and compared results of D-mannital solutions and PEG solutions subjected to various temperature regimes.

They concluded the more temperature diverged from optimum, the more the final germination was influenced by osmotic potential.

ECOTYPES

Natural selection has resulted in the development of geographically segregated plant populations, commonly referred to as ecotypes. Turesson (1922) originally defined ecotype as the "ecological unit to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat." Gregor (1939) contributed to the theoretical understanding of ecotype by advocating the use of the following terms:

Cline: any gradation in measurable characters.

Ecocline: a cline apparently correlated with an observable ecological gradient.

Ecotype: a particular range on an ecocline.

The use of the word ecotype has resulted in many interpretations as to its theoretical meaning, but as Quinn (1978) pointed out, ecotype has "been used by botanists and ecologists to indicate almost any degree of genetic difference below the level of the species." In terms of studying local genetic adaptations of plant species to a particular habitat, Quinn recommends use of the term "population" to describe these phenomenon. However, in the context of this review, the meaning of ecotype will correspond to Turreson's original definition. Words such as type, race, collection or population will be used synonymously with ecotype.

Examination of ecotypic variation in natural settings has included common garden analysis of phenologic and morphologic characteristics, differentiation of physiological responses in controlled environments and assessment of germination properties. The following review presents some of the available research on these approaches.

Ecotypic Differences Based Upon Common Garden Studies

Initial examinations of genetic differences in prairie species evaluated photoperiodic response of latitudinal collections. Olmstead (1944) and Larsen (1947) described growth and development of various collections of side-oats grama (*Bouteloua curtipendula*) and little bluestem (*Schizachyrium scoparium*), respectively. They found northern strains initiated an earlier flowering and phenologic response to long day lengths, while plants collected from more southernly sites responded to short day photoperiods. Cornelius (1947) in a further analysis of little bluestem noted earlier flowering types in a common garden came from more western and northern areas and later flowering types from eastern and southern collections.

McMillan (1959) undertook an extensive study of ecotypic development in response to climatic conditions for 12 mid-grass prairie species indigenous to the northern and southern Great Plains. Generally, he found northern races exhibited an earlier floral initiation and a more rapid maturation than plants selected from southern sites. However, species differences did occur from which he recognized three general patterns of flowering behavior:

1. The trend of earlier flowering by clones from northern and western communities and progressively later flowering by southern and eastern transplants. Species exhibiting these

patterns were *Panicum virgatum*, *Schizachyrium scoparium*, *Andropogon gerardi-hallii* complex, *Sorghastrum nutans*, *Sporobolus heterolepis*, *Koeleria cristata*, *Bouteloua gracilis* and *B. curtipendula*.

2. The trend exhibited by *Elymus canadensis* where early flowering clones were selected from southern communities. Increasingly later flowering collections came from nothern, western and eastern collections.

3. The absence of a geographically oriented flowering pattern. This response was shown by transplants of *Stipa spartia*, *S. comata* and *Oryzopsis hymenoides*.

Further, McMillan reported plant height was apparently correlated with maturation dates, with a shorter stature found in those plants initiating earlier growth. Also, later flowering clones were more apt to produce unfilled caryopses.

Ward (1969) reported on ecotypic development in *Deschampsia caespitosa* from collections made in Colorado. Plants from 12 locations were grown in a common garden at Fort Collins, Colorado and phenological and growth measurements taken over a two year period. Results indicated higher elevation types were generally earlier in anthesis than those from lower elevations. Plants which developed later generally had larger culm lengths and generally later dates at which maximum culm heights were attained. Timing and length of leaf growth was not correlated with collection area, but uniform for all plants. Ward felt this was attributable to a uniform response to similar atmospheric conditions and that an ecogenetic control of this trait was relatively minor.

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Ecotypic differentiation in high plains populations of *Panicum virgatum* was studied by Quinn (1969). Plant materials were transplanted to a common garden at Fort Collins and phenological and growth measurements taken. Significant differences in comparative growth and development were evident among the collections. The patterns of relative phenologic development were correlated with the length of growing season of the indigenous environment. An increase in the periods of active growth, maximum plant height, plant production and number of inflorescences was noted for plants collected along a north-south gradient.

Quinn and Ward (1969) reported on ecotypic differentiation in *Sporobolus cryptandrus*. Significant differences in phenology and rate of development among plant materials from different collections were found. Growth initiation and plant dormancy showed a consistent correlation with the relative length of growing season from the collection environment. However, no geographic or latitudinal patterns were exhibited in phenological development. Clones from northern and higher altitudinal sites attained maximum leaf area and culm expansion earlier than southern and eastern collections at lower elevations.

Genotypic development in plants of *Koeleria cristata* were indicated by marked heritable differences in phenology and morphology between races (Robertson and Ward 1970). Moisture regime of the native habitat was felt to be a more important selective force than growing season length.

Clary (1975) examined ecotypic differentiation as a response to climatic conditions in *Sitanion hystrix*. He sampled 12 sites from seven western states and grew collections under uniform conditions in a transplant garden and growth chamber. His results indicated that rates of phenological development differed among collections, but were not correlated with the growing season of the collection sites. Also, no differences in water use efficiency were found between sites. In response to phenological timing under common garden conditions, the following relationships were noted:

1. plants from warm, dry habitats flowered early and had low dry matter production,
2. plants from habitats with moderate environments flowered latest and had relatively high dry matter production, and
3. plants from cool, wet habitats flowered early and had relatively high dry matter production.

Evaluations of ecotypic development in _Festuca idahoensis_ have revealed both geographical variation and elevational differences. Tisdale (1959, 1960) reported morphological and phenological differences in plant sources collected from the Pacific Northwest and grown in a common greenhouse. Stocker (1975) performed a transplant study of high and low populations of eight perennial grasses and forbs indigenous to Washington. _F. idahoensis_ was included for study and showed significant differences between collections in plant height, leaf length, time of anther dehiscence and seed germination ability.

Ecotypic Differences of Geographically Isolated Populations Based Upon Physiologic Studies

Separations of plant populations by physiological analyses have been reported by numerous authors. Hiesey _et al_. (1958-1959) discussed guidelines and methodology for developing a physiologic approach to the study to climatic races. They indicated through the use of cloned plants, separation of interacting ecologic, physiologic and genetic factors was possible.

Milner *et al.* (1958-1959) examined in detail the physiology of two climatic races of *Mimulus cardinalis*. One race was collected from a coastal site and the other from a mid-Sierran population. Cloned plants were used in the study. Results indicated greater light intensities were required by the high elevation population to saturate photosynthesis than for the coastal race. Further, the mid-Sierran collection exhibited higher photosynthetic rates from 10-40°C and dark respiration levels in comparison to the other race.

Mooney and Billings (1961) compared the physiological ecology of arctic and alpine populations of *Oxyria digna* transplanted to a common environment. Results of their study indicated:

1. Arctic plants produced rhizomes, while alpine did not.
2. Phenological development in response to photoperiod was different for the alpine versus arctic populations.
3. Arctic populations exhibited characteristics which indicated they were better adapted to lower temperatures during growth than alpine populations. These included an ability to carry on photosynthesis at higher rates under lower temperatures, and also attain their maximum rates at lower temperatures. Northern populations had higher respiration rates under all temperature conditions.

Baruch (1979) examined elevational differentiation in 3 populations of *Espeletia schultzii* in relation to CO_2 exchange, plant water relations and morpho-anatomical characters. In response to higher elevations, plants exhibited pronounced morphological adaptations. These included thick leaves, dense pubescence and water storing parenchyma. This was in response to the harsher drier environment of higher elevations. Degree of morpho-anatomical development was inversely related to photosynthetic rate. Higher elevation populations showed higher photosynthetic rates when cold acclimated, while lower elevation populations exhibited higher photosynthetic rates when acclimated under warmer temperature conditions.

An examination of the effect of light intensity and temperature on apparent photosynthesis in altitudinal ecotypes of _Trifolium repens_ was reported by Mächler and Nösberger (1977). They found higher altitude plants had greater photosynthetic rates, especially at lower temperatures, than did low elevation populations. Ecotypic differences were related to the environment from which plants were collected. Mächler _et al._ (1977) discussed differences in photosynthates produced from two _Trifolium repens_ ecotypes representing high and low elevational populations. The authors concluded alpine types exhibited higher photorespiration than low elevation collections, although the high elevation ecotypes required low temperatures for optimum photosynthesis. It was suggested low temperatures compensated for potentially high photorespiration activity in the high elevation types; the reduced photorespiration of the low elevation collections was interpreted as an adaptation to warmer habitat conditions. Mächler and Nösberger (1978) further discussed adaptation to temperature of photorespiration and photosynthesis in elevational ecotypes of _Trifolium repens_. CO_2 compensation point increased as temperature increased for both populations, with the lower elevation genotype showing higher values at all temperatures.

McNaughton (1967) reported on differences in photoreduction of 2,6-dichlorophenol-indophenol between high elevation and maritime populations of Typha latifolia. Efficiency of photosystem II for this reaction was negatively correlated to growing season. Photochemical reduction was greatest for a high altitude race selected from a Wyoming population. McNaughton suggested an increased efficiency of reaction represented a compensatory mechanism for plants growing under short growing seasons.

McNaughton (1973) examined photosynthesis and transpiration on Quebec and California ecotypes of Typha latifolia. The two sites were chosen to represent a long growing season and a short growing season genotype. Results indicated under an environmental regime chosen to simulate long growing season conditions, assimilation rates were identical for the two T. latifolia samples. Also, in both populations, photosynthesis declined as a function of leaf age and the rate of decrease was identical for the two populations. Transpiration rates were found to be similar between the two populations and unrelated to leaf age. Significant differences were found in optimum photosynthetic temperatures, with the California collection peaking at 28.6°C and the Quebec population giving optimum photosynthesis at 25.3°C. The primary difference reported between the photosynthetic properties of the two populations was the greater temperature sensitivity exhibited by the Quebec plants. When plants were grown under conditions simulating the Quebec environment, enhanced photosynthesis at the optimum temperature was observed in the Quebec collection. In both populations, broadening of the temperature/photosynthetic curves with leaf age was indicated. A greater photorespiration rate in the Quebec ecotype was also reported. McNaughton concluded differences in assimilation rate between T. latifolia populations were relatively minor in comparison to reports recorded for other species.

McNaughton et al. (1974) examined photosynthetic properties and root chilling response of two low-altitude and two high-altitude populations of T. latifolia. The low-elevation ecotypes were chosen from California populations while the high-elevation types each represented selections from a California and Colorado population. Photosynthetic rates at high CO_2 concentrations were found to be greater for the high elevation population although, light saturation rates and light saturation characteristics were identical between the collections. Root chilling was reported to decrease leaf water content and phosphorus uptake in the low altitude ecotypes. It was suggested that photosynthetic differences between ecotypes plays a minor ecological role in population differentiation, but reduction in water and nutrient uptake may impart strong natural selection in the high elevation types.

An examination of temperature effects in biochemical and morphological traits in T. latifolia populations originating from different ends of a thermal gradient was performed by Jones et al. (1979). The study was conducted along a shoreline of a South Carolina cooling reservoir, with plants sampled at the effluent end of the pond and the far (cool) end of the reservoir. Their results indicated plants selected from locations reacted in similar fashion to a controlled temperature environment.

Germination Response of Ecotypes to Various Incubation Environments

Successful regeneration of sexual species within a plant community is dependent upon the production of propagules adapted to germinate and establish under existing environmental conditions. Because climates, soils and organisms, vary spatially and temporally, natural selection has resulted in the development of differential germination characteristics within populations of a species. The following review describes these ecotypic differences.

Intraspecific variation in germination to controlled incubation conditions has been shown for numerous species. Workman and West (1967), in a study of *Ceratoides lanata* indicated ecotypic variation between collections in germination response to moisture stress and temperature. Selection of alfalfa (*Medicago sativa*) on the basis of their ability to germinate under high osmotic stress has been shown by Dotzenko and Haus (1960) and Redmann (1974). Dewey (1960) examined various strains of *Agropyron* and their ability to germinate under conditions of simulated moisture stress. His results indicated salt tolerance differences of genotypes within a species. Wright (1973) evaluated germination and seed dormancy differences in various cultivars of *Eragrostis lehmanniana*. Seed development and shedding differences for *Lolium multiflorum* has indicated ecotypic development (Harun and Bean 1979).

Germination response of ecotypes has been shown to have adaptive significance in the regeneration strategies of plant species. Young and Evans (1981) have differentiated collections of *Elymus cinereus* from saline and non-saline sites on the basis of germination characteristics. Seeds from non-saline sources exhibited greater germinability to simulated moisture stress than seeds indigenous to saline sites. This aspect was related to natural environmental conditions. It was felt, germination in saline tolerant genotypes was triggered when soils were saturated and dilution reduced moisture stress conditions. This observation for *E. cinereus* was supported by Choudhuri (1968). However, an opposite effect was noted for *Lepidium perfoliatum*. Seeds collected from plants indigenous to saline sites exhibited greater germinability to moisture stress than seeds collected from non-saline areas.

Genotypic response of natural populations to varying temperature environments and pretreatments have indicated differentiation on the basis of natural selection. Within populations of *Salvia columbariae*, ecotypic differences in relation to germination properties and heat pretreatments have been indicated by Capon and Brecht (1970) and Capon *et al.* (1978). They reported germination in warm site ecotypes was enhanced by high temperature pretreatments. Fowler and Dwight (1964) examined the effects of stratification treatments on the germination of *Pinus strobus* L. seeds from eleven provenances. They determined significant differences between seed sources and chill pretreatment, with seeds from northern sources requiring less stratification than seed from southern sources. Lindauer and Quinn (1972) reported on seed germination and ecotypic development in populations of *Danthonia sericea*. Factors examined were temperature, light, prechilling, scarification and after-ripening. Collections from similar habitat types exhibited similar germination responses.

Stocker (1975) in evaluating germination characteristics of common garden plants found differences in high elevation and low elevation populations. He found seeds of _F. idahoensis_ and _A. spicatum_ from high elevation populations had lower germination percentages than seeds from low elevation sources.

Criticism of assessing ecotypic development of natural populations on the basis of seed germination has come from Baskin and Baskin (1973) and Nelson _et al._ (1970). They recommended plants be grown in common gardens and bred true among populations. Seeds would then be collected from these plants and used in the germination trials. This approach would conceivably eliminate environmental factors from differentially affecting seed germination characteristics among populations. However, Lindauer and Quinn (1972) disagree with this approach because in so moving plants to a common garden, the genetic-environmental interactions which occur in a population's natural habitat would be ignored. They feel it is these responses that have adaptive significance and are acted upon by natural selection.
Germination trials of seed collected from natural sources should then reflect the developmental environment of any particular site.

CHAPTER I

SOIL CHEMICAL PATTERNS UNDER PLANT COMMUNITIES DOMINATED BY BIG SAGEBRUSH (ATREMISIA TRIDENTATA NUTT.) IN EASTERN OREGON

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SOIL CHEMICAL PATTERNS UNDER PLANT COMMUNITIES DOMINATED BY BIG SAGEBRUSH (*ATREMISIA TRIDENTATA* NUTT.) IN EASTERN OREGON

ABSTRACT

The objectives of this study were 1) to examine soil nutrient patterning in eastern Oregon plant communities dominated by subspecies of *Artemisia tridentata* Nutt., and 2) to compare soil nutrient levels between adjacent good and poor condition rangeland.

Marked horizontal and vertical soil chemical patterns were evident on all sites. Surface concentrations of nutrients were greatest under shrub and bunchgrass influenced soils in comparison to interspace areas. Values of total nitrogen, organic matter, potassium and phosphorous tended to decrease with depth, while magnesium concentrations generally increased in lower soil horizons. Levels of calcium tended to accumulate in surface soils under shrub canopies, but increased with depth within the interspace and bunchgrass influenced soil zones. Soil pH was generally lower in upper soil horizons. Soil chemical differences between shrub, interspace and bunchgrass influenced soils became less distinct with increased soil depth.

Differences in soil chemical levels between good and poor condition sites were noted, however no consistent patterns were evident. These changes represented a structural rearrangement of the soil nutrient capital, but how they affected functional relationships could not be determined by results of this research.

INTRODUCTION

In semi-arid rangelands, modification of the functional environment by vegetation has resulted in distinct plant-induced soil chemical patterns. Numerous studies have shown this to be a common occurrence in shrub dominated ecosystems (Fireman and Hayward 1952; Rickard and Keough 1968; Sharma and Tongway 1973; Charley and West 1975). Localization and decomposition of above and below ground litter has led to nutrient accumulations under shrubs as compared to adjacent bare soil zones (Bjerregard 1971). Increased surface concentrations of total nitrogen, organic phosphorous, organic sulfur, monovalent and divalent cations and organic carbon generally occur beneath shrub canopies (Fireman and Hayward 1952; Tiedemann and Klemmedson 1973; Charlie and West 1975). Changes in soil pH have been shown to be a function of the vegetation present on a site. Increased pH levels generally exist under halophytic shrub species when compared to adjacent bare soil areas (Sharma and Tongway 1973), but tend to be lower than surrounding soils for non-saline xerophytic shrub communities (Charley and West 1975). The net effect of these changes in soil nutrient capital for semi-arid shrublands has been the partioning of structural and functional relationships in a horizontal and vertical fashion.

Although a few studies have documented soil nutrient patterns in big sagebrush (Artemisia tridentata Nutt.) communities (Fireman and Hayward 1952; Charley and West 1975), a comprehensive evaluation of sites differentiated by subspecies of big sagebrush has not been performed. Further, studies have not included comparisons of the perennial herbaceous component in the evaluation of soil nutrient patterns and also examined differences between adjacent good versus poor condition rangelands.

The primary objectives of this research were: 1) to examine soil chemical patterning in eastern Oregon plant communities dominated by subspecies of big sagebrush, and 2) to compare soil nutrient levels between adjacent good and poor condition rangeland. The importance of examining soil nutrient patterns for sagebrush grassland ecosystems are as follows: First, because rooting depth, litter quality and plant phenology differ for species within a community, an evaluation of soil nutrient patterns that exist as a result of synecological interactions and outside environmental factors, may provide an increased understanding of structural and functional relationships in big sagebrush sites. Second, a comparison of these patterns for good versus poor condition range might indicate shifts in soil fertility resulting in declining ecological condition. These changes may conceivably enhance the competitiveness and perpetuation of big sagebrush on sites in poor condition.

DESCRIPTION OF STUDY AREA

In order to facilitate the contrast between range condition classes, selection of sample areas was on the basis of locating adjacent mature, even-aged good and poor condition sites. An *Artemisia tridentata* spp *vaseyana*/*Festuca idahoensis* - *Agropyron spicatum* (ARTRV/FEID-AGSP) habitat type was identified near Baker, Oregon. Both an *Artemisia tridentata* spp *tridentata*/*Elymus cinereus* (ARTRT/ELCI) and an *Artemisia tridentata* spp *wyomingensis*/*Stipa thurberiana* (ARTRW/STTH) habitat type were located at the Squaw Butte

Experiment Station west of Burns, Oregon. At each sample area, a fence line contrast separated past land use activities.

For the ARTRV/FEID-AGSP site, the good condition range had a history of fall sheep grazing, while the poor condition community had been consistently grazed spring and summer by cattle. The dominant grass species in the high seral stand were *Agropyron spicatum* and *Festuca idahoensis*, with *Poa sandbergii* the only understory perennial present on the poor condition site at the Squaw Butte location. The good condition ARTRW/STTH and ARTRT/ELCI communities were located in areas excluded from grazing the past 40 years, while both poor condition communities were presently being used as spring and summer range by cattle. *Elymus cinereus* was the dominant understory species on the good condition ARTRT/ELCI habitat type. *Sitanion hystrix* and *Stipa thurberiana* were most prevalent in the understory of the poor condition range. Vegetation of the high seral ARTRW/STTH stand was characterized by an understory dominance of *Sitanion hystrix* and *Stipa thurberiana*. *Sitanion hystrix* was the only grass species present in the adjacent low seral community.

At each study site, cover of big sagebrush plants and dominant grass species not directly under the sagebrush canopy were recorded. Soil characteristics were also noted for each location. Vegetative and soils information in each of the three study areas is given in Table 1.

MATERIAL AND METHODS

For each plant community and condition class, the vegetative-soil resource was stratified into the following 3 horizontal functional groups: under-shrub canopy (S), bare soil interspace (I), and under-grass crown area (G). At each study site, 10 mature big sagebrush plants were randomly located and served as collection areas for the S soil samples. These 10 sagebrush plants were also used as reference points for the selection of an equal number of I and G sampling areas. Interspace soils adjacent to the selected sagebrush plants were sampled for assessment of nutrient levels. The immediate area around the selected sagebrush plant frequently was void of a dominant perennial bunchgrass individual not influenced by the sagebrush canopy. When this occurred, the nearest plant or plants which provided sufficient soils material for evaluation were selected for sampling. If 2 grass species were judged to be dominant within the same plant community, sampling of the G functional group was evenly split between the two species. These samples were then collectively analyzed. *Agropyron spicatum* and *Festuca idahoensis* were sampled in the high seral stand of the ARTRV/FEID-AGSP habitat type, while *Poa sandbergii* was assessed on the adjacent low seral community. For the ARTRT/ELCI habitat type, *Elymus cinereus* was evaluated on the good condition site and *Stipa thurberiana* and *Sitanion hystrix* sampled on the poor condition site. Grass species sampled in the good condition community of the ARTRW/STTH habitat type included *Stipa thurberiana* and *Sitanion hystrix*, while *Sitanion hystrix* was the only species assessed on the adjacent low seral site.

Vertical sampling of soils material was performed at 3 depths which corresponded to different morphological units. At the ARTRV/FEID-AGSP and ARTRW/STTH study sites, depths of 0-10 cm, 10-20 cm and 20 cm down to restrictive horizon were assessed. Soils on the

ARTRT/ELCI habitat type were deeper and samples taken from depths of 0-10 cm, 10-25 cm and 25 cm to restrictive horizon. Approximately 0.5 kg of soils material was collected from each of these depths. Under all surface conditions, superficial organic debris was removed prior to sampling. Following recommendations of Charley and West (1975), the zone of maximum surface litter accumulation under the shrub canopy was used as the site for vertical soil sampling. Excavation of soils under bunchgrass plants were made directly under the crown area.

Sampling the ARTRV/FEID-AGSP and ARTRT/ELCI study sites was performed during August, 1980. The ARTRW/STTH community was sampled during the same time period in 1981. Within condition classes at each habitat type 180 soil samples were collected. Obvious root material and organic debris were removed prior to chemical analysis.

Soils analysis was performed at the Oregon State University Soil Testing Laboratory and the following evaluations performed: total nitrogen was determined using the Kjeldahl method as outlined by Bremner and Edwards (1965); organic matter was estimated utilizing the wet oxidation-titration method of Walkley and Black (1934); extraction of soil phosphorous was conducted using the procedure of Olsen and Dean (1965). A modification of the technique outlined by Pratt (1965) was used to assess soil potassium. Instead of a multiple extraction of soil by extractant a single equilibration of the sample was used. Calcium and magnesium levels were determined using an ammonium acetate method (Peech _et al_. 1947). Soil pH was measured by utilizing a 1:2 soil to solution ratio and glass electrode pH meter (Jackson 1958).

Analysis of variance with a completely randomized design and Tukey's w-procedure were used to test differences ($\alpha = 0.05$) between functional groups at a given soil horizon and between soil horizons under a given functional group. A student t-test was utilized to assess differences ($\alpha = 0.05$) between adjacent good vs. poor condition rangeland (Steele and Torrie 1980).

RESULTS

Horizontal and Vertical Changes

The presence of vegetation significantly affected the horizontal and vertical distribution of soil nutrients in the sagebrush-grassland habitat types studied (Figures 1-3). Trends in the spatial distribution of soil chemical patterns indicated:

1) greater concentrations of nutrients under S and G influenced soils than adjacent I soils,

2) decreased levels of total nitrogen, organic matter, potassium and phosphorous as soil depth increased,

3) generally lower soil pH levels in the upper horizons than the lower horizons regardless of functional group, although no significant change with depth was detected for shrub influenced soils on the ARTRV/FEID-AGSP habitat type,

4) greater concentrations of magnesium in the lower soil horizons, especially on the ARTRT/ELCI and ARTRW/STTH habitat types,

5) surface accumulations of calcium under S influenced soils,

6) either no change or an increased calcium concentration as depth increased for the I and G functional groups,

and, 7) less distinct soil chemical differences between S, I and G functional groups as soil depth increased.

In addition to the patterns described above, accumulations of certain soil chemicals were often significantly greater in surface soils under the shrub canopy than soils influenced by the G functional group. This relationship was evident for 1) total nitrogen, phosphorus, potassium and calcium in the poor condition stand of the ARTRV/FEID-AGSP habitat type, 2) total nitrogen, organic matter and phosphorus in the good condition community and phosphorus, potassium, calcium and magnesium in the poor condition community of the ARTRT/ELCI habitat type, and 3) total nitrogen, organic matter and potassium within the low seral stand, plus phosphorus and calcium in the high seral stand of the ARTRW/STTH habitat type.

Good vs. Poor Condition Rangeland

The percentage of land area occupied by each functional group changed in response to ecological condition. Shrub cover increased and bunchgrass cover declined going from high seral to low seral plant communities within each habitat type (Table 1). Although coverage of interspace areas was not recorded, the percentage of bare ground was noticeably greater in the poor condition communities. Grass species in the low seral sites were characteristically reduced in vegetative growth and basal area. This was in contrast to the robust and vigorous appearance of grasses in the good condition stands. From observations of the G functional group during soil excavation, rooting depth and volume of soil occupied by roots were considerably less on the poor condition sites than the adjacent high seral plant communities.

Distributions of total nitrogen, soil chemicals, organic matter, phosphorus and potassium with respect to soil sampling position and habitat type for good versus poor condition rangeland are presented in Figures 1-3. The relationship between declining nutrient level with increasing soil depth and the impact vegetation has on horizontal soil chemical concentrations is apparent from these depictions.

Although differences between absolute levels of soil nutrients between good and poor condition sites were indicated in some instances, generalized trends across the three habitat types were not evident. In general, the good condition ARTRT/ELCI site had higher levels of soil chemicals at the three sampling depths when compared to the adjacent poor condition site. Only phosphorous did not exhibit significant differences at the >25 cm soil sampling depth. Except for a decreased level under good condition shrub canopies, soil pH did not significantly differ between good and poor condition plant communities.

Surface concentrations of potassium and entire soil profile levels of calcium and magnesium on the ARTRW/STTH habitat type tended to be higher within the poor condition area than the good condition exclosure. Consistently, lower values of total nitrogen, and organic matter were noted on the good condition site as depth increased. Surface levels of these soil chemicals generally did not significantly differ. Soil pH in the upper horizon was not distinguishable between the two condition classes. However, as soil depth became greater, pH levels increased under S and I zones for the high seral community. Phosphorous concentrations below the 10 cm sampling depth were not significantly different between the good and poor condition sites.

For the ARTRV/FEID-AGSP habitat type, surface concentrations of phosphorous, potassium, total nitrogen and calcium tended to be greater under the shrub canopy on the poor condition sample site than the good condition range. Organic matter and potassium in surface G horizons declined on the poor condition site, but I soils did not significantly differ in surface nutrient levels. Soil pH and magnesium values were similar between the two plant communities in the upper soil horizons. Subsurface concentrations of soil chemicals varied in response to condition class, but as in the surface horizons, no clear cut trends between ecological condition and soil nutrient response were evident. differences in total nitrogen, organic matter, and potassium between the poor and good condition range for the I and G influenced soils tended to become nonsignificant as depth of soil increased. However, S values for organic matter, total nitrogen and phosphorous on the good condition soils were significantly greater at 10-20 cm depth, and with the addition of potassium become significantly less than the levels on the poor condition site for the >20 cm soil horizons. Magnesium and calcium concentrations were generally greater deeper in the profile on the high seral community in comparison to the low seral stand.

At all locations, potassium levels were greater under the good condition G functional group when compared to the poor condition plant community. No other soil chemical exhibited this trend.

Comparisons Between Habitat Types

Owing to differences in year sampled, parent material and geographic location, statistical analyses of soil chemical characteristics between plant communities were not performed. However, an examination of the information provided in Figures 1-3 revealed certain obvious trends existing between sites. Levels of soil organic matter and total nitrogen tended to be higher in I areas and at lower depths on the more mesic ARTRV/FEID-AGSP habitat type in relation to the ARTRT/ELCI and ARTRW/STTH habitat types. Soil phosphorous, however, was noticeably greater only in the lower horizons of the ARTRV/FEID-AGSP site when compared to the other two habitat types. Further, soil pH levels were generally found to be higher on the ARTRT/ELCI and ARTRW/STTH sites than those encountered in the ARTRV dominated communities. This may be attributed to parent material differences and/or differential organic matter decomposition rates between the sites. Relative accumulations of potassium under the S influenced soil in comparison to adjacent I areas appeared to be enhanced within the ARTRT/ELCI and ARTRW/STTH communities.

DISCUSSION

Regardless of range condition class or habitat type, the sagebrush/gasssland plant communities evaluated in this research show distinct horizontal and vertical soil chemical patterning. Under vegetation influenced soil, surface accumulations of total nitrogen, organic matter, phosphorous and potassium are most likely the result of localization and concentration of litter. Greater amounts of magnesium are found at lower soil depths under all functional groups, probably originated from soil developmental factors. Accumulations of calcium under the shrub canopy may be attributed to relatively higher concentration of calcium in sagebrush leaf litter (Mack 1978) in comparison to perennial bunchgrasses (Uresk and Cline 1976). Decreased pH values on the soil surface were probably caused by decomposition of organic matter and production of organic acids and leaching of soil carbonates to deeper soil horizons. Differences in soil pH between plant communities probably result from an interaction of soil parent materials with differential soil leaching and rates of organic matter decomposition.

The examination of soil nutrient patterns for sagebrush/grassland ecosystems provides insights into the functional and structural relationships that exist on these sites. Results of this research tend to support the contention of Tiedemann and Klemmedson (1973) that accumulations of soil chemicals enrich the soil nutrient capital of vegetation influenced soils, at the expense of bare soil areas. This is an important adaptation by arid land species which enable them to better cope with a moisture limited environment. During relatively brief periods of adequate soil moisture, optimization of uptake by having a readily available source of nutrients in close proximity to the plant would seemingly enhance growth. Nutrient accumulations conceivably improve competitiveness and perpetuation of plants in semi-arid ecosystems.

One interesting relationship that appeared in the results of this research was the high surface accumulations of potassium under sagebrush plants at all locations and grasses in the good condition ARTRT/ELCI and ARTRV/FEID-AGSP plant communities. Potassium is generally considered one of the most mobile ions in leaves and is rapidly leached during decomposition (Mack 1978). Why these species accumulate potassium in upper soil horizons is not entirely clear. Results for other nonhalophytic shrub species do not indicate a similar pattern of surface potassium accumulation under shrub influenced soils (Tiedemann and Klemmedson 1973; Brotherson and Osayande 1980).

The enhancement may be related to the volume of soil available to the plant for root exploration, and the subsequent uptake of potassium in excess of the plants' needs. From observation of plants present on the various sites, the big sagebrush individuals and understory perennial grasses accumulating potassium would have to be considered larger and deeper rooted than those which did not show this affect.

A possible ecological advantage which may be conferred to plants which enrich their upper soil horizons with potassium may be related to interactions with soil nitrogen. Evidence suggests internal potassium recirculation to be an important factor in facilitating the uptake and distribution of nitrate (Ben Zioni _et al_. 1971; Armstrong and Kirby 1979). Because nitrate tends to be the dominant form of nitrogen in the upper soil layers for semi-arid shrublands (Charley and West 1977) and plant roots generally fully occupy these soil horizons (Sturges 1977; Cline _et al_. 1977), enhanced levels of soil potassium may promote rapid absorption and internal translocation of nitrate during relatively brief periods of active surface mineralization. Thus, mineral nutrition of the plant may be improved, and growth accelerated when soil moisture is available.

These observations may help to explain the persistence of sagebrush on denuded rangelands, even after excessive livestock grazing has been removed. As ecological condition declines, the composition and percentage of the various functional groups apparently shift in relation to one another. The pattern of change is one of an increased proportion of land area occupied by S and I zones at the expense of the G component (Shown _et al_. 1972).

Associated with the decline in the prevalence of the G functional group is a decrease in the depth and volume of the root network. This is the result of 1) a change from deep-rooted high seral species to inherently shallower rooted low seral species, and 2) repeated defoliation which may further reduce individual plant basal area and root biomass. The net effect of a limited root system is a decreased proportion of soil available for extraction of soil nutrients. Because sagebrush plants typically exhibit a well developed lateral and vertical root network (Sturges 1977), they appear better adapted on poor condition sites to remove soil nutrients from adjacent interspace areas and deeper in the soil profile than the grasses present within the community. Thus, the persistence and competitiveness of sagebrush plants may be promoted on deteriorated rangelands.

Although no consistent patterns of increase or decrease in quantitative levels of soil nutrients were noted as range condition declined, these changes may be associated with subsequent alterations in mineral cycling properties of the ecosystem. For instance, the increased density and biomass of sagebrush on poor condition rangelands, may represent a shift from a system characterized by a high herbaceous litter turnover, to one which has a smaller yearly organic input and slower decomposition rates. This would be the result of two factors: 1) the production of woody perennial structures which persist on the plant for long term periods and tie-up a portion of the nutrient pool, and 2) the relatively slow decomposition rates of sagebrush foliage due to its high terpenoid content and woody nature of stems and roots. The net effect of these modifications are not clear, but functionally mineral cycling rates should be retarded on poor condition sagebrush-grasslands. Because plant succession is a dynamic process, the slowing of mineral cycling within the system coupled with the longevity of big sagebrush individuals should enhance the perpetuation of the shrub component within the community. The extent to which these changes have altered plant community interrelationships requires additional research.

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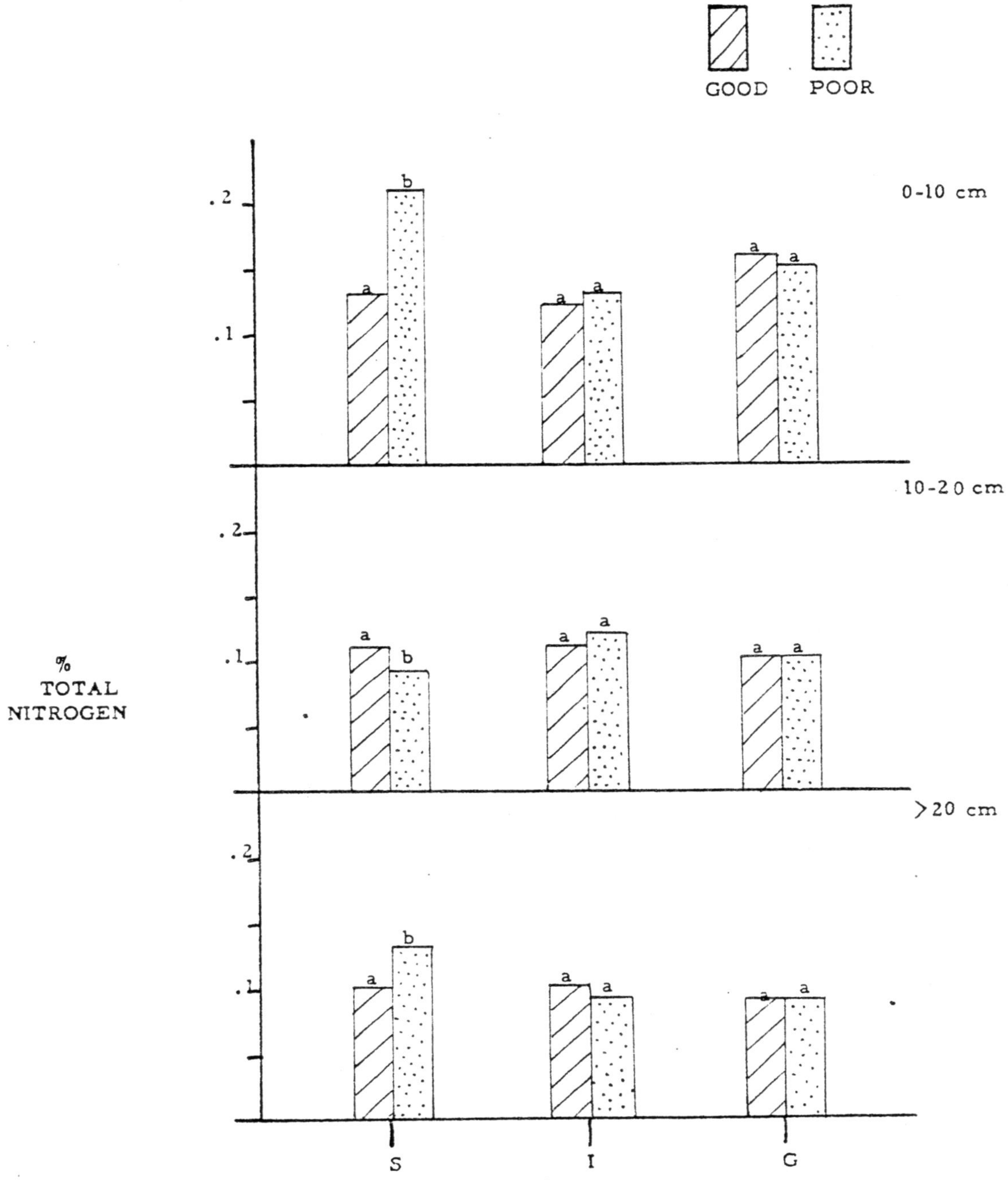
Table 1. Vegetation and soil characteristics of the study areas.

Habitat Type	Elevation (meters)	Site Location	Shrub Cover %		Grass Cover %		Soil Classification	Soil Texture of Surface Horizon
			Good	Poor	Good	Poor		
ARTRV/FEID-AGSP	1066	NE¼NE¼S24 T7SR41E	9.5	19.1	17.5	3.6	Typic haploxeroll	Loam
ARTRT/ELCI	1372	SE¼SW¼S24 T24SR25E	20.0	26.0	27.5	8.2	Xerollic durorthid	Sandy Loam
ARTRW/STTH	1372	SW¼NE¼S35 T24SR25E	15.3	21.3	21.3	2.3	Xerollic durorthid	Sandy Loam

Figure 1. Spatial distribution between shrub (S), interspace (I) and grass (G) influenced soils at 3 depths for adjacent good and poor condition stands of an *Artemisia tridentata* ssp. *vaseyana*/*Festuca idahoensis*-*Agropyron spicatum* habitat type. (Similar letters denote non-significant differences (α=.05) between adjacent bar graphs.)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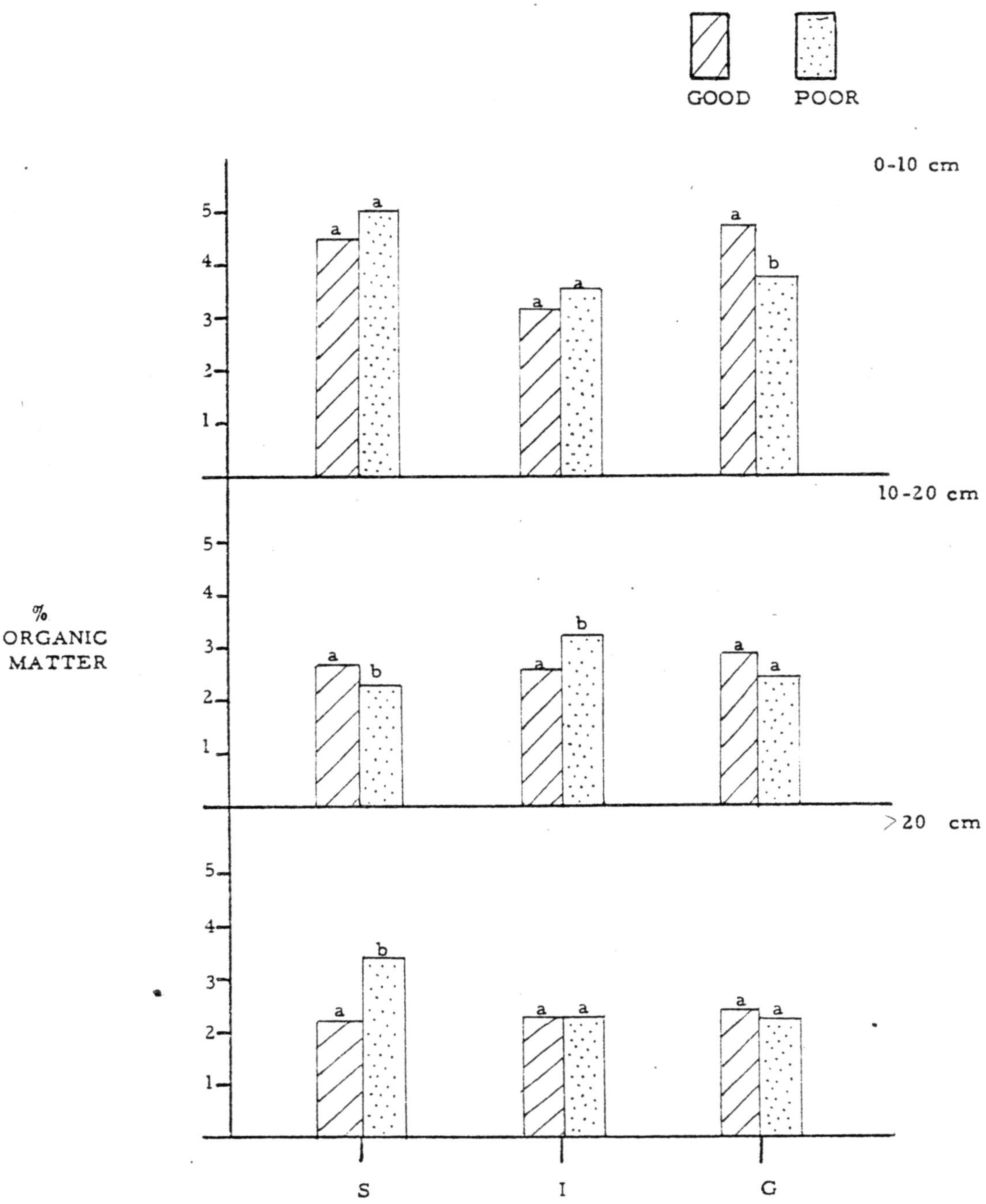
POOR
% TOTAL NITROGEN
0-10 cm
10-20 cm
>20 cm
.2
.1
a
b
S
I
G


GOOD
POOR
0-10 cm
10-20 cm
>20 cm
% ORGANIC MATTER
1
2
3
4
5
a
a
a
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b
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a
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a
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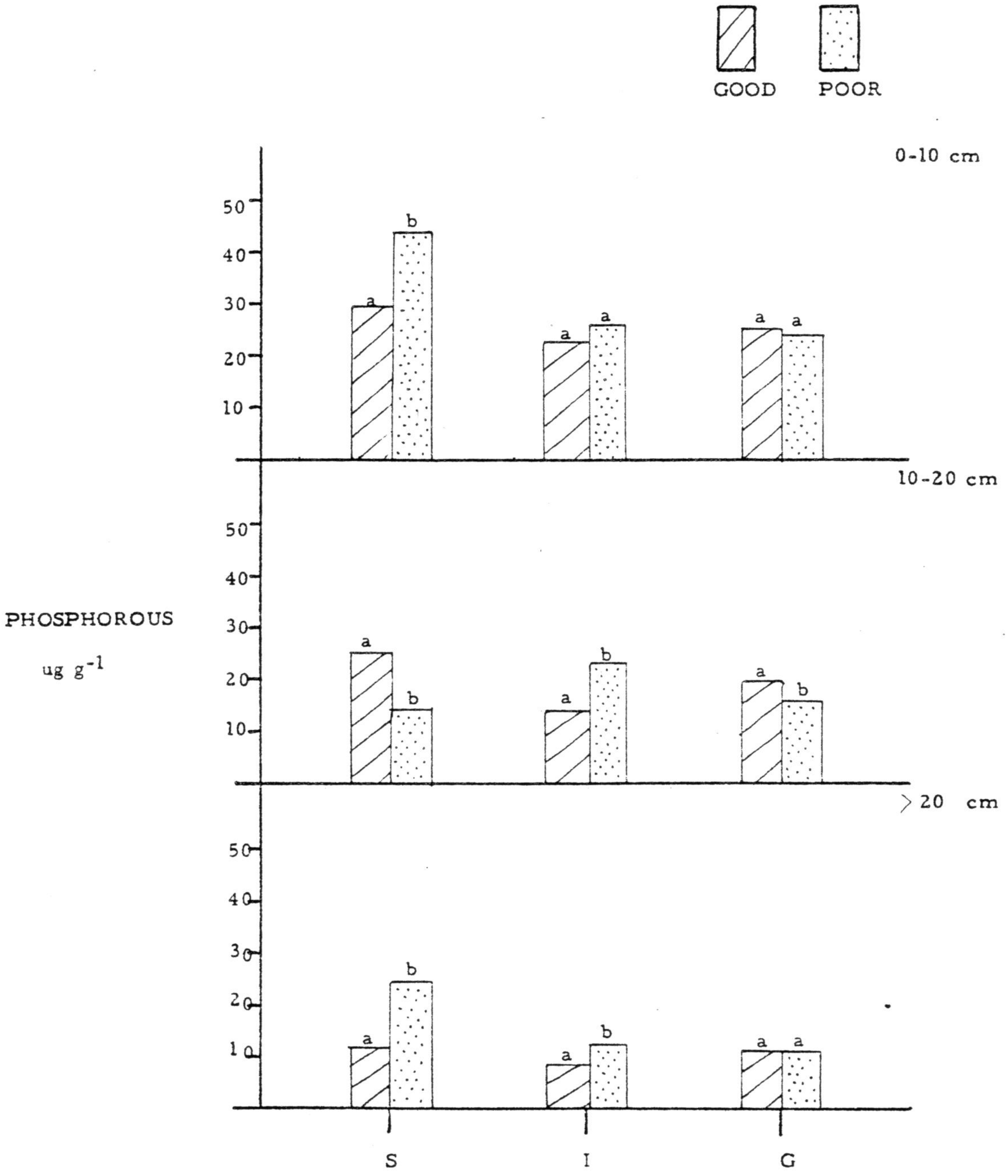
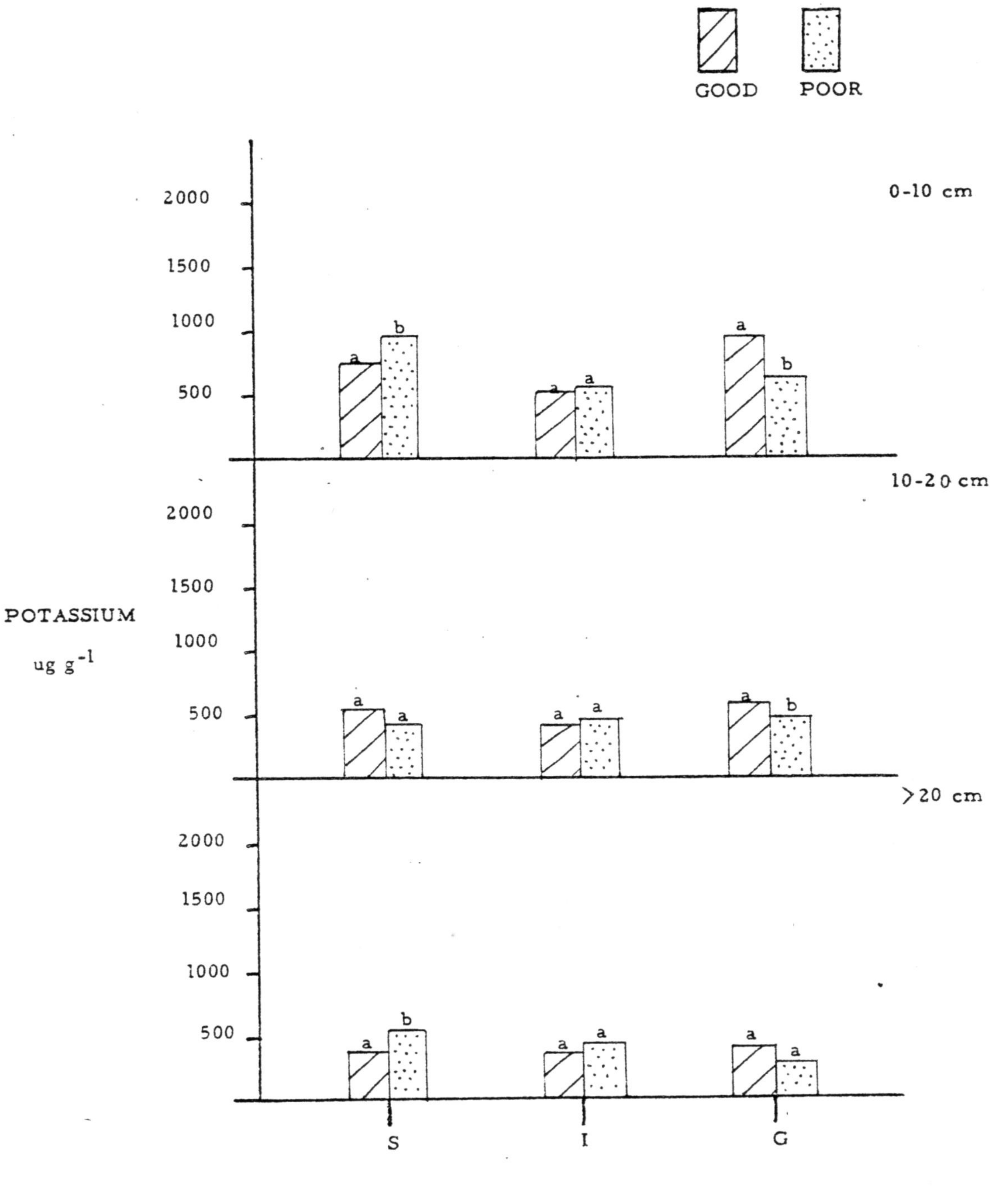
a
a
a
S
I
G


GOOD
POOR
0-10 cm
10-20 cm
> 20 cm
PHOSPHOROUS
ug g-1
50
40
30
20
10
a
b
S
I
G


GOOD
POOR
0-10 cm
10-20 cm
>20 cm
POTASSIUM
ug g^{-1}
2000
1500
1000
500
a
b
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a
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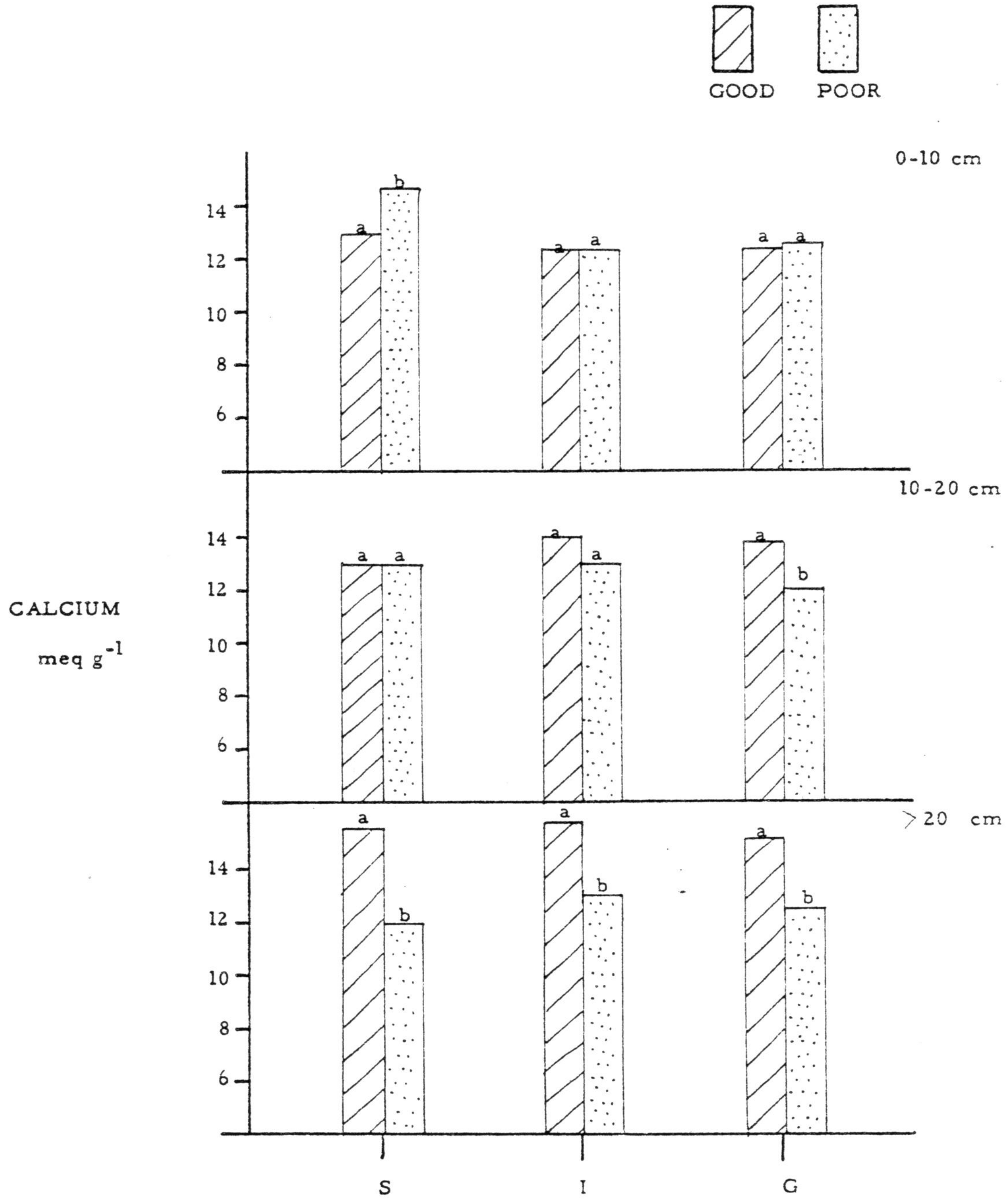
a
a
a
a
S
I
G


GOOD
POOR
0-10 cm
10-20 cm
> 20 cm
CALCIUM
meq g^{-1}
14
12
10
8
6
a
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a
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a
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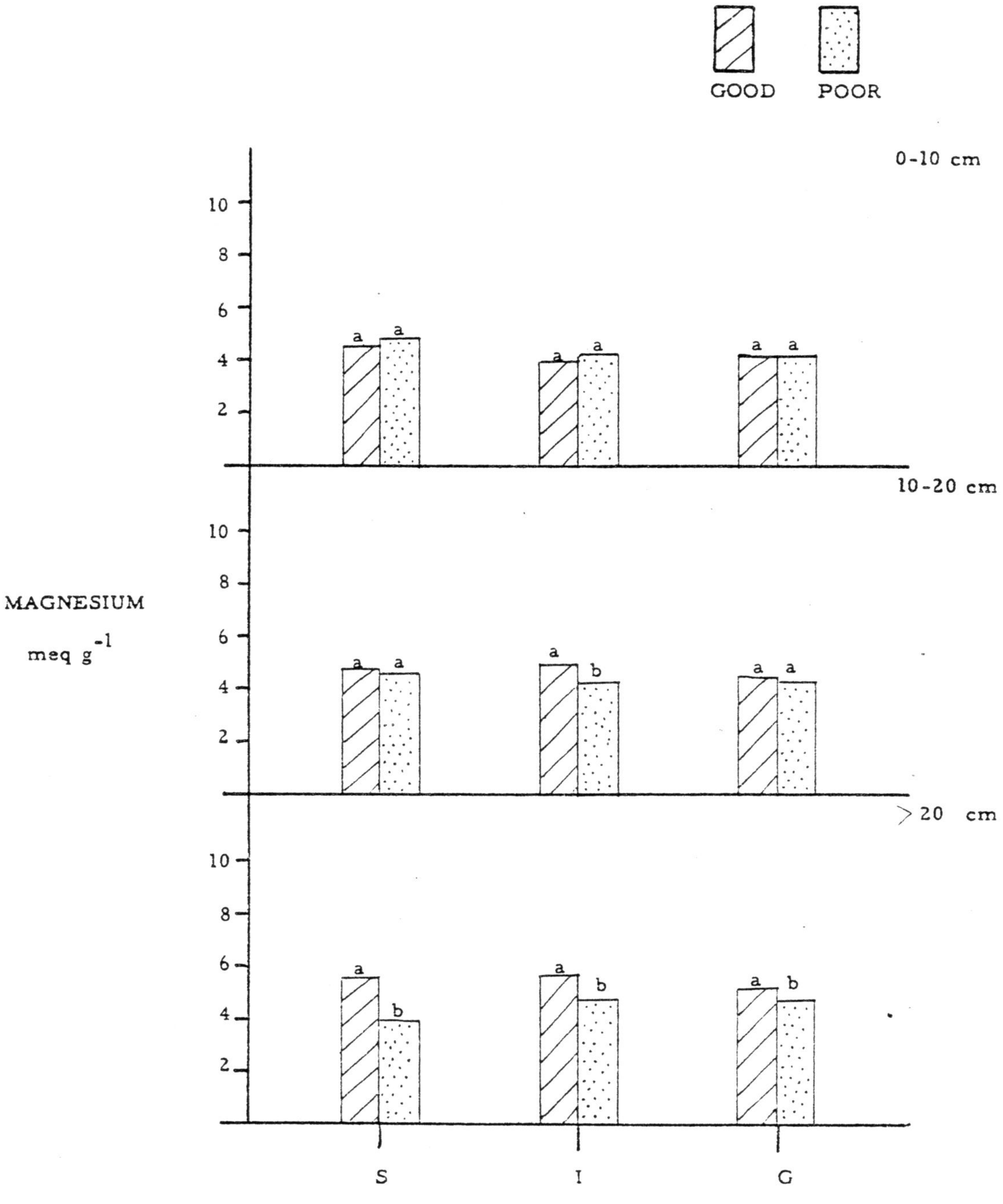
a
b
a
b
S
I
G


GOOD
POOR
0-10 cm
10-20 cm
> 20 cm
MAGNESIUM
meq g-1
10
8
6
4
2
a
b
S
I
G

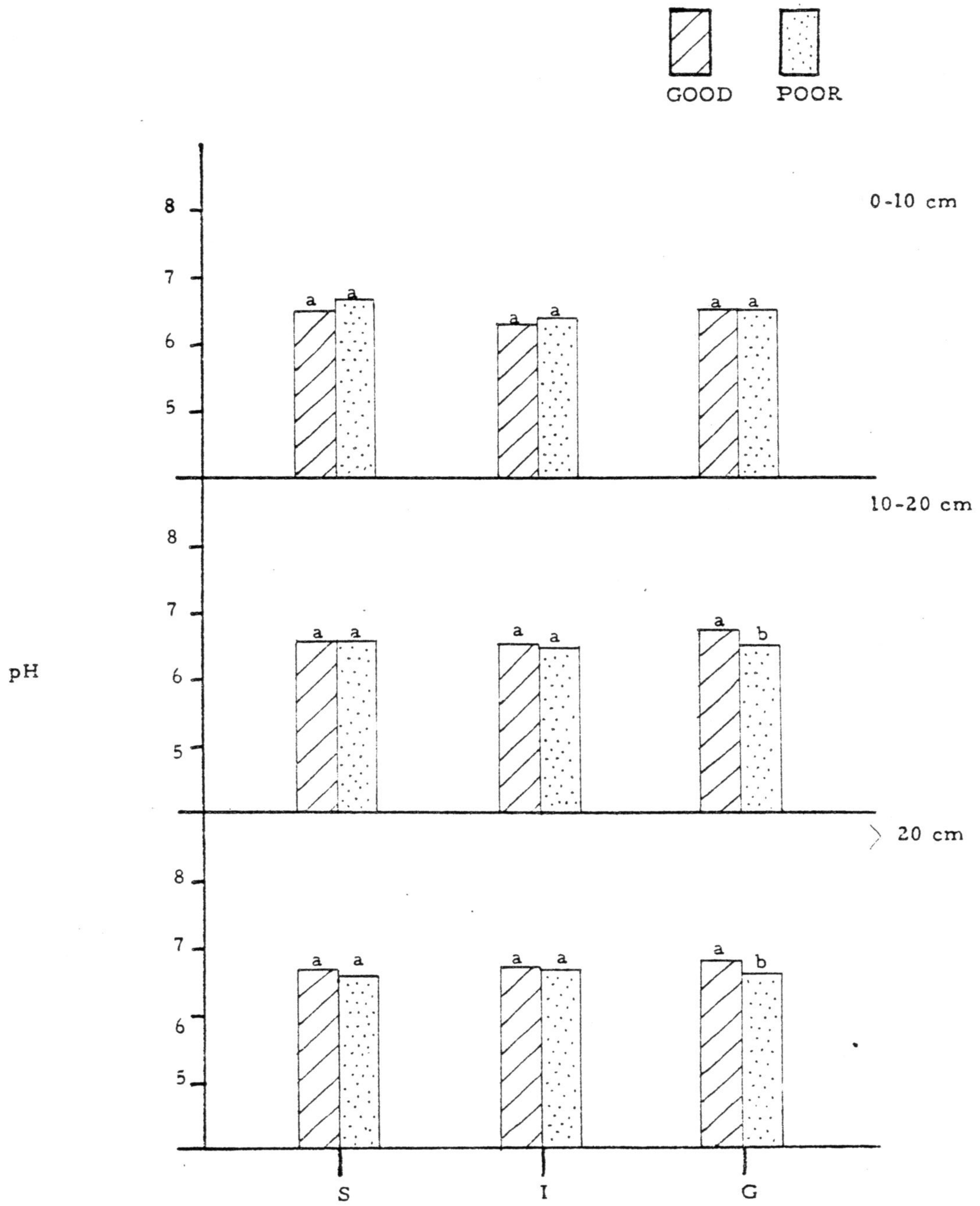
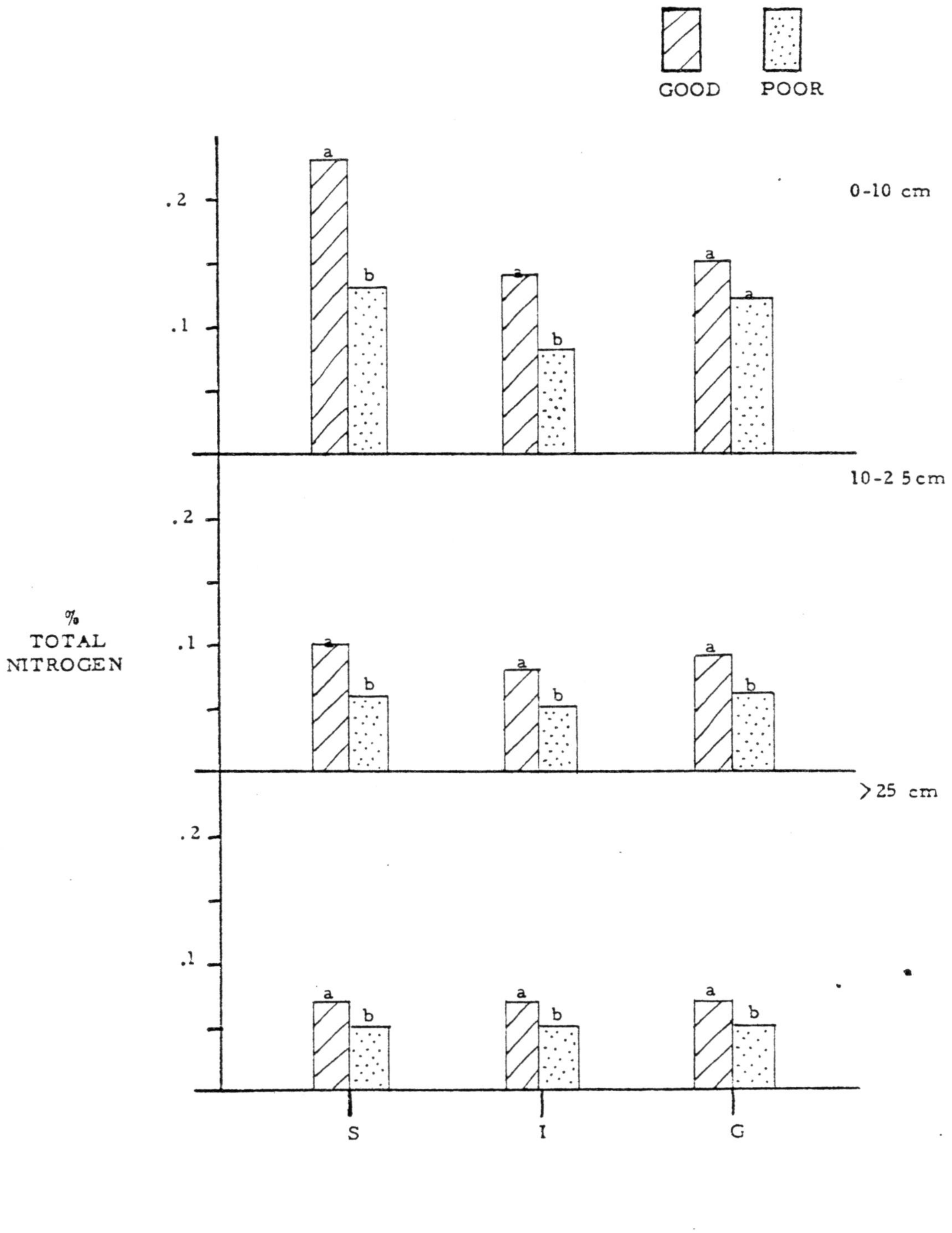
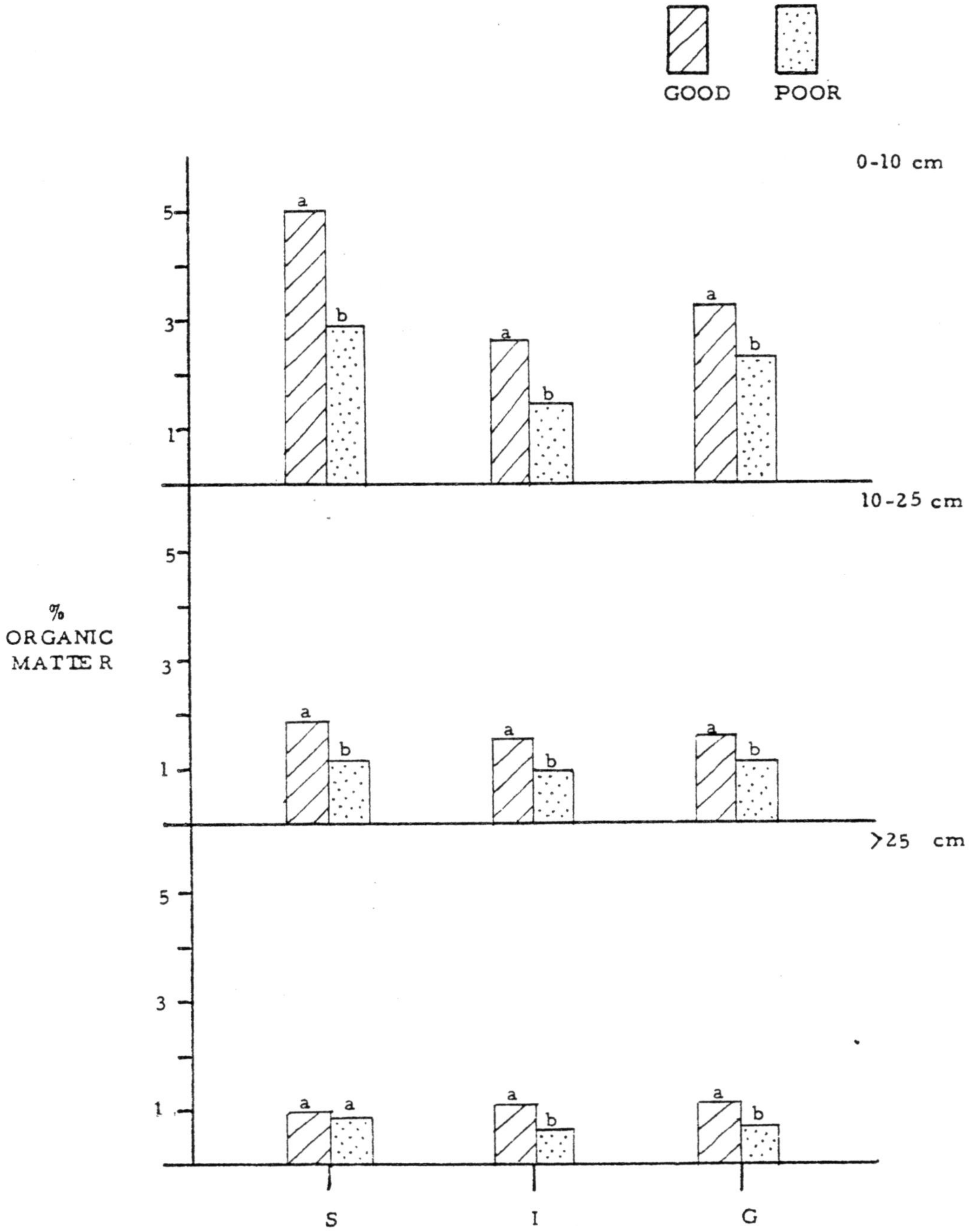
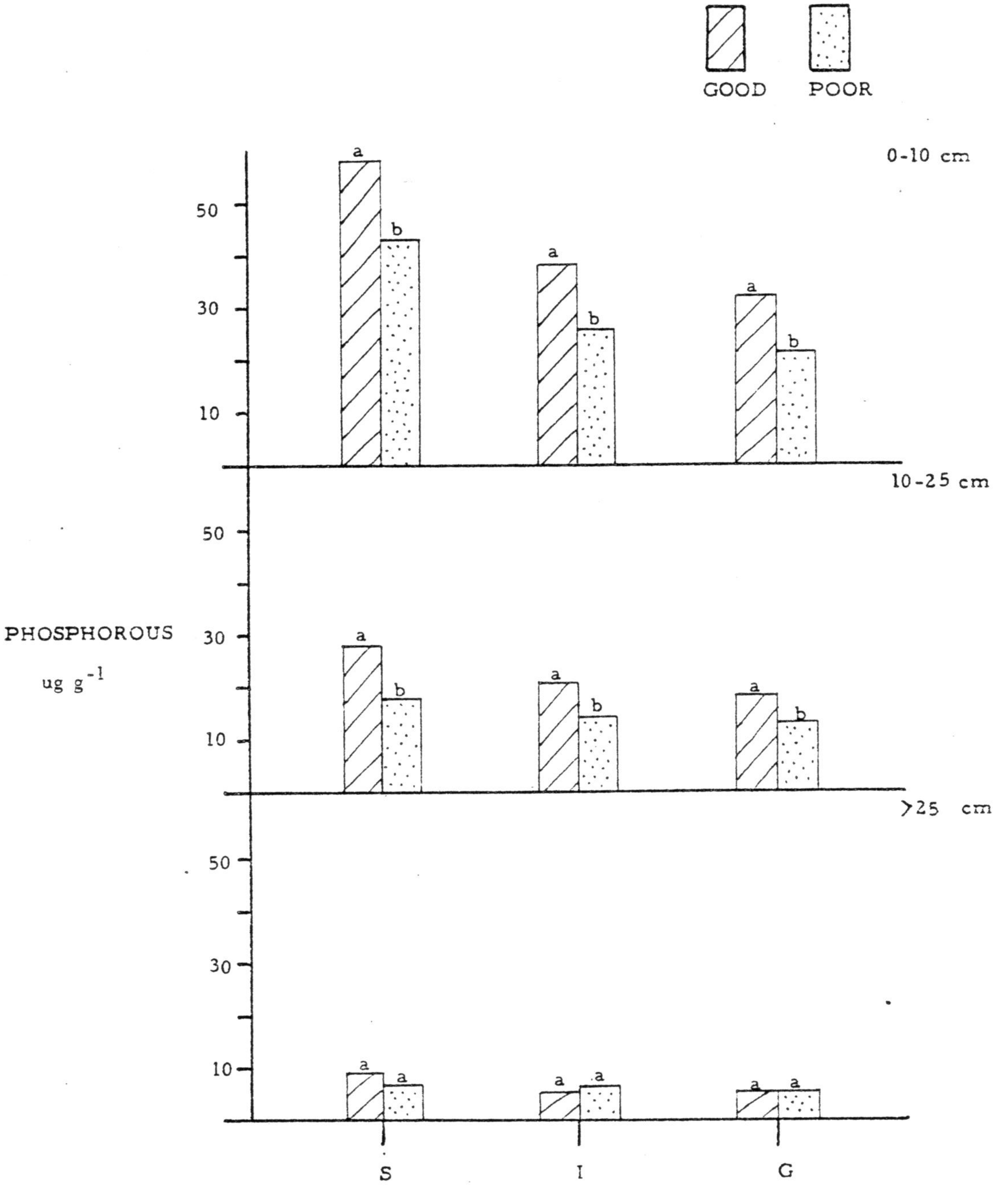
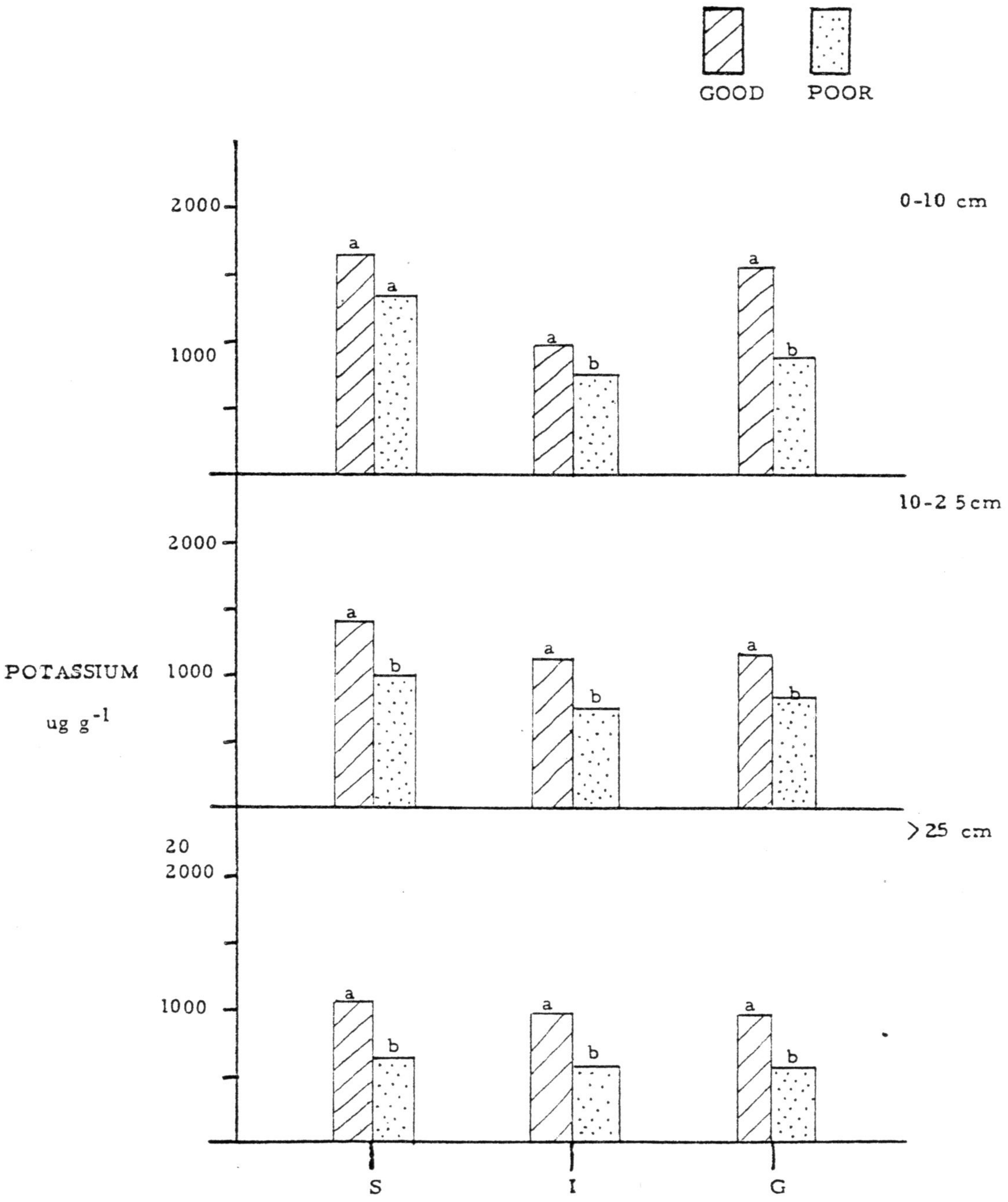

GOOD
POOR
pH
0-10 cm
10-20 cm
> 20 cm
8
7
6
5
a
a
a
a
a
a
a
a
a
a
a
b
a
a
a
a
a
b
S
I
G

Figure 2. Spatial distribution between shrub (S), interspace (I) and grass (G) influenced soils at 3 depths for adjacent good and poor condition stands of an *Artemisia tridentata* ssp. *tridentata*/*Elymus cinereus* habitat type. (Similar letters denote non-significant differences (α=.05) between adjacent bar graphs.)


GOOD
POOR
0-10 cm
10-2 5cm
>25 cm
%
TOTAL
NITROGEN
.2
.1
a
b
S
I
G


GOOD
POOR
0-10 cm
10-25 cm
>25 cm
%
ORGANIC
MATTER
5
3
1
a
b
S
I
G


GOOD
POOR
0-10 cm
10-25 cm
>25 cm
PHOSPHOROUS
ug g⁻¹
50
30
10
a
b
S
I
G


GOOD
POOR
0-10 cm
10-2 5cm
>25 cm
POTASSIUM
ug g-1
2000
1000
2000
1000
20
2000
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a
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b
a
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a
b
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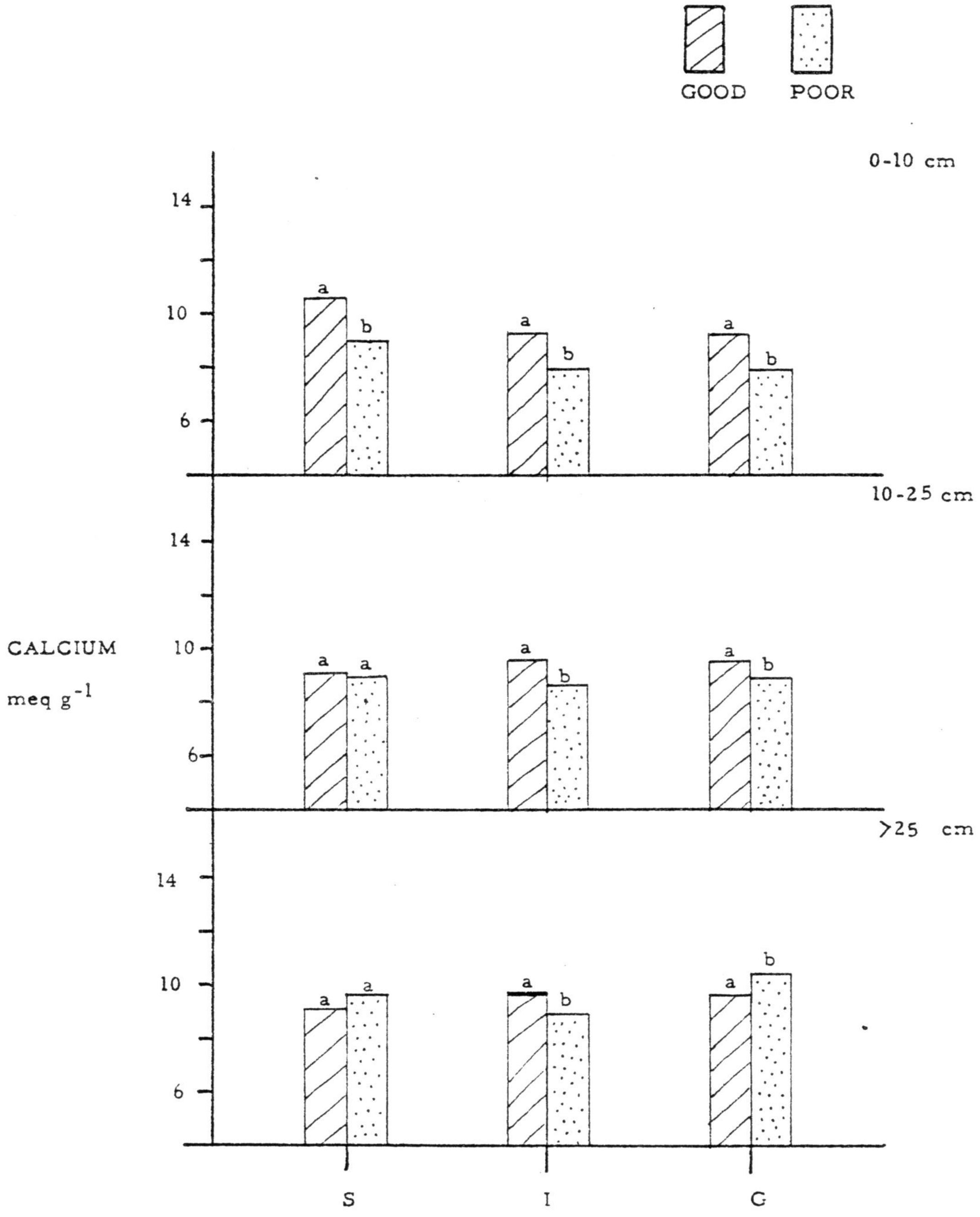
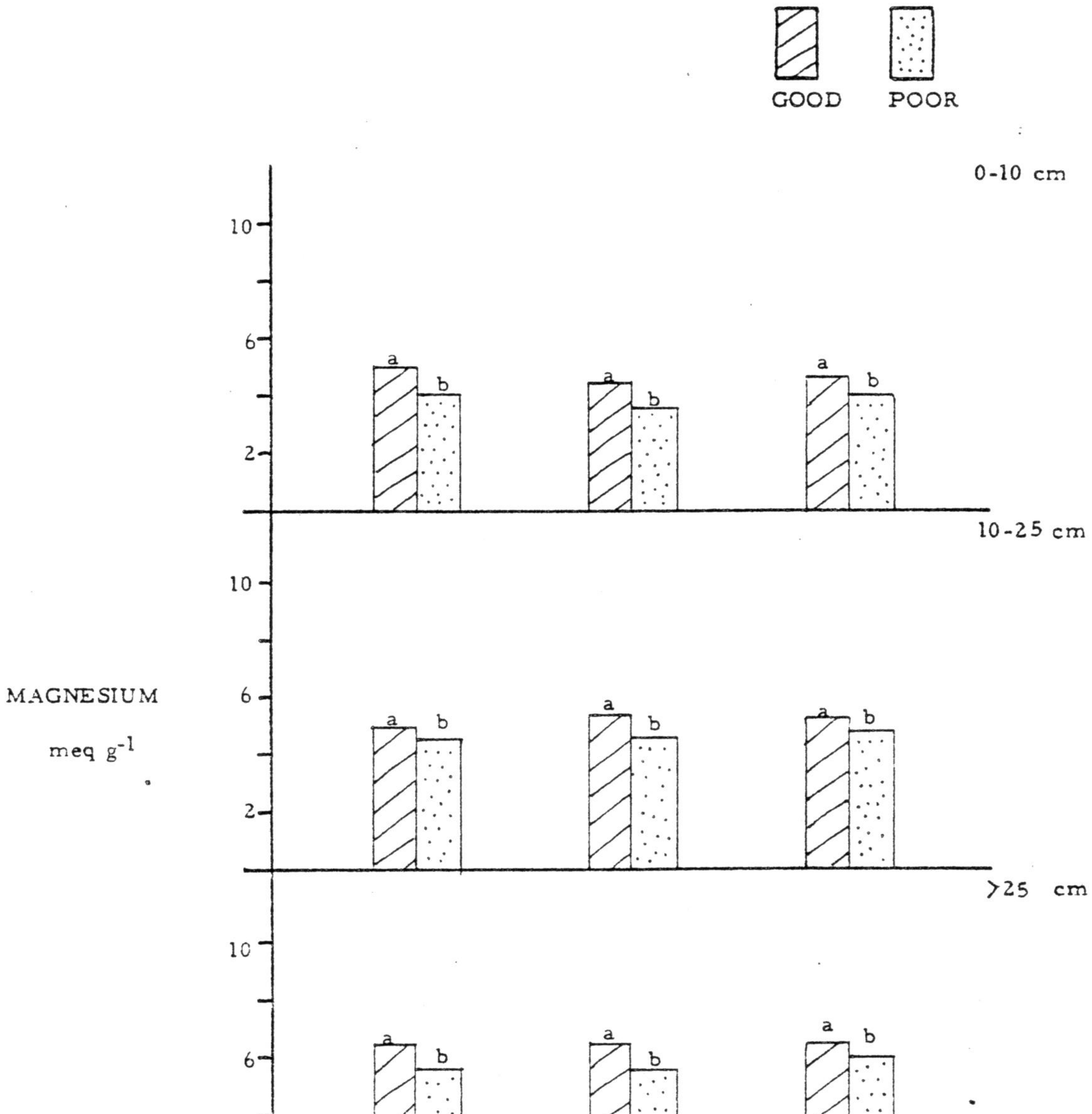
a
b
a
b
S
I
G


GOOD
POOR
0-10 cm
10-25 cm
>25 cm
CALCIUM
meq g-1
14
10
6
a
b
S
I
C


GOOD
POOR
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10-25 cm
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MAGNESIUM
meq g-1
10
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2
a
b
S
I
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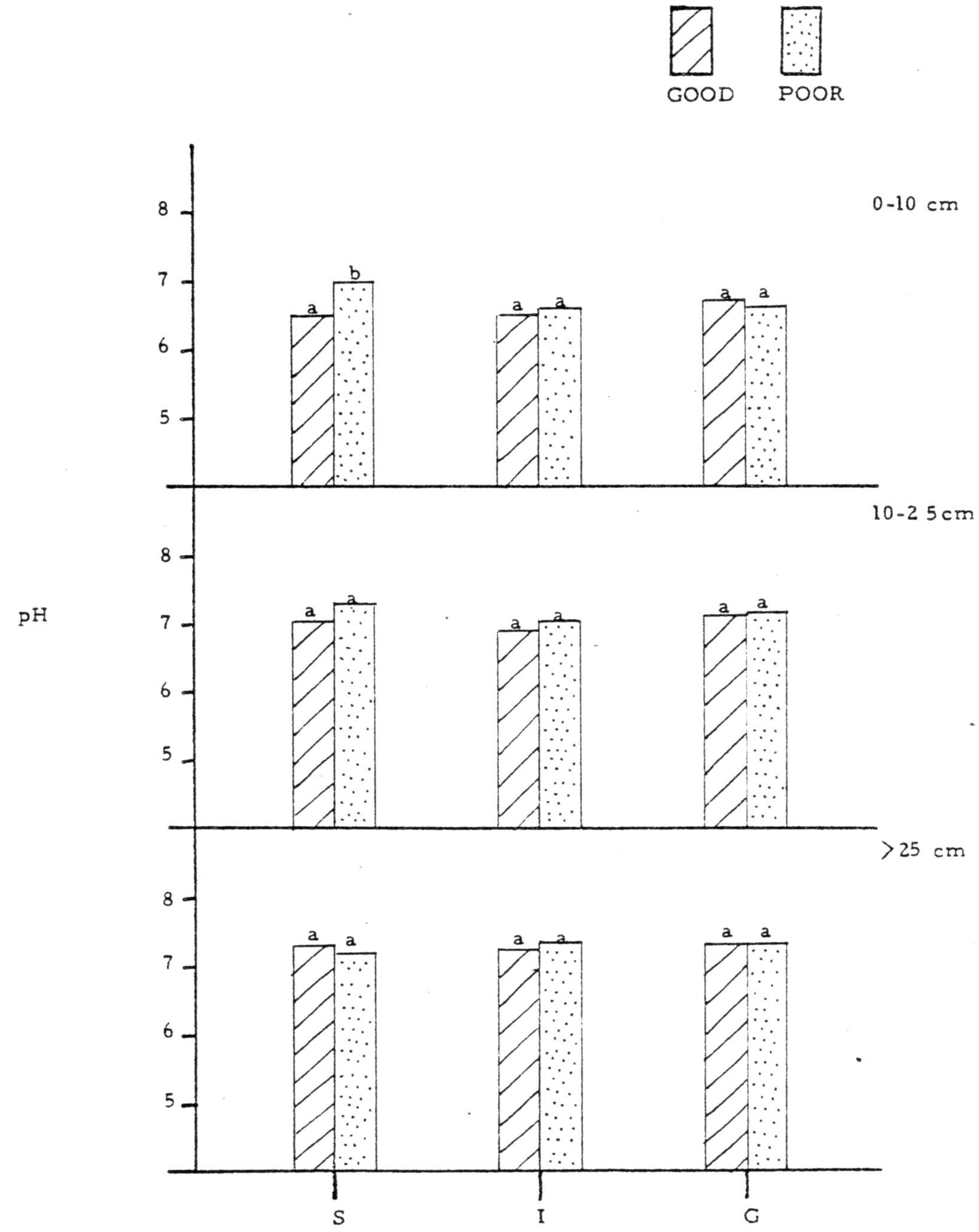
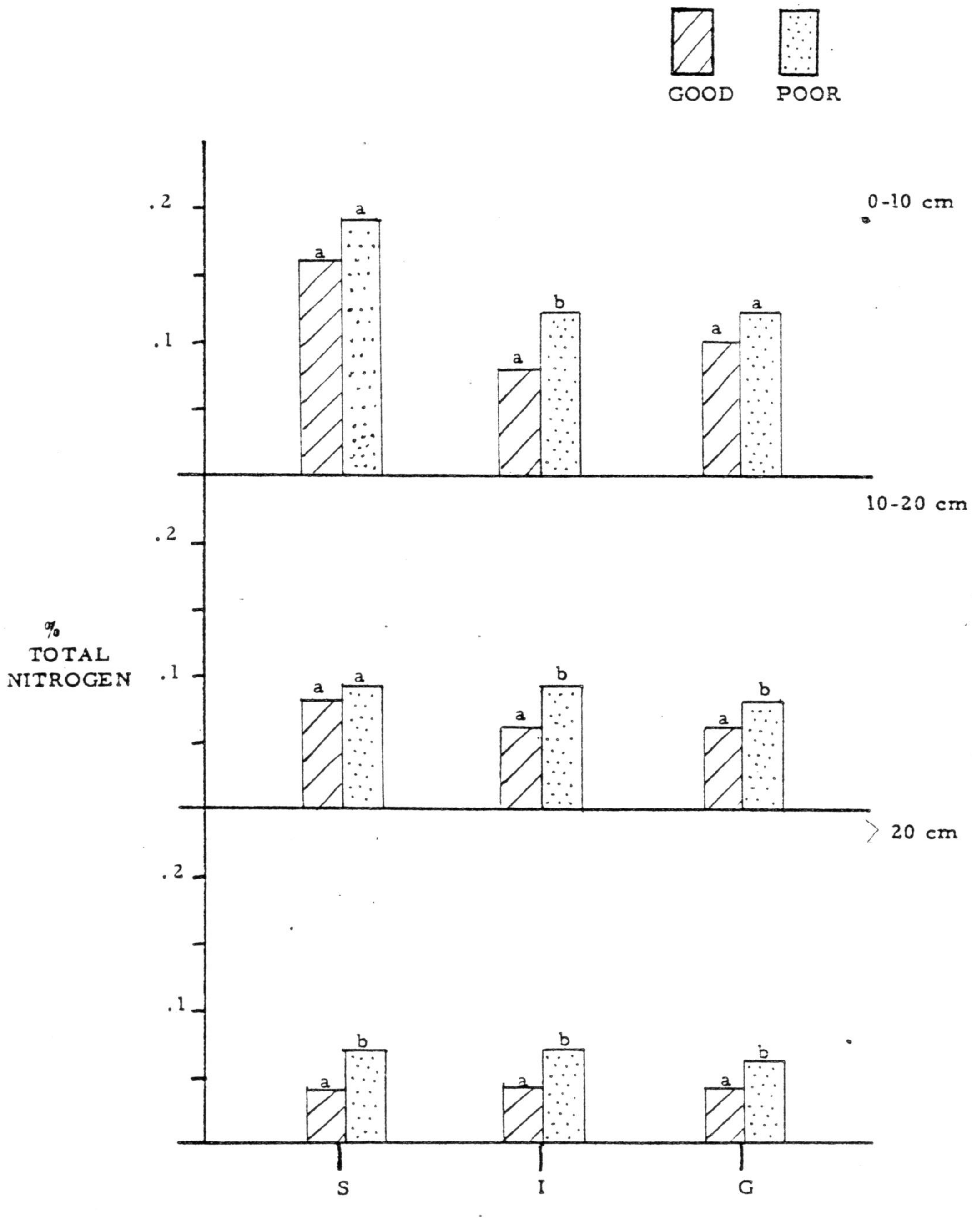
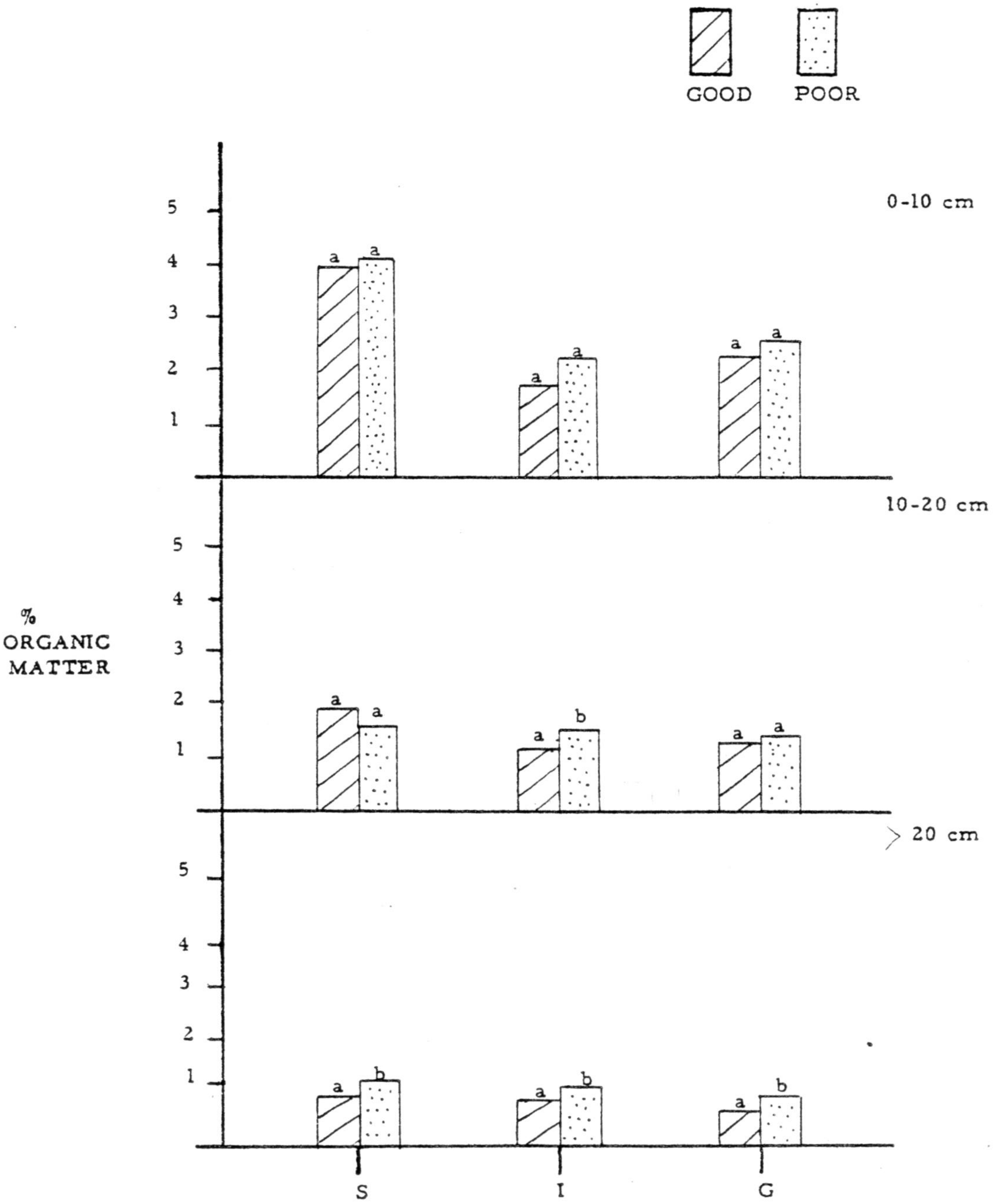

GOOD
POOR
0-10 cm
10-2 5cm
>25 cm
pH
8
7
6
5
a
b
S
I
G

Figure 3. Spatial distribution between shrub (S), interspace (I) and grass (G) influenced soils at 3 depths for adjacent good and poor condition stands of an *Artemisia tridentata* ssp. *wyomingensis*/*Stipa thurberiana* habitat type. (Similar letters denote non-significant differences (α=.05) between adjacent bar graphs.)


GOOD
POOR
0-10 cm
10-20 cm
> 20 cm
% TOTAL NITROGEN
.2
.1
a
b
S
I
G


GOOD
POOR
0-10 cm
10-20 cm
> 20 cm
%
ORGANIC
MATTER
5
4
3
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a
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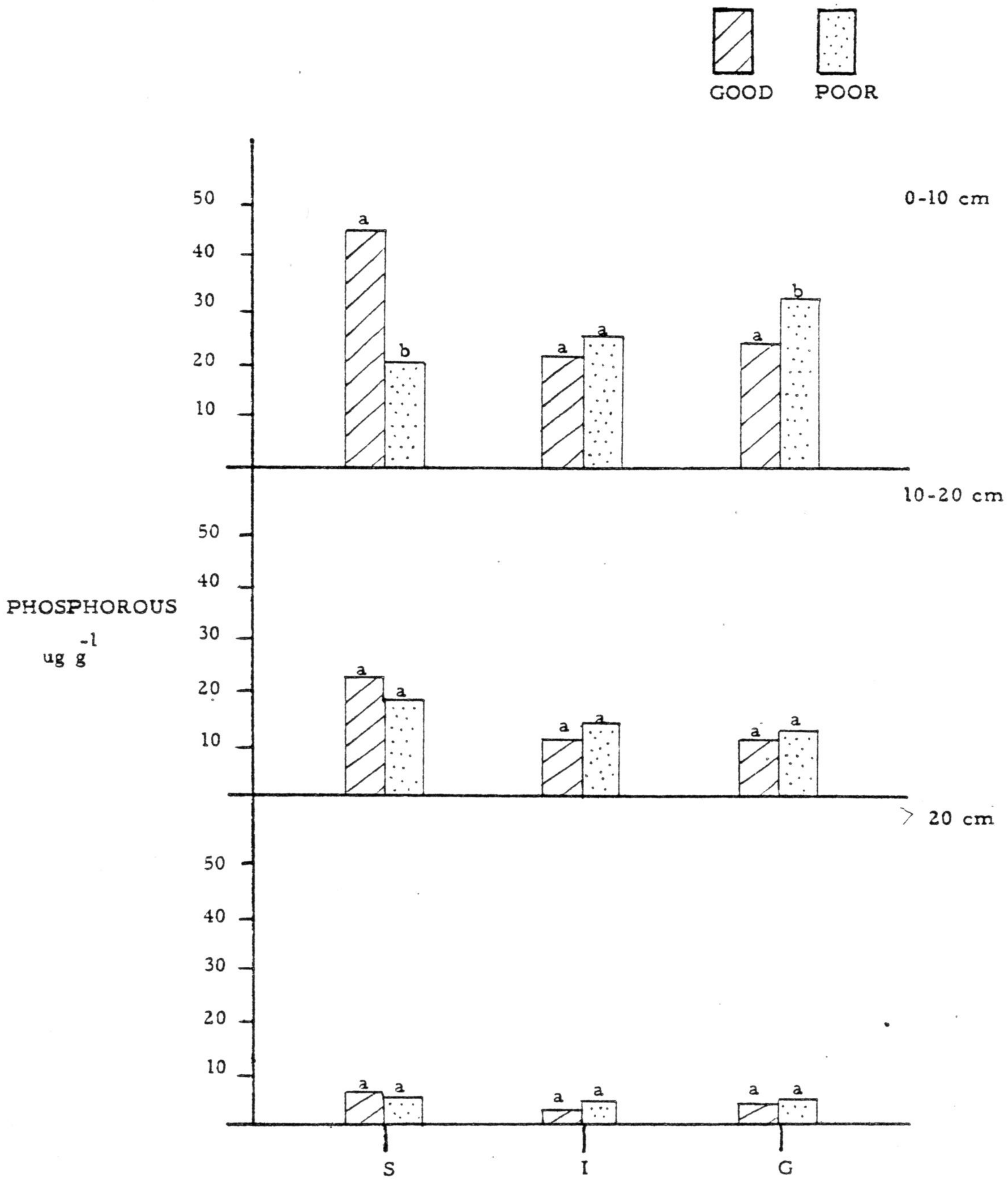
S
I
G


GOOD
POOR
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> 20 cm
PHOSPHOROUS
ug g^{-1}
50
40
30
20
10
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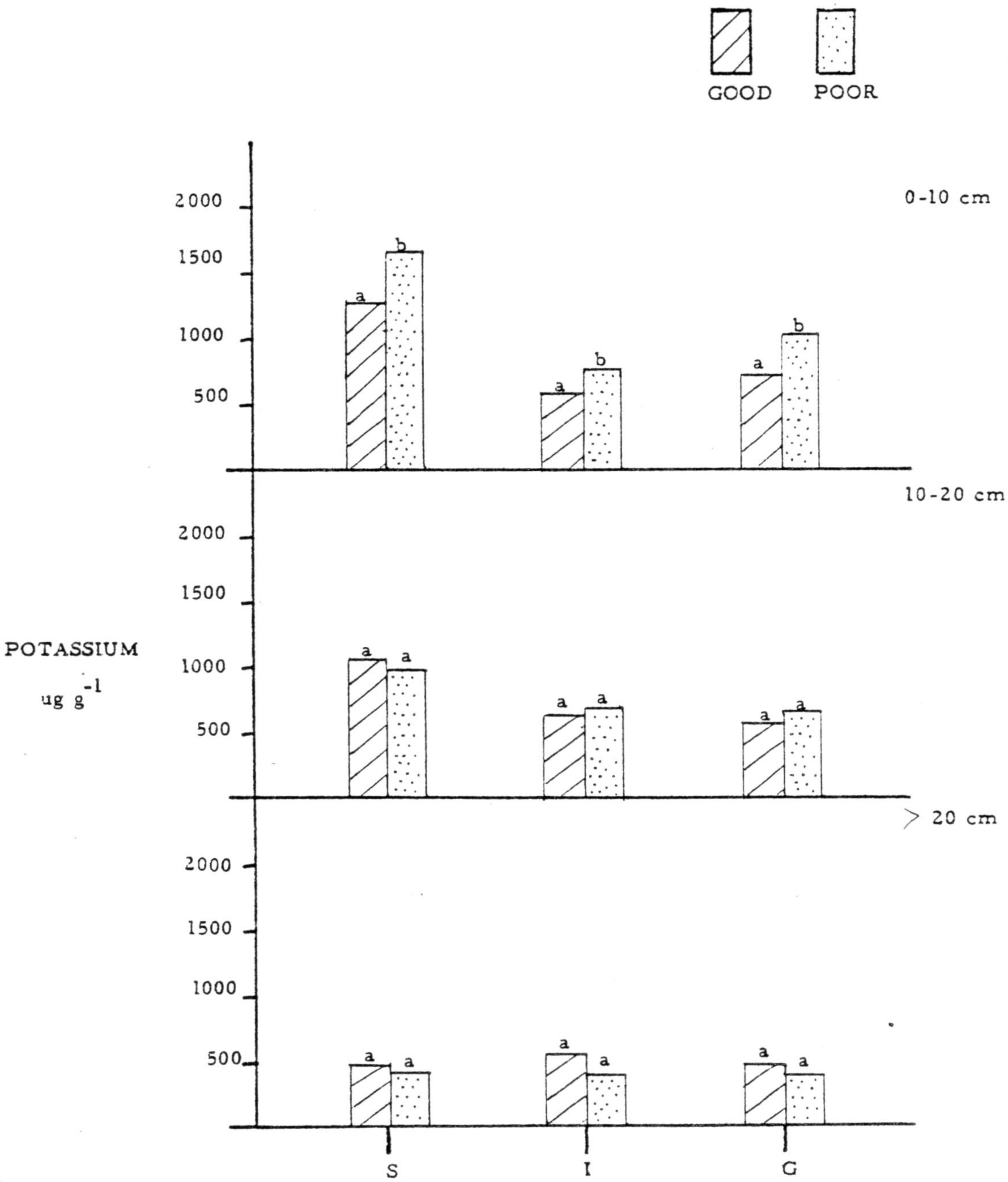
S
I
G


GOOD
POOR
POTASSIUM
ug g^{-1}
0-10 cm
10-20 cm
> 20 cm
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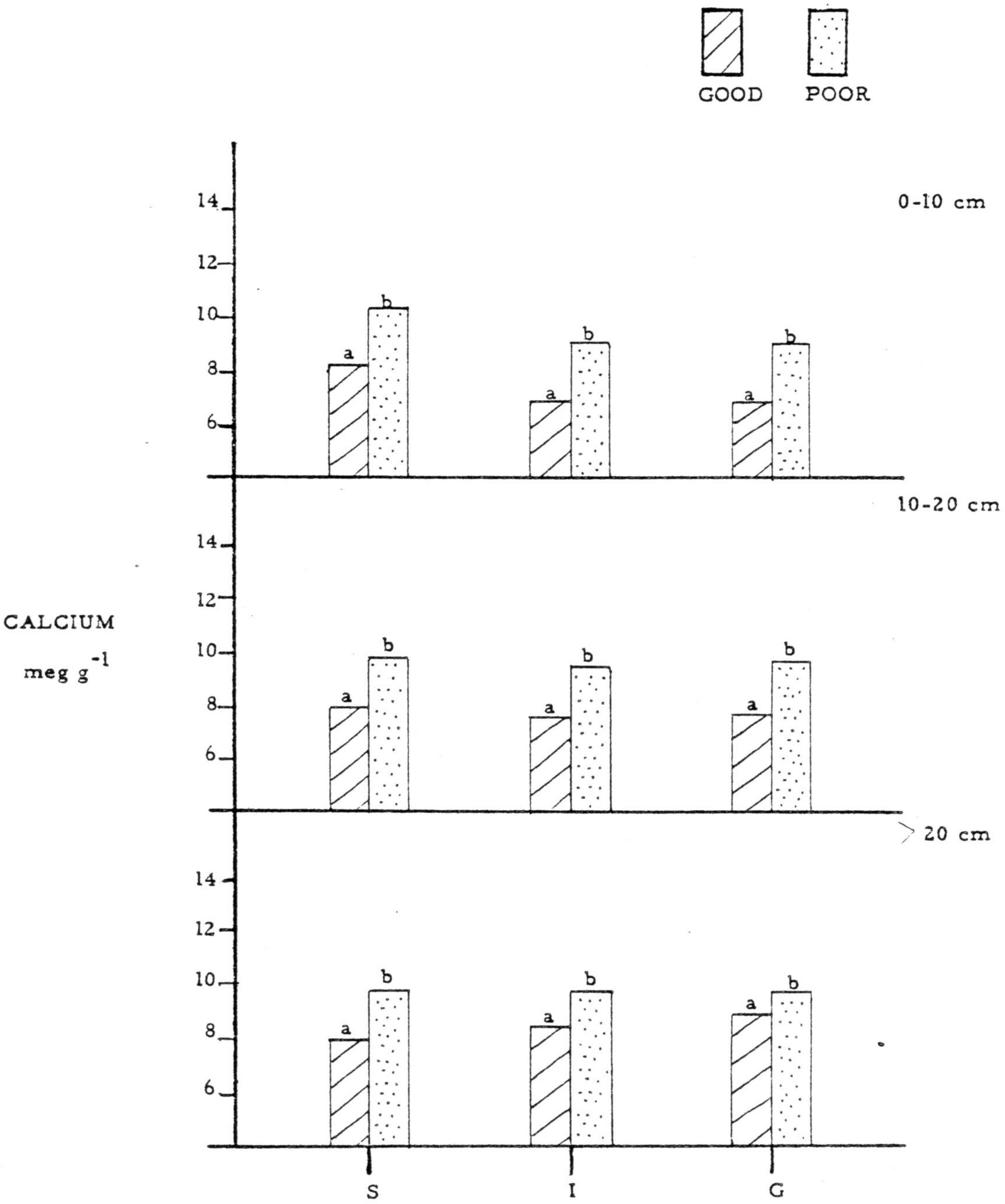
GOOD
POOR
CALCIUM
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0-10 cm
10-20 cm
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I
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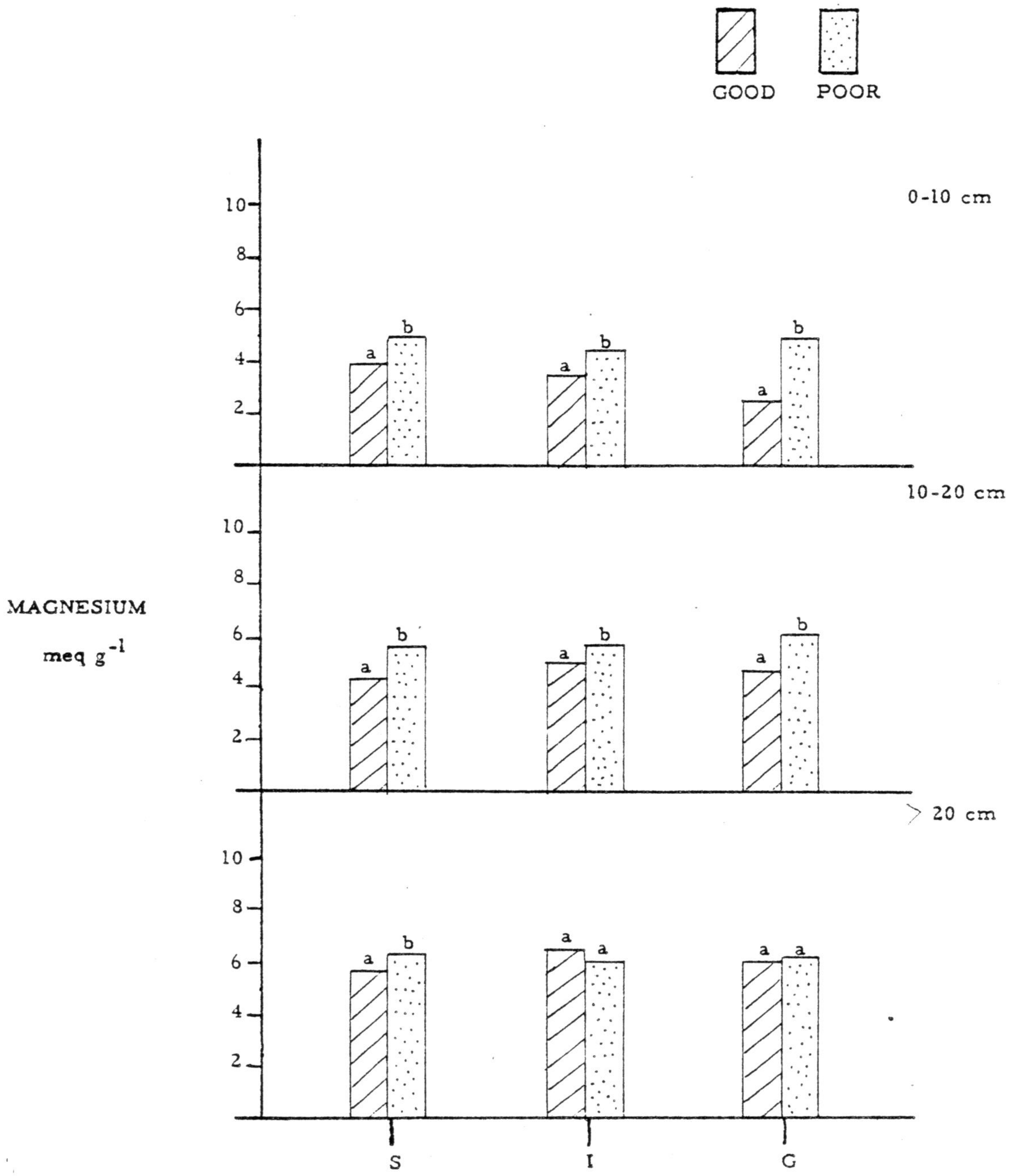
GOOD
POOR
MAGNESIUM
meq g-1
0-10 cm
10-20 cm
> 20 cm
10
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6
4
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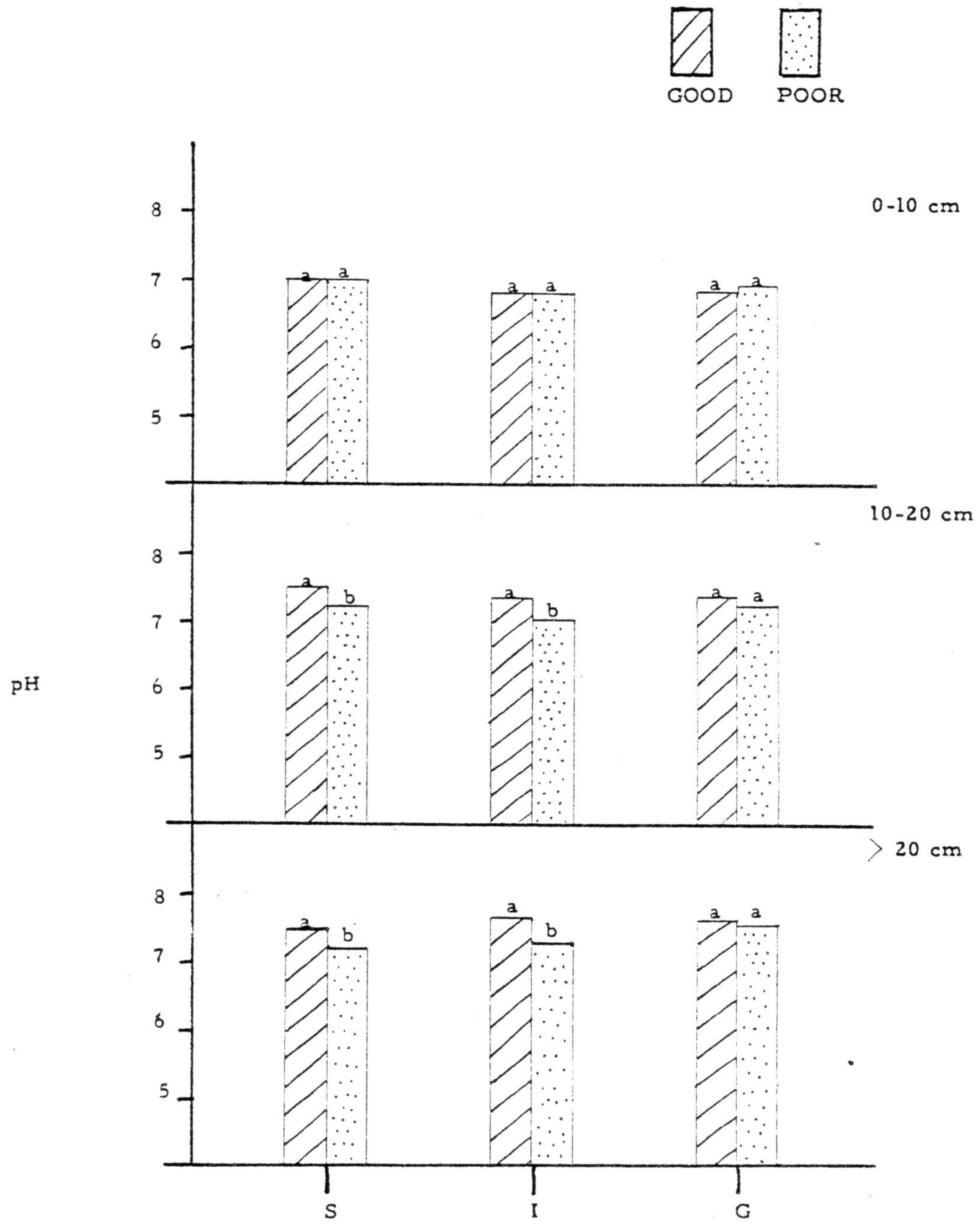
GOOD
POOR
pH
8
7
6
5
0-10 cm
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a
a
a
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a
8
7
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5
10-20 cm
a
b
a
b
a
a
8
7
6
5
> 20 cm
a
b
a
b
a
a
S
I
G

CHAPTER II

THE EFFECT OF MOISTURE STRESS AND TEMPERATURE ON GERMINATION OF FOUR EASTERN OREGON IDAHO FESCUE COLLECTIONS

Paul S. Doescher
Richard F. Miller

THE EFFECT OF MOISTURE STRESS AND TEMPERATURE ON GERMINATION OF FOUR EASTERN OREGON IDAHO FESCUE COLLECTIONS

ABSTRACT

Germination response to varying temperature and moisture stress levels during a 30 day incubation period was observed in four eastern Oregon collections of *Festuca idahoensis*. Seeds were selected from the following habitat types: *Artemisia tridentata* ssp. wyomingensis/ *Festuca idahoensis* (ARTRW/FEID), *Artemisia tridentata* ssp. *vaseyana* "P"/*Festuca idahoensis* (ARTRV"P"/FEID), *Artemisia tridentata* ssp. *vaseyana*/*Festuca idahoensis* (ARTRV/FEID), *Pinus ponderosa*/*Festuca idahoensis* (PIPO/FEID). Incubation temperatures were held constant (±2°C) and ranged from 5°C to 35°C. At 15°, 20° and 25°C, moisture stress levels of -.6 MPa and -.9 MPa were simulated using polyethylene glycol 6000.

Collectively, optimum germination amount for all collections was obtained at 10°C. Germination percentages for seeds from the ARTRW/FEID, ARTRV"P"/FEID, ARTRV/FEID and PIPO/FEID habitat types were 93.0, 97.0. 91.9 and 88.8%, respectively. Seed germination was maintained at higher levels over a wider temperature range for the sagebrush collections in comparison to seeds selected from the PIPO/FEID site.

Maximum germination rates for all collections occurred between 20-25°C. At temperatures above 10°C, germination rates were significantly greater in the three collections from the sagebrush sites than seeds from the forested community.

As moisture and temperature stress increased, both germination amount and rate for the four collections declined. Seeds from sagebrush sites exhibited significantly higher germination amounts and rates over wider temperature/moisture stress ranges in comparison to seeds collected from the PIPO/FEID habitat type.

The pattern of germination response observed in this research probably reflects adaptational genetics of genotypes adapted to a particular site. Seeds from the sagebrush habitat types appeared to be better able to germinate and survive under more variable temperature and moisture stress conditions than seeds selected from the forested community. On the basis of germination response, it was concluded *Festuca idahoensis* from the PIPO/FEID site represented a distinct ecotype in comparison to plants from the sagebrush dominated communities.

INTRODUCTION

Persistence of a plant species on an area is dependent upon the continued capability of the population to maintain an adequate reproductive potential. Seed production and germination are particularly important for the survival of many species given the variable conditions of most natural ecosytems. Many environmental factors interact to influence both the reproductive and establishment characteristics of a species, but dissimilar habitats generally result in natural selection for different adaptive genotypes (Turesson 1922).

Parameters which may influence the adaptability and regeneration success of a species or species' population may include moisture stress and temperature. Waring (1969) and Zobel _et al._ (1976) in analyses of forest communities in western Oregon have shown plant moisture stress during summer drought and an integration of soil and air temperature during the growing season of primary importance in delineating various community types. These factors may also be important during the germination and establishment phases of a plant's life cycle. Selective forces have probably resulted in the development of genotypes sensitive to the climatic regimes of a given area. Timing and amount of seed germination in controlled environments should reflect the developmental parameters which exist under natural conditions.

Various reports examining native species response to simulated incubation conditions, have shown germination characteristics which reflect environmental conditions of the indigenous habitat. Choudhuri (1968) and Young and Evans (1981) reported differences in germination under controlled moisture stress conditions for populations of species' found in saline and non-saline environments. Genotypic response of natural populations to various controlled temperature regimes have been indicated by Lindauer and Quinn (1972) and Stocker (1975). Response of winterfat (*Ceratoides lanata*) to an interacting moisture stress and temperature environment has also indicated ecotypic development (Workman and West 1967). An examination of differential germination properties to temperature pretreatment of populations representing an elevational gradient of *Salvia columbariae* Benth. was reported by Capon *et al.* (1978). Collectively, these studies suggest population differences in germination response to variable environmental conditions. However, it has been suggested environmental pre-conditioning of seeds, especially by variable temperature regimes, may distort the perceived genotypic response of populations under controlled germination conditions (Nelson *et al.* 1970; Baskin and Baskin 1973). This appears to be particularly true of species which require a stratification period in order to break seed dormancy.

The purpose of this research was to evaluate the germination response of four eastern Oregon Idaho fescue (*Festuca idahoensis* Elmer.) collections to varying conditions of temperature and simulated moisture stress. Each collection represented a different habitat type with an Idaho fescue synusiae. Idaho fescue is a cool-season, native perennial bunchgrass indigenous to a wide range of Pacific Northwest community types and environmental conditions (Humphrey 1945; Franklin and Dyrness 1973). It generally has been reported most common on rangelands in relatively good ecological condition (Humphrey 1945). Previous germination studies have indicated optimum germination temperatures for Idaho fescue occurring between 15-20°C (Eddleman 1978; Young and Evans 1981; Stocker 1975), and that three month old seeds do not appear dormant (Eddleman 1978).

MATERIALS AND METHODS

Seed Collection and Processing

The four habitat types selected for comparison represented the following eastern Oregon communities with an Idaho fescue synusiae:

Artemisia tridentata ssp. *wyomingensis/Festuca idahoensis* (ARTRW/FEID),

Artemisia tridentata ssp. *vaseyana/Festuca idahoensis* (ARTRV/FEID),

Artemisia tridentata ssp. *vaseyana* "P"/*Festuca idahoensis** (ARTRV"P"/FEID),

Pinus ponderosa/Festuca idahoensis (PIPO/FEID).

All habitat types were chosen in the same general geographic region (Table 1) and represented clinal variation along an elevational and moisture gradient. It was felt the ARTRW/FEID and ARTRV"P"/FEID habitat types were more xeric in relation to the ARTRV/FEID and PIPO/FEID sites. Each site was in relatively good ecological condition, thus minimizing genotypic differences due to grazing pressure.

Seeds of Idaho fescue at each site were hand stripped at various times during the 1979 growing season and transported to Oregon State University for processing. Seed lots were cleaned by hand threshing and screening to remove caryopses from chaff. Heavy seeds used in

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*This habitat type represents a low elevation association of *A. tridentata* ssp. *vaseyana* and *Festuca idahoensis*. The "P" signifies this habitat type occurs on relatively coarse pumice soils.

germination trials were separated from light and unfilled seeds by use of a seed blower. Abnormally developed embryos observed on a light table were not included in the germination trials. Test of seed viability with tetrazolium chloride indicated better potential germination from seeds collected later in the growing season. These seed lots were used for the germination comparisons.

Experimental Procedure

Filled seeds approximately 8 months of age were concurrently germinated in environmental chambers under 7 constant temperatures and 6 interacting temperature/moisture stress conditions. A wide range of incubation environments were chosen so as to clarify ecotypic response and establish trends in germination characteristics. Temperature treatments (± 2°C) were 5, 10, 15, 20, 25, 30 and 35°C. Seeds were also subjected to moisture stress levels of -.6MPa and -.9MPa at temperatures of 15, 20 and 25°C. The water potential (ψw) of each solution was depressed using polyethylene glycol (PEG) 6000 and specific ψw values were computed using the procedures outlined by Michel and Kaufmann (1973).

Four replications each containing 25 seeds were utilized for each treatment/population combination. Seeds were placed on cellulose pads (Kimpak*) in petri dishes with either distilled water or PEG 6000 solutions added in sufficient quantities to saturate the germination medium but cause puddling only on the bottom of the petri dish. Petri dishes were placed four deep on a metal tray containing a single layer of saturated cellulose on the bottom. Trays were enclosed by two

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*Burrows Equipment Co., Evanston, IL 60204 black plastic bags in order to maintain dark germination conditions and a high humidity environment during the germination trial. Trays were factorially arranged, randomly placed within the growth chamber and rotated daily. Seeds were imbibed for 30 days and germination recorded daily. A seed was considered germinated when both radicle and plumule had elongated at least 3 mm. Ungerminated seeds were tested for viability by backliting. Germination counts were converted into percentages for statistical interpretation.

Data Analysis

Germination treatments were tested (α = .05) using standard Analysis of Variance techniques. Values for total germination percent were transformed using an arcsine square-root transformation in order to make the statistical distribution more normal (Sokal and Rohlf 1969). Two values were computed to evaluate germination rate.

1. Maquire's (1962) Coefficient of Rate of Germination - a value which considers speed of germination as well as total number of seeds which germinate on a given day.
2. Days to 50% of Total Germination - an indication of germination rate independent of total number of seeds which germinate. The smaller the value, the greater the germination rate.

In addition, the mean daily germination amount was accumulated and plotted against time. Differences between collections, temperatures and moisture stress levels were assessed using Tukey's - w procedure (α = .05) (Steel and Torrie 1980). When significant interactions existed between main effect means, only those having ecological significance were interpreted.

RESULTS

Germination Response to Constant Temperatures

The characterization of germination properties over temperatures of 5, 10, 15, 20, 25 and 30°C indicated a differential response within the four Idaho fescue collections (Figure 1). Germination did not occur for any of the collections at 35°C. Analysis of Variance revealed a significant collection x temperature interaction for both the assessment of mean total percent germination and mean CRG. Evaluation of two-way interaction means for percent germination and CRG and main effects for days to 50% germination revealed the following germination patterns:

1. Collectively, optimum germination for all collections was obtained at 10°C. Germination percentages for seeds from the ARTRW/FEID, ARTRV"P"/FEID, ARTRV/FEID and PIPO/FEID habitat types were 93.0, 97.0, 91.9, 88.8%, respectively.
2. Seed germination was maintained at higher percentages over a wider temperature range for the sagebrush collections than was evident for seeds collected from the PIPO/FEID site. Optimum germination percentages significantly declined on either side of the 10°C temperature for the PIPO/FEID selection.
3. Collections ARTRW/FEID and ARTRV"P"/FEID were judged not significantly different at all temperature treatments.
4. Collection ARTRV/FEID significantly differed from collection ARTRW/FEID and ARTRV"P"/FEID at certain temperatures, but never differed from both collections at the same temperatures.
5. Maximum germination rates for all collections were exhibited within the 20-25°C temperature range. At temperatures above 10°C,

mean CRG values were significantly greater in the three collections chosen from sagebrush sites in comparison to seeds from the pine dominated community. The PIPO/FEID collection exhibited a significantly slower response for days to 50% germination in comparison to the other collections at all temperatures.

Germination Response to Temperature/Moisture Stress

Germination characteristics between populations varied in relation to temperature and moisture stress. As moisture stress increased both germination amount and rate declined (Figure 2). A significant collection x temperature x moisture stress interaction was detected for both the analyses of mean % germination and CRG. Evidently, a synergistic response between moisture stress and temperature, which resulted in a disproportionate decline in germination percentage at 25°C, contributed the most to the interaction sum of squares.

Interpretation of three way interaction means for % germination and CRG indicated a similar germination response between the ARTRW/FEID and ARTRV"P"/FEID populations. Seeds collected from the ARTRV/FEID site responded differently than the other two sagebrush collections at temperature/moisture stress levels of 20°C/-.9 MPa for % germination and 25°C/-.6 MPa for mean CRG. Total percent germination of seeds imbibed in solutions of -.6 and -.9 MPa was greatest for all collections at temperatures of 15°C and 20°C. Idaho fescue seeds from sagebrush sites maintained significantly higher germination amounts and rates over wider temperature/moisture stress ranges than seeds collected from the PIPO/FEID habitat type.

A significant interaction was found between temperature and moisture stress for days to 50% germination. Again, a synergistic relationship appeared to exist between incubation temperature and moisture stress. Mean separation of main effects for the four Idaho fescue populations indicated collections ARTRW/FEID, ARTRV"P"/FEID and ARTRV/FEID did not differ in days to 50% germination. Seeds selected from the PIPO/FEID habitat type were significantly slower to reach 50% germination than seeds from the ARTRW/FEID and ARTRV/FEID sites.

DISCUSSION

Examination of germination characteristics of seeds incubated under varying temperature and moisture stress environments revealed differences in relative response among four Idaho fescue collections. Seeds selected from sagebrush dominated habitat types maintained higher germination percentages and rates over wider temperature and moisture stress regimes than did seeds gathered from a relatively mesic PIPO/FEID habitat type.

Assessment of these responses may be related to environmental factors under which population of a plant species have evolved. Numerous studies have shown that germination patterns reflect the seasonal and climatic environments which naturally occur during germination (McDonough 1977; Eddleman 1978; Young and Evans 1981). Selective processes have probably resulted in the development of genotypes which optimize germination under certain incubation regimes.

In Idaho fescue, seeds collected from sites with a sagebrush overstory seem to be better adapted to germinate and survive under a more variable environment than seeds gathered from a higher elevation PIPO/FEID community. Within the pine site, amelioration of the microclimate near the ground surface by aspect, elevation or vegetative overstory conceivably reduces the need to germinate a large number of seeds under a wide range of temperature and moisture stress conditions. This is not to say seeds will not germinate under other incubation regimes, but rather to infer high elevation populations are conditioned to germinate optimum amounts under the naturally cooler temperature and higher moisture environments of these sites. Conversely, seed beds on sagebrush sites probably exhibit a wider fluctuation of temperature and moisture conditions under which seeds germinate. It would seem ecologically advantageous for genotypes adapted to drier sites to be able to germinate a large number of seeds over a broader range of moisture and temperature environments.

The importance of speed of germination in the establishment of seedlings has been stressed by Harper (1977). He states the faster a seed germinates, the greater is its potential for establishing under conditions of competition. It seems likely germination rate is a heritable trait selected for by environmental factors. Results indicating differential germination rates seemingly correlate well with developmental factors which occur for a particular area. Collections of Idaho fescue seeds from sagebrush sites are adapted to germinate faster under wider conditions of moisture and temperature stress than are seeds from a PIPO/FEID habitat type, where conditions may not be as variable.

The relative order of population germination response in Idaho fescue to a wide range of temperature and moisture stress environments roughly conforms to the environmental gradient that exists under natural conditions. Seeds from the warm, dry sagebrush sites are most responsive to extremes of moisture and temperature stress. Additionally, similar Idaho fescue habitat types in terms of environmental characteristics appear to have similar germination properties. This inference can be attributed to similar selective forces and/or compensatory factors that occur under natural conditions.

On the basis of these results, it seems possible to distinguish between eoctypes within the four Idaho fescue collections. It is felt the pattern of germination response in seeds from the PIPO/FEID habitat type was sufficiently distinct to warrant classifying Idaho fescue on this site as a separate ecotype in comparison to plants found within the sagebrush dominated communities. This relationship is enhanced by the comparatively similar germination all collections exhibited at 10°C and the significant decline in response for the PIPO/FEID collection as temperature and/or moisture stress increased. Unlike the PIPO/FEID collection, seeds from the ARTRV/FEID site exhibited different germination characteristics only at a few temperature/moisture stress environments. Whether or not this represented a genetically or environmentally induced response is hard to determine within the constraints of this research. However, because the pattern of germination was similar within all sagebrush collections, further evaluation of ecotypic development may need to be performed. These assessments could include additional germination trials under different incubation condition and/or growth response of plants in uniform growing conditions.

The type of research presented in this report has application in the revegetation of rangelands with native species. Reports by Chapin and Chapin (1981) and Robertson (1977) indicate in common garden studies indigenous populations are often best suited to surviving long term local environmental conditions. Daubenmire (1968) stressed the importance of revegetating a specific habitat type with planting stock representing that particular community. At the very least, genetic heterogeneity within a species should be taken into consideration when land managers plan to revegetate native rangelands. Certainly, genotypes either exist naturally or could be developed which would be suitable for the revegetation of a large proportion of the distributional area of Idaho fescue. However, until these sources are identified, it would be best to utilize seeds native to the particular habitat type being revegetated.

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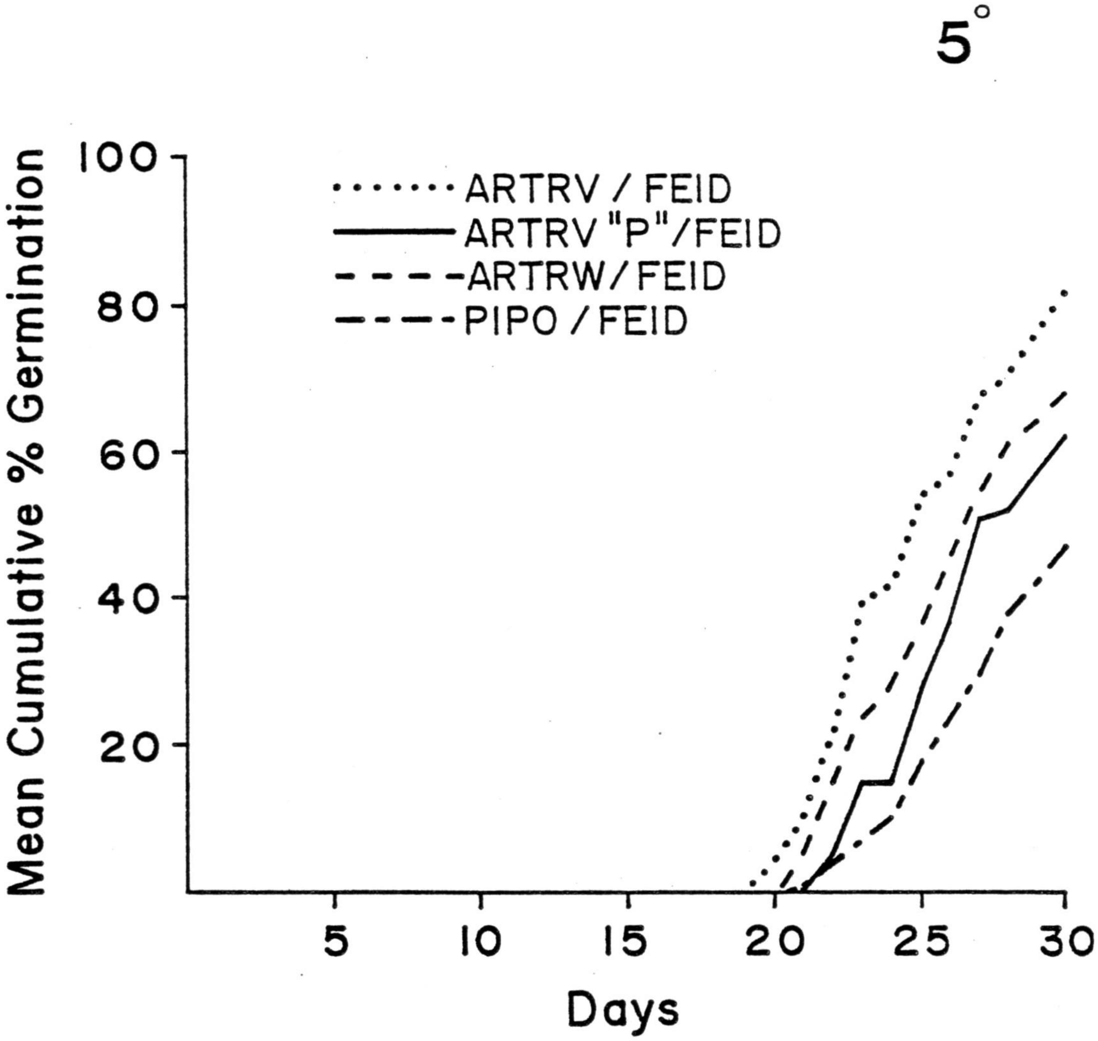
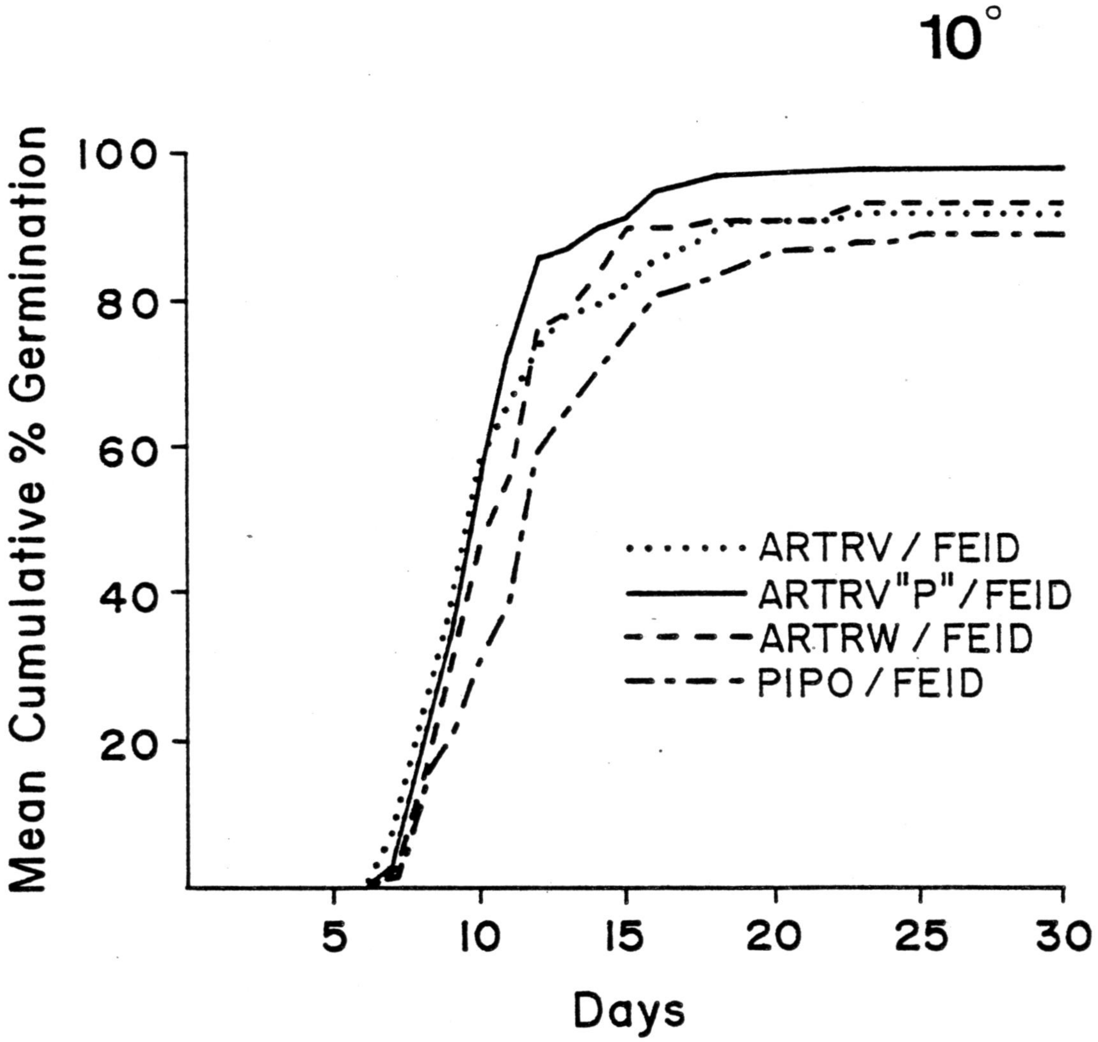
Table 1. Sampled plant communities and site characteristics of four eastern Oregon *Festuca idahoensis* collections.

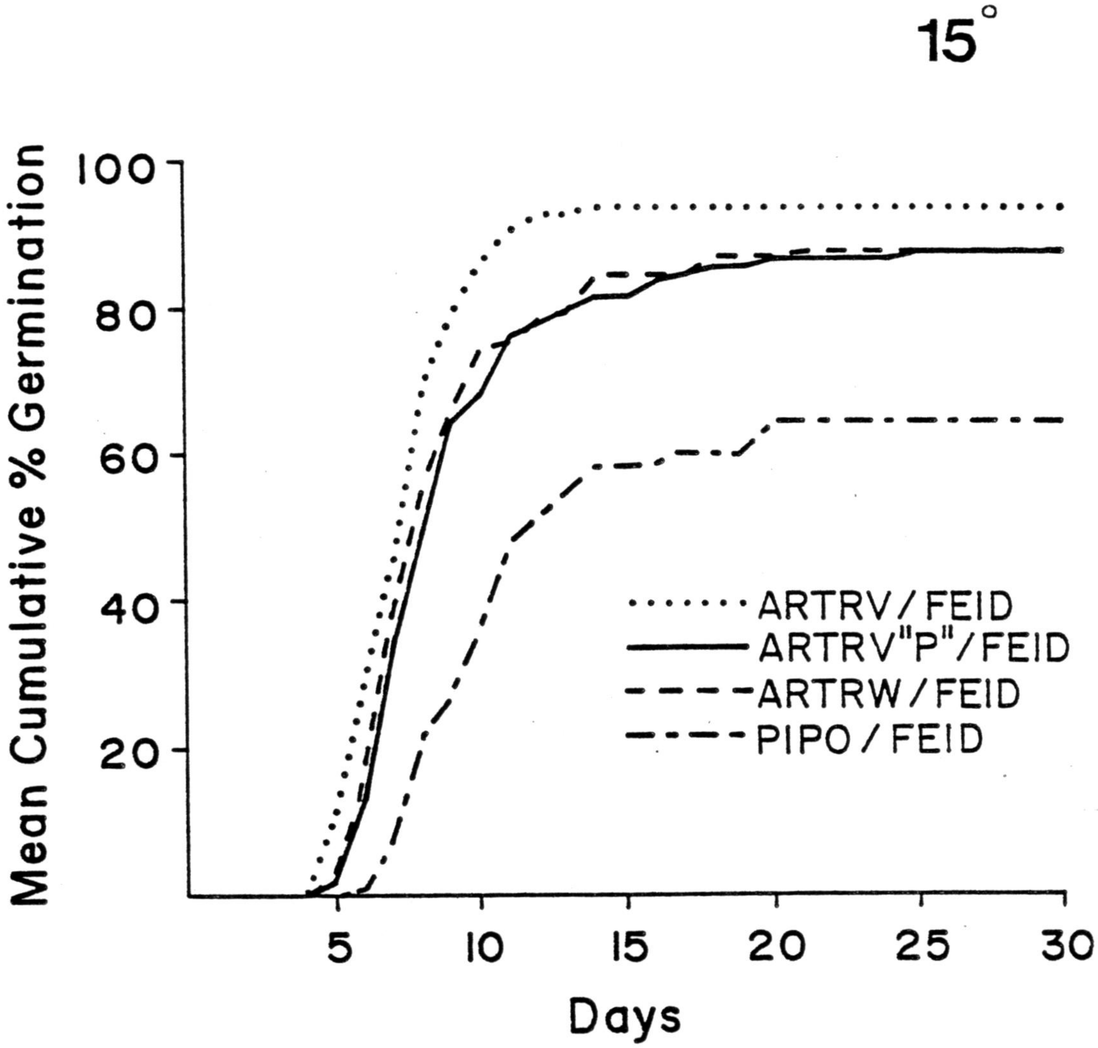
Habitat Type	Abbreviation	Elevation (meters)	Site Location	Soil Description	Texture of Surface Soil
Artemisia tridentata ssp. *wyomingensis*/ *Festuca idahoensis*	ARTRW/FEID	1350	SW¼NW¼S33 T21S,R21E Near Hampton, OR	Xerollic Durargid	Loamy Sand
Artemisia tridentata ssp. *vaseyana* "*P*"*/ *Festuca idahoensis*	ARTRV"P"/FEID	1400	SE¼NE¼S20 T20S,R18E Near Brothers, OR	Xerollic Durargid	Sandy Loam
Artemisia tridentata ssp. *vaseyana*/ *Festuca idahoensis*	ARTRV/FEID	1700	SE¼NW¼S12 T21S,R20E Near Hampton, OR	Argic Cryboroll	Sandy Loam
Pinus ponderosa/*Festuca idahoensis*	PIPO/FEID	1750	NW¼SE¼S22 T20S,R15E Near Millican, OR	Typic Cryboroll	Loam

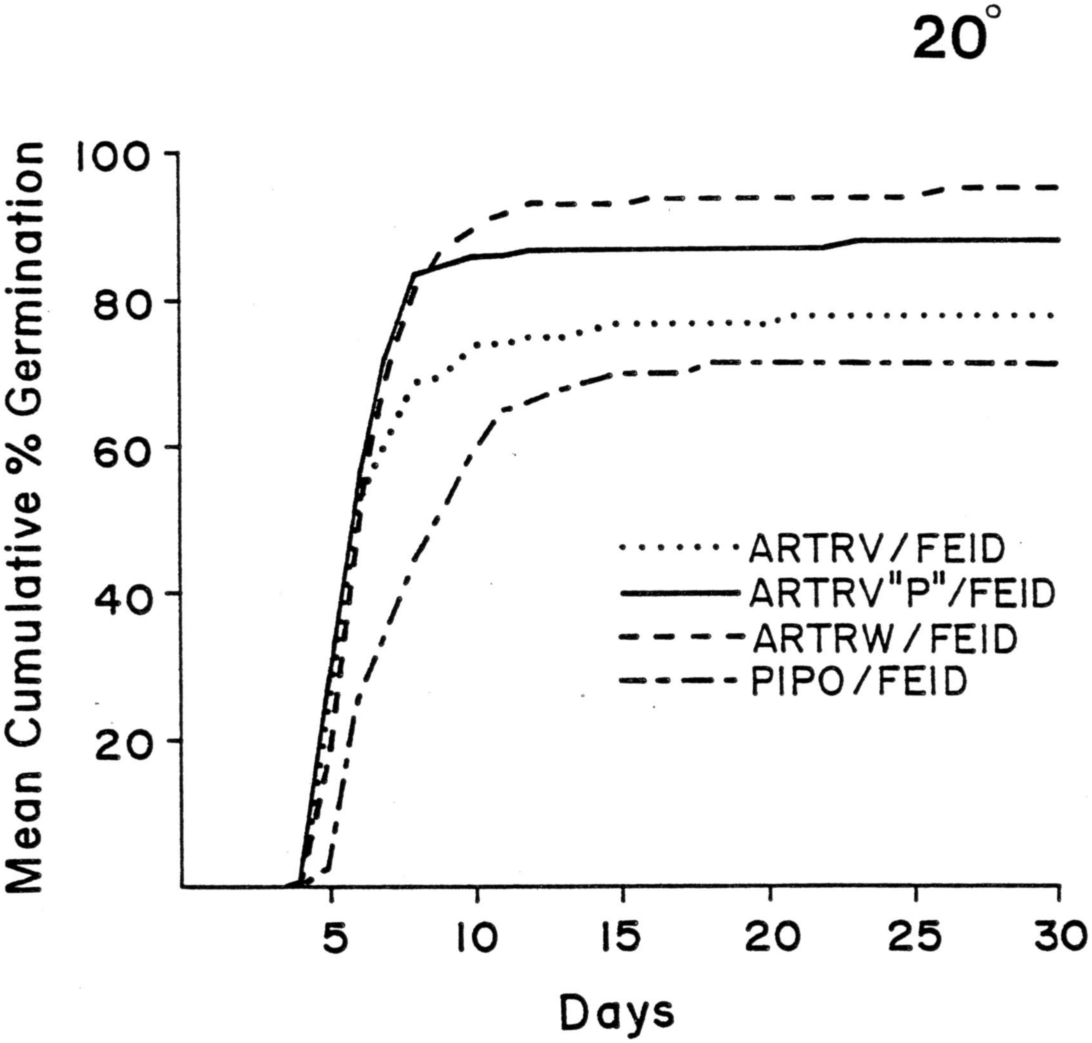
*A low elevation plant community dominated by *A. tridentata* spp. *vaseyana*. Not much information is known about this association, expect that it occurs on relatively coarse pumice soils and has a unique physiognomy in comparison to higher elevation stands.

Figure 1. Mean cumulative percent germination of four eastern Oregon *Festuca idahoensis* collections at 6 constant temperatures (°C). Seeds were selected from the following habitat types: *Artemisia tridentata* ssp. wyomingensis/*Festuca idahoensis* (ARTRW/FEID), *Artemisia tridentata* ssp. *vaseyana* "P"/*Festuca idahoensis* (ARTRV"P"/FEID), *Artemisia tridentata* ssp. *vaseyana*/*Festuca idahoensis* (ARTRV/FEID), and *Pinus ponderosa*/*Festuca idahoensis* (PIPO/FEID).


5°
Mean Cumulative % Germination
100
80
60
40
20
Days
5
10
15
20
25
30
ARTRV / FEID
ARTRV "P"/FEID
ARTRW/FEID
PIPO / FEID


10°
Mean Cumulative % Germination
100
80
60
40
20
5
10
15
20
25
30
Days
ARTRV / FEID
ARTRV"P"/FEID
ARTRW / FEID
PIPO / FEID


15°
Mean Cumulative % Germination
100
80
60
40
20
5
10
15
20
25
30
Days
ARTRV/FEID
ARTRV"P"/FEID
ARTRW/FEID
PIPO/FEID


20°
Mean Cumulative % Germination
100
80
60
40
20
5
10
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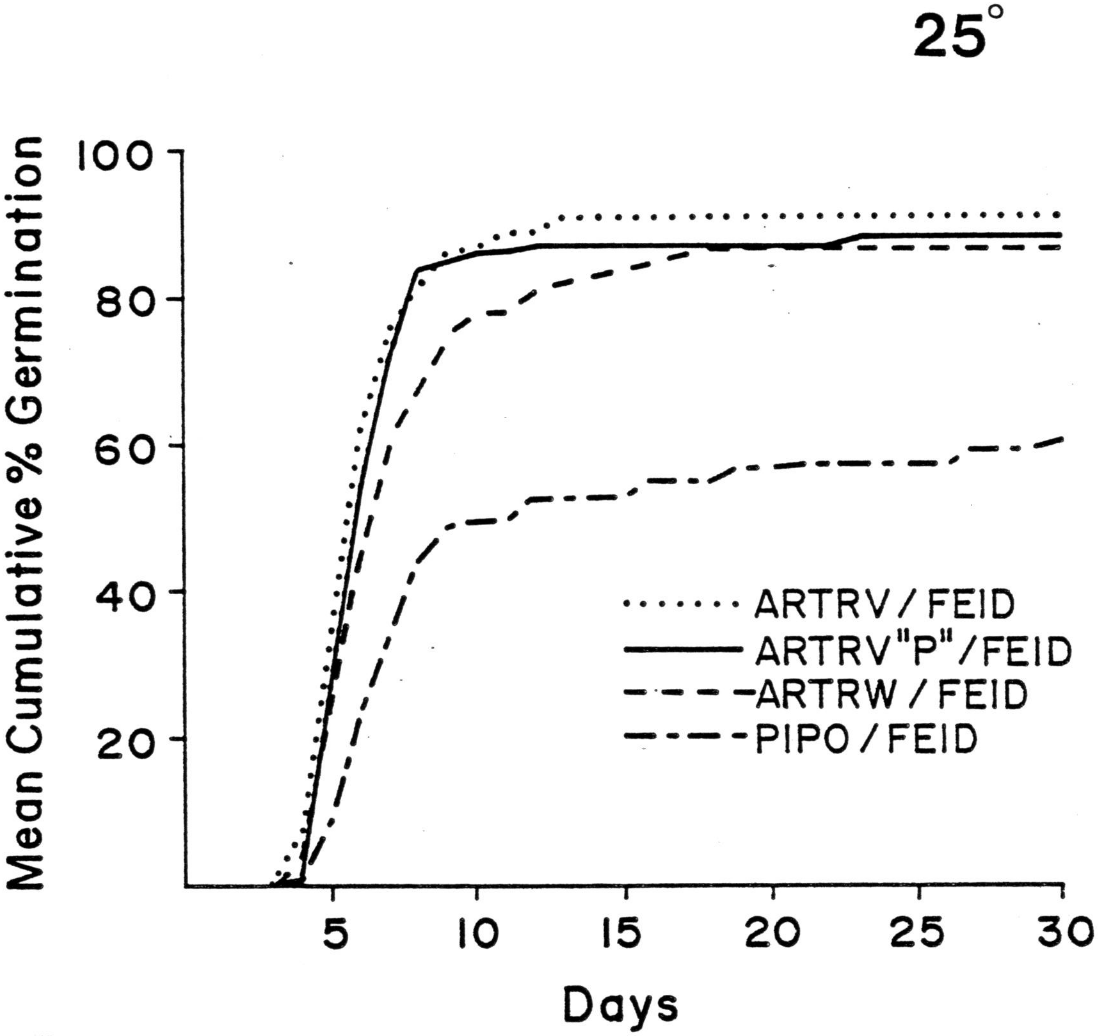
25
30
Days
ARTRV/FEID
ARTRV"P"/FEID
ARTRW/FEID
PIPO/FEID


25°
Mean Cumulative % Germination
100
80
60
40
20
5
10
15
20
25
30
Days
ARTRV / FEID
ARTRV"P"/FEID
ARTRW / FEID
PIPO / FEID

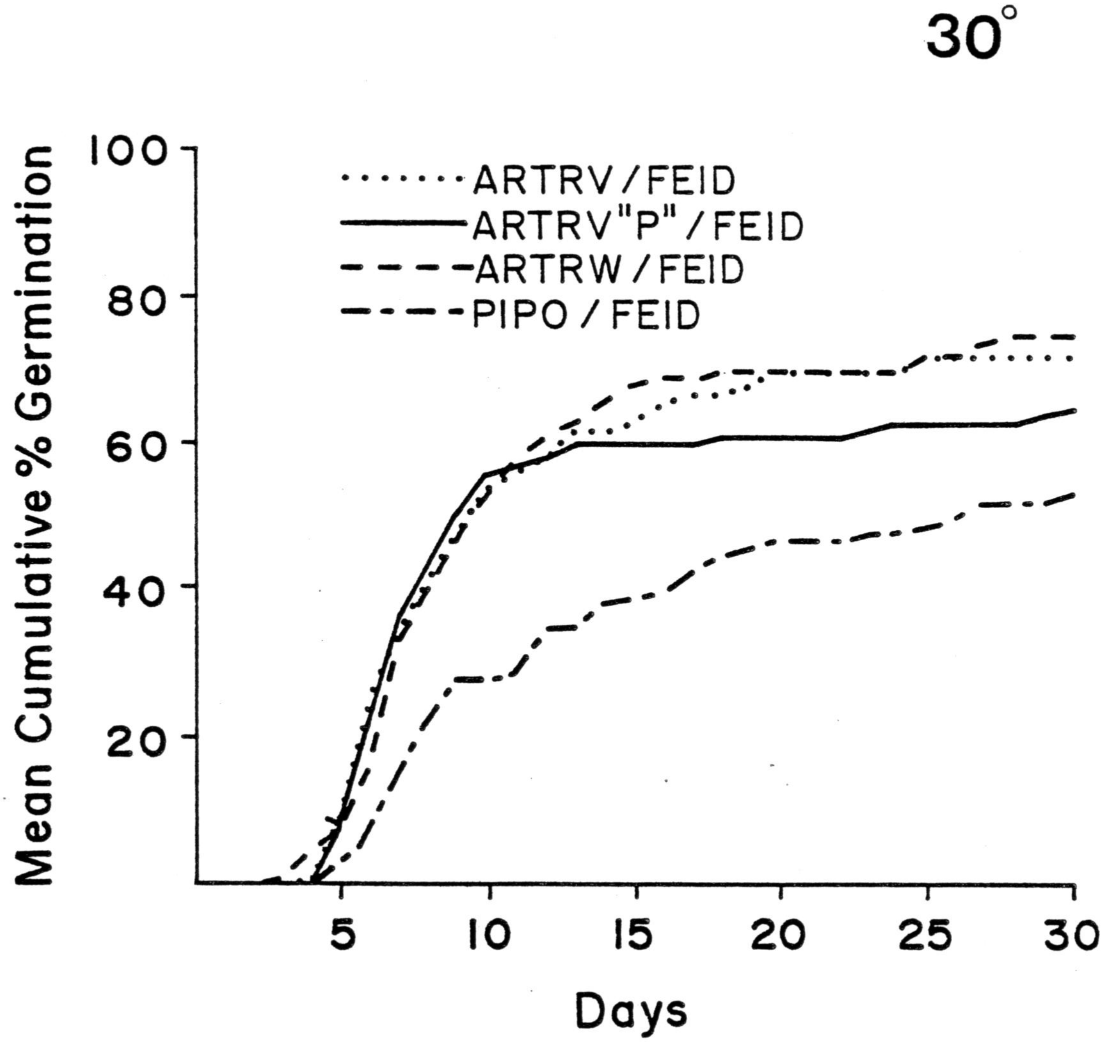
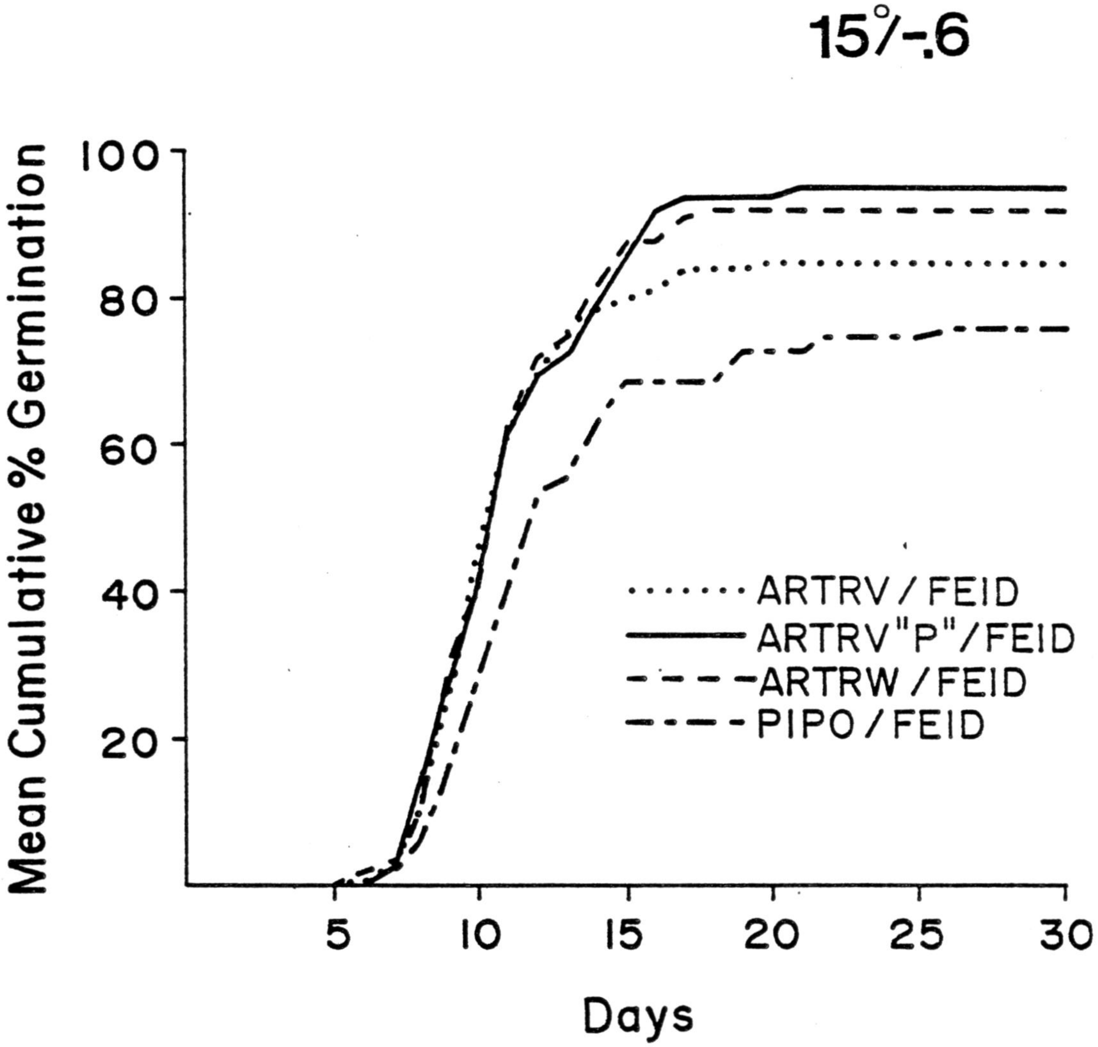
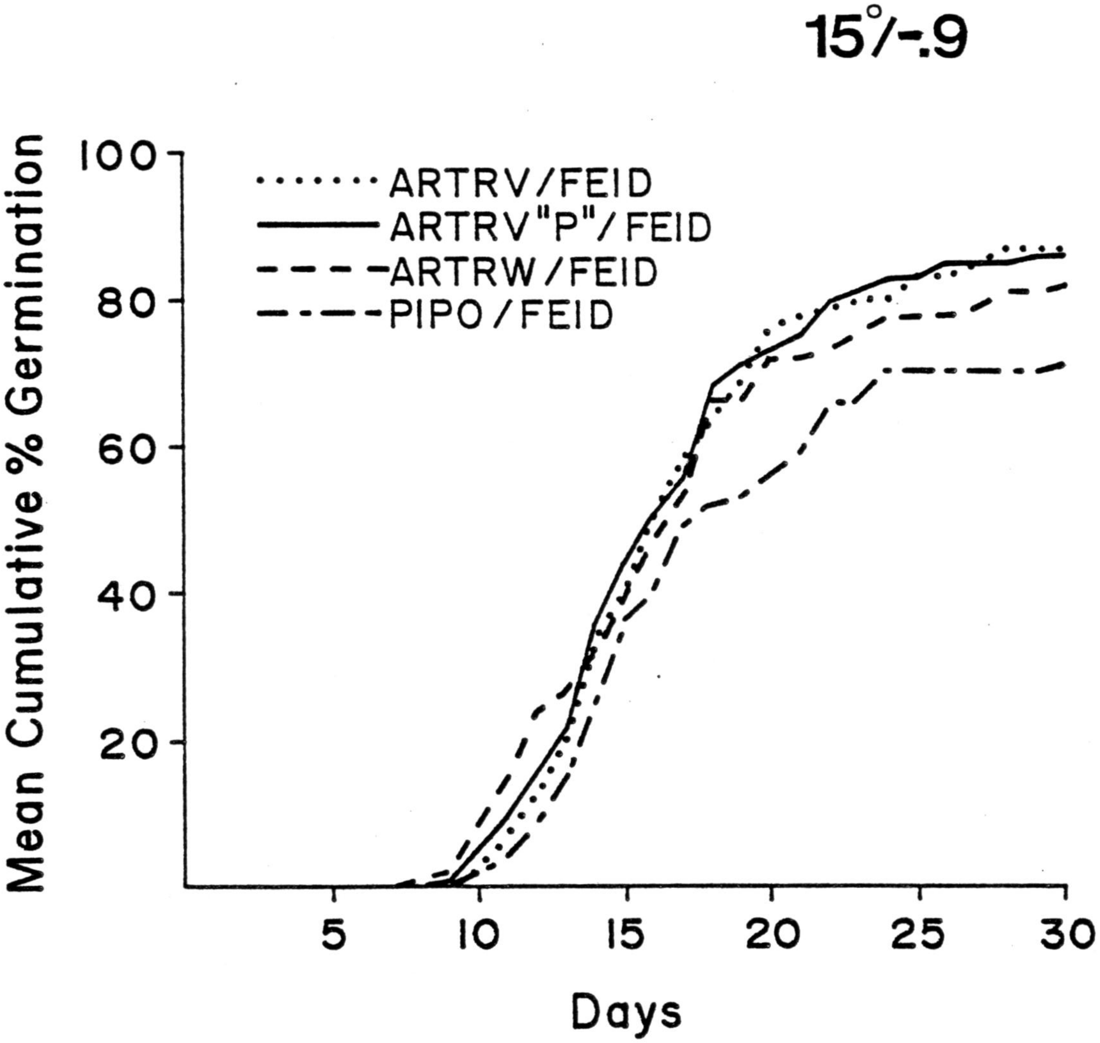

30°
Mean Cumulative % Germination
100
80
60
40
20
5
10
15
20
25
30
Days
ARTRV/FEID
ARTRV"P"/FEID
ARTRW/FEID
PIPO/FEID

Figure 2. Mean cumulative percent germination of four eastern Oregon *Festuca idahoensis* collections at 3 constant temperatures and 2 simulated moisture stress regimes (°C/MPa). Seeds were selected from the following habitat types: *Artemisia tridentata* ssp. wyomingensis/*Festuca idahoensis* (ARTRW/FEID), *Artemisia tridentata* ssp. *vaseyana* "P"/*Festuca idahoensis* (ARTRV"P"/FEID), *Artemisia tridentata* ssp. *vaseyana*/*Festuca idahoensis* (ARTRV/FEID), and *Pinus ponderosa*/*Festuca idahoensis* (PIPO/FEID).


15°/-.6
Mean Cumulative % Germination
100
80
60
40
20
5
10
15
20
25
30
Days
ARTRV / FEID
ARTRV"P"/FEID
ARTRW / FEID
PIPO / FEID


15°/-.9
ARTRV/FEID
ARTRV"P"/FEID
ARTRW/FEID
PIPO/FEID
Mean Cumulative % Germination
100
80
60
40
20
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10
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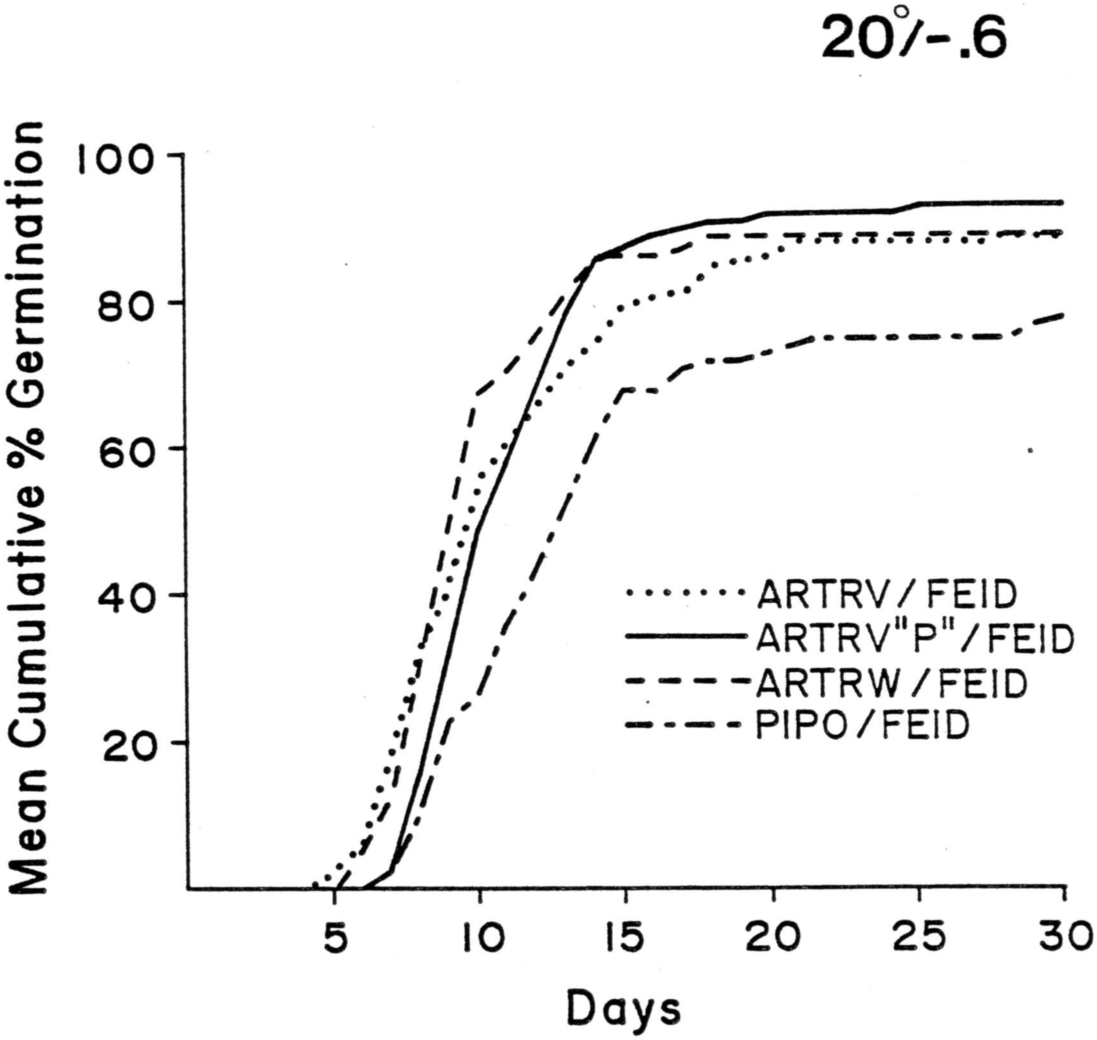
20
25
30
Days


20°/-.6
Mean Cumulative % Germination
100
80
60
40
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5
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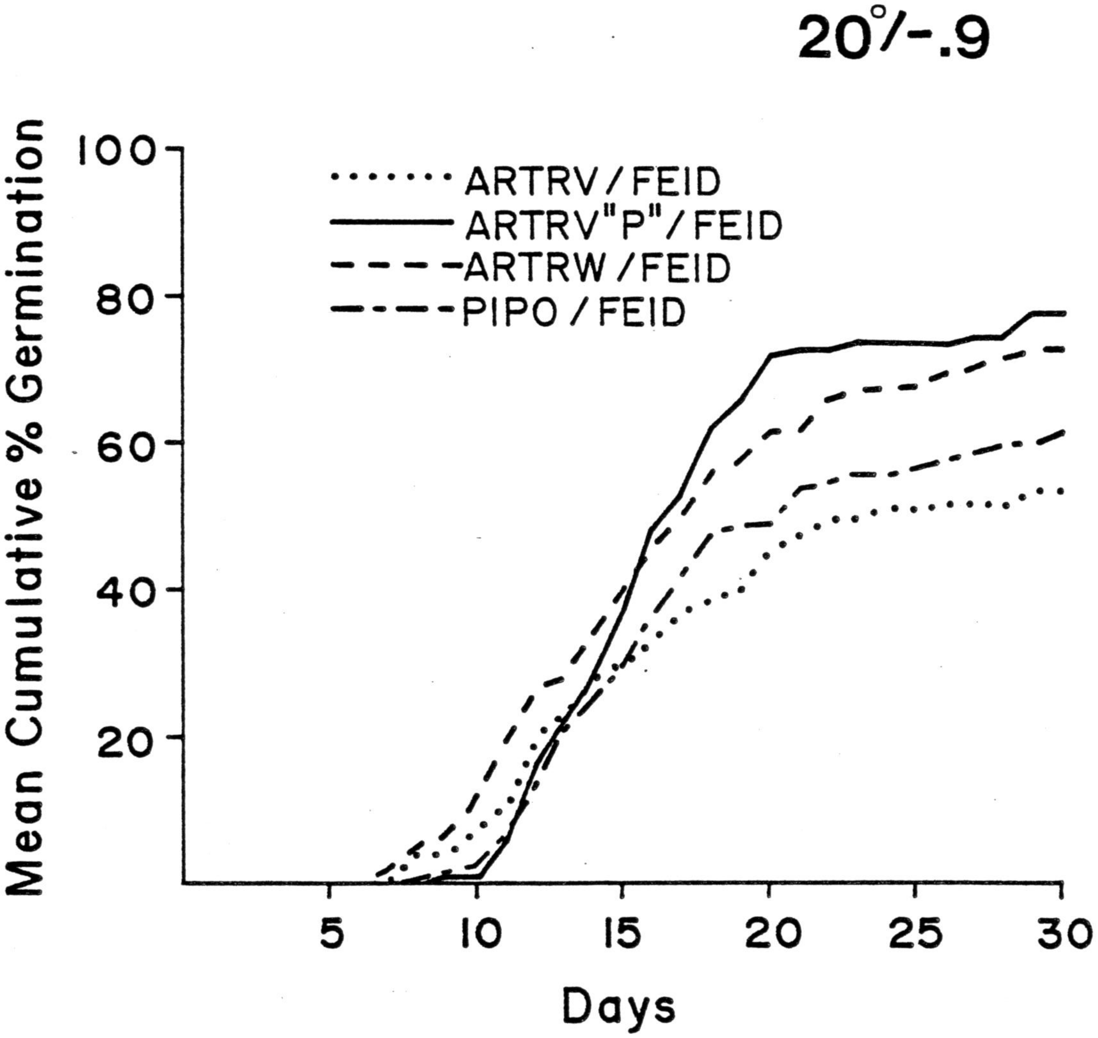
25
30
Days
ARTRV/FEID
ARTRV"P"/FEID
ARTRW/FEID
PIPO/FEID


20°/-.9
Mean Cumulative % Germination
100
80
60
40
20
ARTRV/FEID
ARTRV"P"/FEID
ARTRW/FEID
PIPO/FEID
5
10
15
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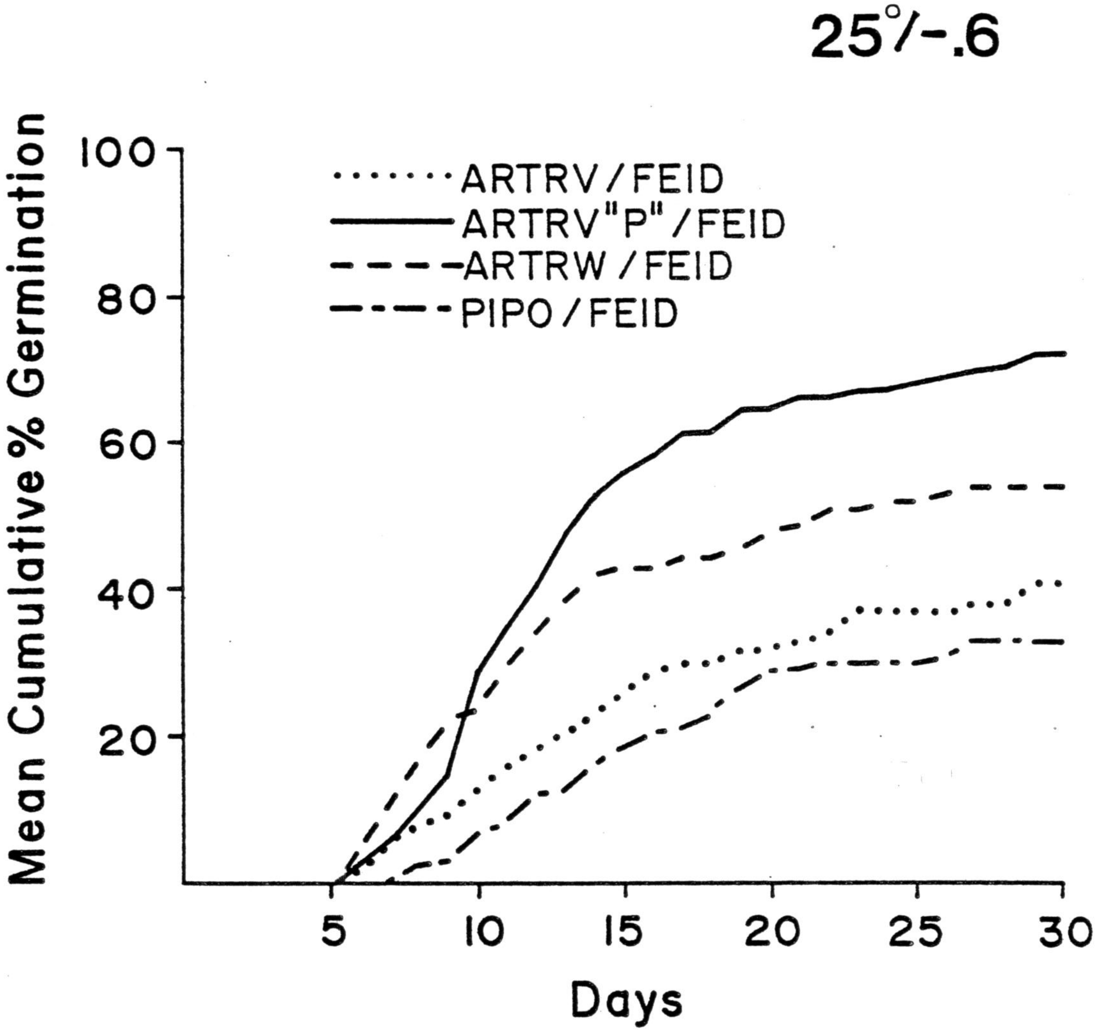
25
30
Days


25°/-.6
Mean Cumulative % Germination
100
80
60
40
20
ARTRV / FEID
ARTRV"P" / FEID
ARTRW / FEID
PIPO / FEID
5
10
15
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25
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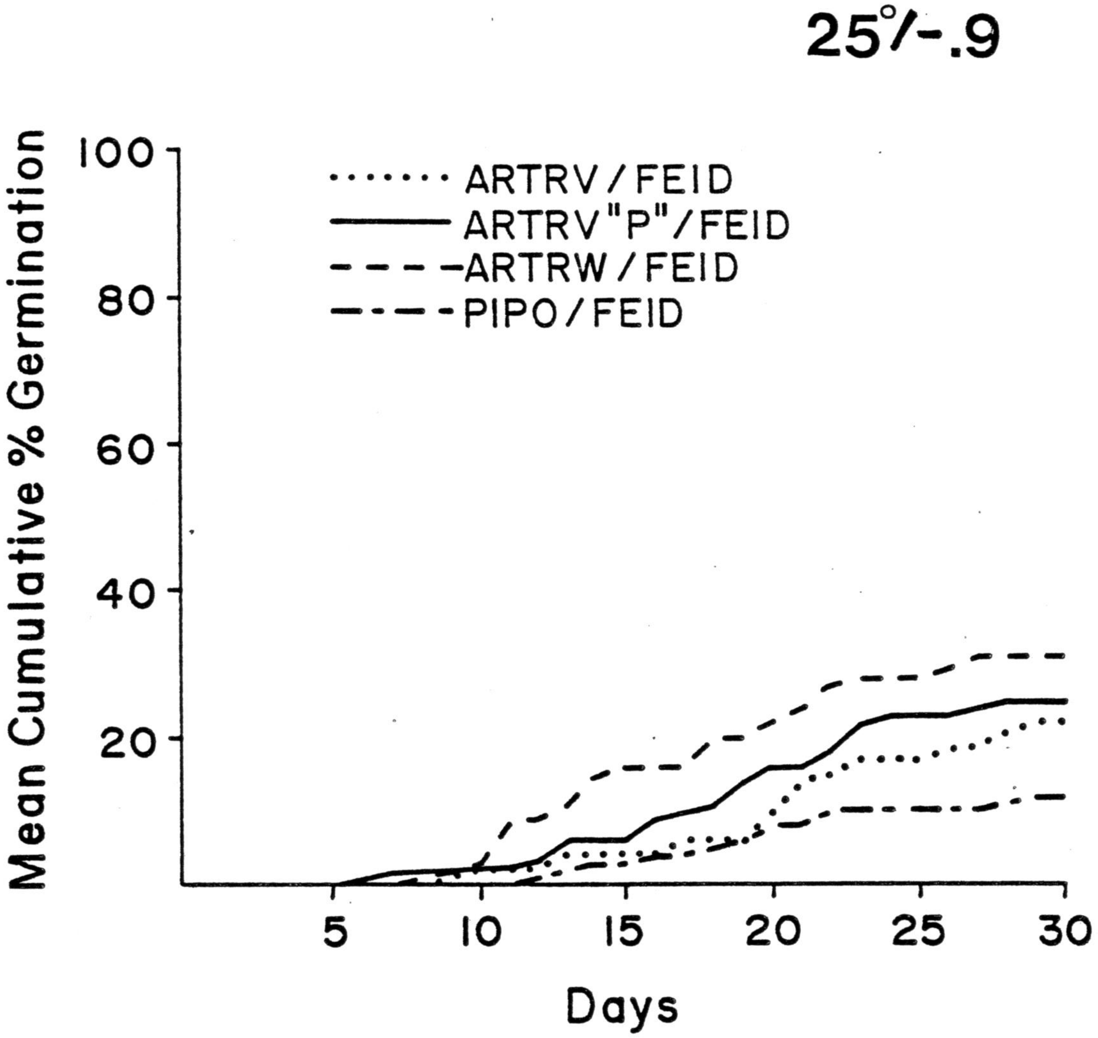
Days


25°/-.9
Mean Cumulative % Germination
100
80
60
40
20
ARTRV/FEID
ARTRV"P"/FEID
ARTRW/FEID
PIPO/FEID
5
10
15
20
25
30
Days

CHAPTER III

MORPHOLOGICAL AND PHENOLOGICAL RESPONSE OF FOUR CENTRAL OREGON IDAHO FESCUE COLLECTIONS IN A COMMON GARDEN

Paul S. Doescher
Richard F. Miller

MORPHOLOGICAL AND PHENOLOGICAL RESPONSE OF FOUR CENTRAL OREGON IDAHO FESCUE COLLECTIONS IN A COMMON GARDEN

ABSTRACT

Transplants of Idaho fescue (*Festuca idahoensis*) from four central Oregon habitat types were grown in a common garden and assessed for ecotypic differentiation. Habitat types studies were: *Pinus ponderosa/Festuca idahoensis*, *Artemisia tridentata* ssp. *wyomingensis/Festuca idahoensis* and a high and low elevation *Artemisia tridentata* ssp. *vaseyana/Festuca idahoensis*.

Ramets from the *Pinus ponderosa/Festuca idahoensis* habitat type were slower in phenological development and had greater vegetative growth than plants selected from three lower elevation *Artemisia tridentata* dominated communities. Within Idaho fescue collections chosen from big sagebrush sites, similar phenological timing was observed. Vegetative and floral development was reduced in plants selected from a relatively xeric *Artemisia tridentata* ssp. *wyomingensis/Festuca idahoensis* habitat type in comparison to ramets gathered from a high and low elevation *Artemisia tridentata* spp. *vaseyana/Festuca idahoensis* community. It was felt phenological and morphological response reflected those environmental factors influencing the selection of genotype adapted to a particular site. On the basis of these results, Idaho fescue collections from the *Pinus ponderosa* and *Artemisia tridentata* ssp. *wyomingensis* sites appeared to represent distinct ecotypes in comparion to the other two collections.

INTRODUCTION

The ecotype concept in range science is an important one, because management prescriptions are often enhanced by a knowledge of population differentiation within a plant species. Evaluations of ecotypic development across broad geographic regions (McMillan 1959; Clary 1975) and state-wide areas (Ward 1969; Robertson and Ward 1970; Dobrowolski 1979) have indicated phenological and morphological differences based upon collection latitude, longitude and elevation. However, less information has been gathered assessing ecotypic differentiation within relatively short geographic distances. Since a species commonly exists as a component of many plant associations and under a wide range of habitat conditions, population differences at the local level may be as distinguishable as those over wide regional distances.

The purpose of this study was to assess ecotypic development based upon phenological and morphological measurements in local populations of Idaho fescue (*Festuca idahoensis* Elmer) indigenous to central Oregon. Idaho fescue was chosen for study due to its relative importance as a forage species on rangelands in good ecological condition. Few studies evaluating ecotypic development in Idaho fescue have been performed. Tisdale (1960) collected seeds from numerous locations in the Pacific Northwest and established plants under uniform growing conditions. Differences in plant phenology and morphology were noted among collections. In a transplant study of selections from a high and low elevation steppe community, Stocker (1975) found shorter leaf length and plant height in plants collected from the high altitude site. Additionally, anther dehiscence was faster in the high elevation collection.

MATERIALS AND METHODS

Collection of plant materials were made during the summer of 1980 from the same geographic region in central Oregon. Vegetation of the area has been described and consists of big sagebrush (*Artemisia tridentata*) communities at the lower elevations and coniferous forests at the higher elevations (Franklin and Dyrness 1973). Idaho fescue commonly occurs as an important herbaceous component in communities dominated by subspecies of big sagebrush and ponderosa pine (*Pinus ponderosa*).

Sites were selected so as to represent clinal variation along an elevational and moisture gradient. Following recommendations of Daubenmire (1968), potential Idaho fescue populations were stratified on the basis of habitat type. Each community had as an understory synusiae, an Idaho fescue component. Site locations ranged from arid sagebrush grasslands to ponderosa pine forest. One stand each of four habitat types were identified and had as overstory dominates the following species:

Artemisia tridentata ssp. *wyomingensis* - Wyoming big sagebrush

Artemisia tridentata ssp. *vaseyana* - Mountain big sagebrush

Artemisia tridentata ssp. *vaseyana* "P" - a low elevation form of ssp. *vaseyana* which occurs on course pumice soils. Little is known about this variant.

Pinus ponderosa - ponderosa pine

Stands were in good ecological condition so as to minimize genetic selection on the basis of grazing tolerance. Habitat type, stand location and site information are given in Table 1.

Twenty five plants occurring in each habitat type were collected during the summer dormant period of 1980. Immediately after collection, root systems were wetted and individual plants placed in pots for transport. Pots were kept moist until plants could be transplanted to a common garden.

Each plant was divided into two ramets, approximately 7 x 7 cm in size and planted in a common garden at the Squaw Butte Experiment Station near Burns, Oregon. Garden elevation was 1412 meters and surface soils had a sandy loam texture. Yearly precipitation during the years 1962-1977 averaged 26.7 cm. Ramets were planted one meter apart in a completely randomized design and watered immediately upon placement in the common garden. Cultivation was performed at frequent intervals during the course of the trial to keep the interspace between Idaho fescue plants bare.

During the 1981 growing season, phenological and morphological measurements were recorded to assess ecotypic differentiation between collections. The following phenological stages, expressed as days of development past May 1, 1981, were recorded:

1. Boot stage - period of flowering culm elongation.
2. Early flowering - initial exsertion of the inflorescence from the flowering culm.
3. Inflorescence fully exserted - full exsertion of flowering culm from the boot.
4. Inflorescence fully expanded - inflorescence has achieved its maximum spread.

5. Athesis - flowering.
6. Seed shatter - articulation of florets.

In order to qualify for a specific phenological stage, greater than 25% of the flowering culms had to exhibit the desired response.

Morphological characteristics measured prior to seed shatter included:

1. Flowering culm height.
2. Length of inflorescence.
3. Length of spikelet.
4. Number of flowering culms per square centimeter basal area.
5. Vegetative culm height.

Morphological and phenological measurements for the two ramets per plant were averaged to provide a single numerical value for the analysis of collection differences. This approach was recommended by statistical consultation for two reasons: 1) that an average value would tend to minimize variation induced by the transplanting procedure or microsite differences, and 2) when morphological and phenological information was unavailable for one ramet of a pair, the other ramet could still be used in the analysis. Differences in response among collections were assessed using a LSD approach for mean comparisons, only when significance was indicated by analysis of variance (Steele and Torrie 1980). A probability level of 95% was used to assess differences between collections.

RESULTS

All ramets transplanted to the common garden survived the first year. Most individuals exhibited robust and vigorous growth, possibly the result of cultivation and release from competition. However, defoliation by insects and inadequate tiller production prevented the use of a few ramets per collection for analysis of certain phenologic and morphologic comparisons. Climatic conditions during the growing period were characterized by a relatively mild winter, with warm temperatures and low snowfall accumulations. Late spring weather was compensatorily cool and moist with saturated soil conditions and moderate temperatures existing until the middle of June, 1981. Summer conditions were characteristically hot and dry.

Phenological Development

Trends in phenologic progression during the course of the growing season indicated Idaho fescue plants collected from the three sagebrush habitat types to be earlier in development than those selected from the ponderosa pine site (Table 2). This relationship was evident for the following stages: boot, early flowering, anthesis and seed shatter. Within sagebrush collections, no consistent differences in phenological response were apparent. Collections from the ARTRV"P"/FEID site were most similar to plants selected from the ARTRW/FEID habitat type, except in days to anthesis. Phenology of the ARTRW/FEID and ARTRV/FEID differed only in days to exsertion of the inflorescence. Ramets from the ARTRV"P"/FEID were slower in phenological development for early flowering, expansion of inflorescence and anthesis in comparison to plants from the ARTRV/FEID habitat type.

Examination of error mean square values from Table 2 indicated the least variable stage of phenologic development to be anthesis. Very low variation among ramets within collection was evident.

Morphological Development

Examination of relative morphology between the four Idaho fescue collections indicated differences in vegetative and floral characteristics. A summary of the morphological characters assessed in this research is given in Table 3. From this information and on-site observation of plants growing in the common garden, the following trends were evident:

1. Ramets from the ARTRW/FEID habitat type were generally of shorter stature, had fewer flowering culms per unit basal area and exhibited reduced inflorescence characteristics when compared to the other collections.
2. Idaho fescue plants selected from the ponderosa pine community showed larger and greater vegetative culm growth than the other collections, but contained less flowering culms per unit basal area produced. Spikelet and inflorescence length were greatest of any collection.
3. Ramets from the high and low elevation mountain big sagebrush sites were similar in morphological development. However, a significant difference in the number of flowering culms per unit basal area was evident. Plants from the ARTRV"P" dominated site exhibited strong reproductive culm production and an overall stemmy appearance in comparison to the other collections.

DISCUSSION

Phenology

Our results indicated faster phenological development in ramets of Idaho fescue selected from habitat types with an overstory of big sagebrush, than collections made from a higher elevation ponderosa pine community. This observation was in contrast to findings elsewhere, which generally have indicated earlier phenology in high elevation genotypes of such species as Deschampsia caespitosa (Ward 1969), Sporobolus cryptandrus (Quinn and Ward 1969) and even Idaho fescue (Stocker 1975). However, this relationship is by no means clear because variability in phenological response under common garden situations apparently exists within a species. Robertson and Ward (1969) reported high elevation collections of Koeleria cristata to be later in phenology in comparison to low elevation selections, while McMillan (1959a) indicated an opposite response.

One posssible explantation which helps describe the phenological responses observed in this study, may relate to microclimatic conditions which exist between sites in a relatively local geographic area. Sagebrush dominated communities in eastern Oregon are characterized by rapid soil drying during the course of the growing season. Under these conditions, selection of genotypes capable of carrying out their growth cycles rapidly, before moisture conditions become limiting, would seemingly be an obvious evolutionary response. This is in contrast to the pine dominated communities where amelioration of the microclimate by elevation and overstory would tend to favor ecotypes which extended their phenology later into the summer.

Clary (1975), in an evaluation of regional populations of Sitanion hystrix, supports this contention. He suggests, since climatic conditions control length and timing of growing seasons, that these factors have primary selective influence on phenological development in plant populations. Patterns of ecotypic differentiation based upon phenology are probably predictable and result from the climatic conditions of the indigenous environment. Thus, common garden response may reflect the adaptational genetics of genotypes selected for by different habitat conditions.

These explanations may be related to the previously mentioned research where high elevation populations of a species were found to be faster in phenological development than lower elevation collections. In these studies, selections were chosen across wide geographic distances and differences in population response were often represented by ecotypes at the extremes of regional elevation gradients. Because only a few plants were gathered for common garden analysis at any one location, population variation at the local level was not described. Rather, broad intraspecific phenologic patterns were differentiated. If these elevational gradients had been partioned into relatively small segments, ecotypic response in relation to local habitat conditions might resemble the findings of this research. As distance between elevational collections becomes greater ecotypic differentiation would again resemble a more regional pattern.

Morphology

As with phenology, obvious morphological differences existed between pine site collections of Idaho fescue and plants gathered from three sagebrush dominated communities. Ramets from the PIPO/FEID habitat type exhibited greater vegetative growth and longer inflorescence and spikelet lengths than selections from the sagebrush locations. However, unlike the phenological data, differences among the sagebrush collections were evident. High and low elevation populations of Idaho fescue collected from mountain big sagebrush communities exhibited greater growth response both in terms of vegetative and reproductive development than plants selected from the ARTRW/FEID habitat type. Ramets from the Wyoming big sagebrush community were of relatively smaller stature when grown under common garden conditions. Except for the greater number of flowering culms per unit of basal area, Idaho fescue plants from the two mountain big sagebrush sites were similar in morphological development. Whether or not flowering culm production was a genetic or environmental response could not be determined from these results.

Some of the morphological characteristics observed under uniform garden conditions may be of adaptive significance. For instance, differences in vegetative growth between plant collections may be related to water relations that exist under natural conditions. Plant stature, particularly in terms of vegetative development, apparently decreased as collection site became more xeric. Perhaps this represents a xeromorphic adaptation which enables dry site populations of Idaho fescue to reduce transpirational losses.

Another possible morphological adaptation indicated from common garden evaluation was the greater number of flowering culms per unit basal area produced by plants collected from the ARTRV"P"/FEID habitat type. This response may be related to past land use activities associated with the collection area. This site had been cultivated in the early 1900's and after abandonment allowed to revegetate naturally. Under these conditions, genotypes producing a large number of seeds would seemingly be better adapted to establish and invade into new areas than low seed producing plants. Due to the relative similarity in morphological and phenological response between the two Idaho fescue collections from the mountain big sagebrush communities, the differences in flowering culm production may represent genotypes that were a subgroup of a population available for recolonization from high elevation plants. Genotypes with a high reproductive potential would seemingly be favored under these conditions.

Although these trends in morphological development seem logical, caution must be taken in their interpretation. Most of the morphological characteristics measured in this research tend to be highly plastic in response to environmental fluctuations. However, spikelet length is one factor which appears to be relatively inflexible (Robertson and Ward 1970; Dobrowolski 1979). Field measurements of spikelet length in Idaho fescue should correspond to values reported from common garden analysis. Examination of spikelet length alone reveals the same general trend in population response as the other morphological characteristics. Namely, collections from the PIPO/FEID and ARTRW/FEID habitat types exhibit relatively distinct morphology in comparison to the similar ARTRV/FEID and ARTRV"P"/FEID.

CONCLUSIONS

Based upon morphological and phenological development of ramets transplanted to a common garden, ecotypic variation in central Oregon populations of Idaho fescue appeared to be habitat related. The influence of interacting environmental conditions probably resulted in selection for differentially adapted genotypes. Ecotypic response at the local level may be as readily distinguishable as that exhibited by collections separated by wide geographic distances. One the basis of these results, Idaho fescue collections from the PIPO/FEID and ARTRW/FEID sites each appeared to represent distinct ecotypes in comparison to the other two collections.

Although results of this research indicate ecotypic differences in Idaho fescue populations from specific habitat types, one question still remains to be answered. Namely, what is the nature of ecotypic variation as distance between stands of a habitat type becomes greater? That is, do specific ecotypes correspond to particular habitat types as Daubenmire (1968) suggests? An answer to this question may enhance understanding into processes which influence intraspecific variation, and may provide a basis for land managers to select ecotypes of a species for specific management goals. Additional research into this topic apparently is needed.

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Table 1. Sampled plant communities and site characteristics of four eastern Oregon *Festuca idahoensis* collections.

Habitat Type	Abbreviation	Elevation (meters)	Site Location	Soil Description	Texture of Surface Soil
Artemisia tridentata ssp. *wyomingensis*/ *Festuca idahoensis*	ARTRW/FEID	1350	SW¼NW¼S33 T21SR21E Near Hampton, OR	Xerollic Durargid	Loamy Sand
Artemisia tridentata ssp. *vaseyana* "*P*"*/ *Festuca idahoensis*	ARTRV"P"/FEID	1400	SE¼NE¼S20 T20SR18E Near Brothers, OR	Xerollic Durargid	Sandy Loam
Artemisia tridentata ssp. *vaseyana*/ *Festuca idahoensis*	ARTRV/FEID	1700	SE¼NW¼S12 T21SR20E Near Hampton, OR	Argic Cryboroll	Sandy Loam
Pinus ponderosa/*Festuca idahoensis*	PIPO/FEID	1750	NW¼SE¼S22 T20SR15E Near Millican, OR	Typic Cryboroll	Loam

*A low elevation *A. tridentata* spp. *vaseyana* dominated community which has a unique physiognomy in comparison to higher elevation stands. "P" will be used to distinguish this site on the basis of pumice soils found on the site.

Table 2. Phenological development in four collections of *Festuca idahoensis*, expressed in mean number of days since May 1, 1981.

Site	Boot	Early Flowering	Inflorescence Fully Exserted	Inflorescence Fully Expanded	Anthesis	Seed Shatter
Error Mean Square	9.72	21.56	8.11	12.89	2.40	42.05
ARTRW/FEID	7.1^{a*}	14.4^{ab}	30.7^{ab}	45.1^{ab}	51.3^{a}	95.6^{a}
ARTRV"P"/FEID	7.2^{a}	15.7^{a}	30.1^{ac}	47.0^{a}	52.9^{b}	97.3^{a}
ARTRV/FEID	5.8^{a}	13.0^{b}	28.8^{c}	44.9^{b}	51.2^{a}	98.6^{a}
PIPO/FEID	9.3^{b}	19.7^{c}	31.8^{b}	47.1^{a}	54.3^{c}	102.7^{b}

*LSD separations: Values within columns without common letters judged significantly different at the 5% level.

Table 3. Morphological characteristics in four collections of *Festuca idahoensis*.

Site	Mean Flowering Culm Height (cm)	Mean Length of Inflorescence (cm)	Mean Length of Spikelets (cm)	Mean Number of Flowering Culms/cm^2	Mean Foliage Height (cm)
Error Mean Square	64.13	2.80	0.03	0.068	4.50
ARTRW/FEID	38.6^{a*}	8.0^{a}	1.2^{a}	0.17^{a}	12.8^{a}
ARTRV"P"/FEID	56.5^{b}	10.5^{b}	1.4^{b}	0.69^{c}	14.8^{b}
ARTRV/FEID	52.4^{b}	10.3^{b}	1.3^{b}	0.43^{b}	15.9^{bc}
PIPO/FEID	55.1^{b}	12.2^{c}	1.5^{c}	0.19^{a}	17.1^{c}

*LSD separations: Values within columns without common letters judged significantly different at the 5% level.

CHAPTER IV

INITIAL EVALUATIONS OF THE *ARTEMISIA TRIDENTATA* SSP. *WYOMINGENSIS*/*FESTUCA IDAHOENSIS* HABITAT TYPE IN EASTERN OREGON

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INITIAL EVALUATIONS OF THE *ARTEMISIA TRIDENTATA* SSP. *WYOMINGENSIS/FESTUCA IDAHOENSIS* HABITAT TYPE IN EASTERN OREGON

P. S. Doescher, R. F. Miller, S. R. Swanson and A. H. Winward

ABSTRACT

Six stands of the *Artemisia tridentata* ssp. *wyomingensis/Festuca idahoensis* (ARTRW/FEID) habitat type were assessed for vegetation and soils information. *Festuca idahoensis* was the dominant understory species in climax plant communities, while *Poa sandbergii*, *Sitanion hystrix* and *Artemisia tridentata* ssp. *wyomingensis* tended to increase as range condition declined. *Bromus tectorum* was most prevalent on sites with coarse textured soils.

The distribution of the ARTRW/FEID habitat type in eastern Oregon apparently coincides with the occurrence of nearby forested mountain ranges. Further research is needed in order to assess the extent and ecological importance of this plant community.

INTRODUCTION

In eastern Oregon, approximately 10,000,000 hectares of rangeland support sagebrush/grassland vegetation (Winward 1980). The most common woody species on these sites is Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), which is considered more xeric than other members of the big sagebrush group. Habitat types of lands dominated by Wyoming big sagebrush are recognized, however classification of these plant communities has primarily been developed in other regional areas. The most comprehensive evaluations have been performed in Idaho. Common understory associates which have been used to delineate habitat types include: *Agropyron spicatum*, *Stipa thurberiana*, *Stipa comata*, *Poa sandbergii* and *Sitanion hystrix* (Winward 1970; Hironaka and Fosberg 1979).

Although sagebrush dominated lands in Oregon are similar to those encountered in Idaho, one plant community not described is the *Artemisia tridentata* ssp. *wyomingensis*/*Festuca idahoensis* (ARTRW/FEID) association. Generally, Idaho fescue (*Festuca idahoensis*) has been associated with the more mesic portions of the region and has not been reported to occur in conjunction with the relatively xeric Wyoming big sagebrush (Hironaka and Fosberg 1979). During the past several years, as part of a comprehensive study assessing soil-plant relationships in eastern Oregon sagebrush communities, we have gathered basic synecological information regarding this plant community. It appears this habitat type is unique to eastern Oregon and may prove to be of relative interest, both from an ecological and management perspective. The purpose of this report is to describe our initial findings on the ARTRW/FEID habitat type.

MATERIALS AND METHODS

In order to clarify synecological relationships which exist within the ARTRW/FEID habitat type, six stands were located in eastern Oregon and sampled for vegetative and soil characteristics. Three of the sites were situated near Baker (B_1, B_2, and B_3), two at the Squaw Butte Experiment Station west of Burns (S_1 and S_2) and one in close proximity to Hampton (H_1). Site locations are given in Table 1.

The following procedures, modified from Poulton and Tisdale (1961), were used to gather vegetation information. At each site, a circular macroplot with a 25 meter radius was empirically located so as to be representative of the plant species present within the stand. Through the center of each plot, a randomly located baseline was established. During the summer of 1980, three 30 meter x 1 cm transects at distances of 8 and 16 meters on one side of the plot center and 8 meters on the other side of the plot center were established perpendicular to the baseline. Along each transect at 3 meter intervals, frequency of all plant species present was determined utilizing a 30 cm x 60 cm sampling frame. Thirty samples at each site were recorded. Shrub cover using a line-intercept approach was also determined along the 30 m transect. Herbage production of understory species was measured the following year utilizing the same sampling scheme as that used for plant frequency analysis. Plants were clipped and oven dried at 60°C.

At each location, soils were classified and topographic characteristics noted. Soil pH, surface texture, % organic matter and parent material were also determined. In order to provide a mean annual precipitation value for sites, U.S. Department of Commerce records for the closest weather station were averaged during the years 1962 to 1977.

RESULTS AND DISCUSSION

Vegetation and Soils

Results obtained from vegetation analysis are reported in Table 2. Graminoids comprised the bulk of understory species in the ARTRW/FEID habitat type, with Idaho fescue the dominant bunchgrass present on sites judged to be in good ecological condition. *Stipa thurberiana* was found to be a frequent associate in good condition stands, particularly on sites with sandy soil, but appeared to contribute less to understory biomass than Idaho fescue. *Poa sandbergii* and *Sitanion hystrix* were common members of the plant association and tended to increase as range condition declined. At the Squaw Butte and Hampton locations, scattered individuals of *Agropyron spicatum*, *Agropyron smithii* and *Koeleria cristata* were encountered, but did not contribute greatly to the understory component. *Bromus tectorum* achieved its maximum expression within stands found on coarse textured soils and was generally more prevalent on poor condition sites. Although perennial forbs did not constitute a very large percentage of the understory component, *Antennaria dimorpha* was ubiquitous on all areas. Annual forbs as a group tended to be clustered under shrub canopies and less important in the between shrub areas. Canopy coverage of Wyoming big sagebrush ranged from 7% to 25% and as ecological condition declined, sagebrush prevalence generally increased. *Chrysothamnus viscidiflorus* did not appear to be an important component of the ARTRW/FEID habitat type, but did occur on sites with a coarse textured soil. Herbaceous production tended to decline as range condition deteriorated.

Evaluation of soil characteristics within the sampled stands revealed differences in texture in relation to geographic area as soils at the Squaw Butte and Hampton sites were coarser textured than those encountered at the Baker location (Table 1). Soil pH's were basic, ranging from 6.7 to 7.4 and soil parent materials were generally derived from an alluvial source. Soil families keyed principally to xerollic durargids or xerollic durorthids and soil depths were relatively shallow, ranging from 31 cm to 76 cm.

Except for the presence of Idaho fescue and the absence of *Agropyron spicatum*, the ARTRW/FEID habitat type encountered in eastern Oregon appeared to be similar in physiognomy to the *Artemisia tridentata* ssp. *wyomingensis*/*Agropyron spicatum* (ARTRW/AGSP) habitat type described in Idaho (Winward 1970; Hironaka and Fosberg 1979). Both plant communities exist where annual precipitation is generally less than 12" and share common understory species. Further, these two habitat types tend to be less floristically diverse than higher elevation plant communities dominated by *Artemisia tridentata* ssp. *vaseyana*. Whether or not compensatory moisture relationships have enabled Idaho fescue to extend its range into Wyoming big sagebrush stands, or ecotypic development has resulted in the development of genotypes adapted to those sites has yet to be determined. However, it does appear Idaho fescue is at the extreme of its tolerance to moisture stress, whereas Wyoming big sagebrush on these sites occurs at the mesic end of its environmental distribution.

Although the extent of stands of the ARTRW/FEID habitat type in eastern Oregon has not been assessed, it appears to be the dominant plant community on certain specific areas. These sites have one factor in common, the occurrence of nearby forested mountain ranges. Stands in the Baker area are in close proximity to the Wallowa-Whitman range of the Blue Mountains, while sites at the Squaw Butte and Hampton locations are in the vicinity of the Ochoco Mountains. This relationship is consistent with extensive evaluations of other eastern Oregon rangelands. In the southeastern portion of the state, where sagebrush/grassland is the primary vegetation type, similar associations of Idaho fescue and Wyoming big sagebrush have not been located.* On these sites, plant communities are like those described in Idaho, with the ARTRW/AGSP habitat type the most prevalent Wyoming big sagebrush habitat type.

CONCLUSIONS

The ARTRW/FEID habitat type encountered in eastern Oregon represents a unique plant association between Idaho fescue and Wyoming big sagebrush. Its occurrence apparently coincides with nearby forested mountain ranges and it appears to be similar in physiognomy to the ARTRW/AGSP habitat type described elsewhere. Further research is needed to help clarify specific ecological and management characteristics.

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*Observations associated with this research and personal communication with David C. Ganskopp and Michael L. McInnis, Department of Rangeland Resources, Oregon State University.

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Table 1. Site descriptions and soils information for six eastern Oregon stands of the *Artemisia tridentata* ssp. *wyomingensis*/*Festuca idahoensis* habitat type.

Stand	B_1	B_2	B_3	S_1	S_2	H_1
County	Baker	Baker	Baker	Harney	Harney	Deschutes
Township and Section	9S 21(NE¼NE¼)	9S 27(NE¼NE¼)	8S 7(SW¼SE¼)	23S 34(SE¼NE¼)	24S 22(SE¼NW¼)	21S 33(SW¼NW¼)
Range	41E	41E	41E	25E	25E	21E
Elevation (meters)	1100	1100	1100	1341	1432	1341
Aspect and Percent Slope	NE8	W10-15	N3	N2-4	E2	NW5-10
15 Year Precipitation Average (1962-1977) cm/yr		26.2		26.7		24.9
Soil Classification	Xerollic durargid	Xerollic durargid	Xerollic durorthid	Xerollic durorthid	Aridic haploxerol	Xerollic durargid
Soil Depth to Restrictive Horizon (cm)	31	42	48	51	76	61
Soil Surface:						
Texture	Silt Loam	Silt Loam	Silt Loam	Sandy Loam	Sandy Loam	Loamy Sand
pH	7.4	7.4	7.0	7.2	6.7	7.2
% OM	1.4	2.0	2.15	.8	2.1	1.76
Parent Material	Alluvium basaltic	Alluvium	Basalt	Rhyolite alluvium	Alluvium basaltic	Alluvium basaltic

Table 2. Shrub cover, understory herbage production, relative seral stage and plant frequency for six eastern Oregon stands of the ARTRW/FEID habitat type.

STAND	B_1	B_2	B_3	S_1	S_2	H_1
SHRUB CANOPY COVER						
Artemisia tridentata ssp. *wyomingensis*	19.7	13.0	13.7	13.3	25.0	6.7
Chrysothamnus viscidiflorus				6.7	.7	4.3
Herbage Production (1981) kg/ha	304	178	676	393	418	320
Relative Seral Stage	MID	LOW	HIGH	MID	MID	HIGH
PERENNIAL GRAMINOIDS (Frequency)						
Agropyron smithii				3.3		3.3
Agropyron spicatum					10.0	3.3
Carex				30.0		3.3
Festuca idahoensis	36.7	16.7	100.0	23.3	53.3	56.7
Koeleria cristata					36.7	6.7
Poa sandbergii	96.7	96.7	80.0	13.3	50.0	
Sitanion hystrix	40.0	23.3	6.7	30.0	13.3	50.0
Stipa thurberiana	36.7			30.0	13.3	36.7
Stipa comata v. *comata*						13.3
ANNUAL GRAMINOIDS						
Bromus tectorum		30.0	6.7	90.0	86.7	13.3
Vulpia octoflora	3.3	3.3				

Table 2. Continued

STAND	B_1	B_2	B_3	S_1	S_2	H_1
PERENNIAL FORBS						
Achillea millefolium		10.0		3.3		
Allium			10.0			
Antennaria dimorpha	36.7	6.7	16.7	10.0	3.3	3.3
Arabis hirsuta v. *glabrata*				10.0		
Aster scopulorum				3.3		
Astragalus curvicarpa					23.3	
Astragalus salmonensis	53.3		23.3			
Calachortus				10.0		
Chaenactus douglasii				3.3		3.3
Crepis acuminata				3.3		
ERigeron linearis		6.7				
Erigeron poliospermus	70.0		6.7			
Eriogonum heracleoides						3.3
Eriogonum ovalifolium						
Leptodactylon pungens						10.0
Lomatium	3.3	36.7				
Lomatium rollinsii			3.3			
Lomatium triternatum				3.3		
Lupinus caudatus		16.7		16.7		
Phlox hoodii	76.7	60.0	23.3		13.3	
ANNUAL FORBS						
Alyssum alyssoides		26.7	10.0		60.0	
Collinsia parviflora		6.7	83.3	40.0	16.7	86.7

Table 2. Continued

STAND	B_1	B_2	B_3	S_1	S_2	H_1
ANNUAL FORBS (cont.)						
Descurainia pinnata						10.0
Epilobium paniculatum		40.0				
Eriastrum sparsiflorum						3.3
Eriogonum viminceum						16.7
Gayophytum ramosissium						13.3
Lepidium perfoliatum		33.3	3.3			
Microsterus gracilis			60.0	96.7	90.0	76.7
Plectritis macrocerus	33.3	16.7				
Ranunculus testiculatus						
SHRUBS						
Artemisia tridentata spp. wyomingensis	50.0	33.3	23.3	23.3	46.7	6.7
Chrysothamnus viscidiflorus				6.7	3.3	36.7

CHAPTER V

RESEARCH EVALUATIONS

RESEARCH EVALUATIONS

The purpose of this chapter is to evaluate the various research projects undertaken in this dissertation. Suggestions will also be offered which may aid in guiding future research efforts. Because the study areas were relatively distinct from one another, each of the three main projects will be discussed separately.

Ecotypic Development in Idaho Fescue

Examination of ecotypic development in eastern Oregon collections of Idaho fescue provided insights into the nature of population differentiation within a relatively local geographic area. Assessment of both seed germination characteristics and common garden response furnished information which appeared to reflect adaptational genetics of genotypes to a particular set of habitat conditions. Although inferences from the two trials yielded somewhat different conclusions, results from the evaluations tended to compliment one another. The pattern of germination response distinguished seeds gathered within three sagebrush communities from seeds gathered in a PIPO/FEID habitat type. Differential growth characteristics observed in the transplant garden further discriminated ramets from an ARTRW/FEID habitat type with plants selected from a high and low elevation ARTRV/FEID habitat type. On the basis of these results it appeared three Idaho fescue ecotypes were identifiable. Ecotypes from the PIPO/FEID site were characterized by slower phenological development, relatively greater vegetative growth, reduced inflorescence production and restricted germination response in comparison to the sagebrush collections. Ramets from the three sagebrush sites displayed similar phenological development and germination characteristics. However, individuals from the ARTRW/FEID ecotype exhibited reduced vegetative and inflorescence characteristics in relation to plants selected from the two ARTRV/FEID sites. It appeared the use of seed germination trials provided a relatively rapid means to assess readily distinguishable ecotypic patterns within a species. However, evaluation of other growth processes in plants grown under uniform garden conditions seemed necessary in order to further delineate specific ecotypic responses.

One problem associated with the common garden study was the relatively short-time period after transplanting morphological and phenological measurements were taken. Due to time constraints associated with completion of this dissertation, data were gathered on the basis of one years growth. Whether or not the transplant procedures influenced growth response of ramets could not be determined. However, during the initial phase of garden establishment, a relatively large number of plants per collection site were transplanted so as to compensate for expected mortality. The 100% survival of ramets appeared to indicate a successful establishment procedure, and the large number of plants available for analysis may have compensated for transplant effects.

Future research areas which may help to clarify ecotypic development in eastern Oregon populations of Idaho fescue might include the following assessments.

1. Evaluation of common garden plants for phenological and morphological characteristics during successive years. This may help determine if the responses observed in this research were due to ecotypic differences or rather a function of time since transplanting.
2. Examination of plant water relations of collections grown under common garden conditions so as to further assess ecotypic differentiation and relate this information to native environmental conditions.

3. Additional assessments of germination response in order to substantiate the ecotypic patterns established in this research and examine the nature of environmental pre-conditioning in seeds of Idaho fescue. Possible evaluations might include; 1) breeding common garden plants along pure lines and 2) selecting seeds from the 4 collection sites in successive years and germinating them under similar incubation environments as performed in this research.

4. A test of Daubenmire's (1968) contention that the habitat type serves as a means to stratify ecotypic development in a species. Evaluation of seed germination response to controlled temperature and moisture stress environments, replicated for numerous habitat types, may provide an initial means for evaluating this concept.

5. Establishment of reciprocal transplant gardens in order to assess environmental-genetic interactions within Idaho fescue populations.

Soil Chemical Patterns

Although horizontal and vertical soil chemical patterns were established for sagebrush-grasslands, additional research is needed in order to understand functional processes both within and between good and poor condition sites. Several study areas which may help to clarify nutrient cycling relationships include:

1. An examination of litter decomposition rates as influenced by season, land-use activities and plant species present on the site.

2. The assessment of temporal nutrient fluxes both in terms of turnover rates and nutrient availability.
3. An examination of nitrogen cycling dynamics both temporally and spatially and how these might differ between good and poor condition plant communities.

In addition to these evaluations, research examining the role nutrient accumulations have on competitive interrelationships may provide insights into plant succession and community dynamics. One potential study would be assessment of differentially accumulated ions by certain plant species and how these might confer a physiologic advantage of one species over another. For instance, the increased soil potassium concentrations under sagebrush plants in comparison to interspace and some grass influenced soils needs additional evaluation. This is in order to determine if high potassium levels enhance nitrate uptake, or whether they result from luxury consumption.

ARTRW/FEID Habitat Type

The manuscript describing the ARTRW/FEID habitat type originated from a larger project funded to assess plant-soil relationships in eastern Oregon plant communities dominated by subspecies of big sagebrush. Although this information was not originally intended for inclusion in this disseration, the plant association seemed unique enough to warrant its publication as a Technical Note in the Journal of Range Management. Thus, based upon the information available, a brief description of the ARTRW/FEID association was given.

Our initial findings on this habitat type provided insights into plant community interrelationships. However, information gathered in this research established only a cursory vegetation and soils description of this plant association. It is strongly recommended further research be performed in order to clarify specific ecological and management considerations associated with the habitat type.

Potential research evaluations might include:

1. Additional assessments of stands for such synecological information as herbage production, canopy coverage and density for all speices present on these sites.
2. Comparison of this habitat type with other habitat types dominated by big sagebrush, and establishment of a classification system for eastern Oregon rangelands.
3. Physiologic evaluations of Idaho fescue on these sites. This information may help to select cultivars suitable for revegetating relatively xeric sagebrush grassland with Idaho fescue.
4. Assessment of the management importance of this habitat type on eastern Oregon rangelands.

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APPENDICES

APPENDIX A

Soil chemical values on good and poor condition rangeland at three soil depths between canopy, interspace and grass zones for three habitat types of *Artemisia tridentata*.

APPENDIX A

TABLE A-1 Soil chemical characteristics in an *Artemisia tridentata* ssp. *vaseyana*/*Festuca idahoensis*-*Agropyron spicatum* habitat type between canopy, interspace and bunchgrass soil zones, at 3 depths for good and poor condition sites. Similar lower case letters indicate non-significant differences (α = .05) at a particular soil depth and condition class for comparison of S, I and BG soil chemical values.

	0-10 cm			10-20 cm			> 20 cm		
Good	S	I	BG	S	I	BG	S	I	BG
Total N (% D.W.)	$.13^{abA}$*	$.12^{aD}$	$.16^{bG}$	$.11^{aAB}$	$.11^{aD}$	$.10^{aH}$	$.10^{aB}$	$.10^{aD}$	$.09^{aH}$
Organic Matter (% D.W.)	4.45^{aA}	3.11^{bD}	4.73^{aG}	2.69^{aB}	2.56^{aD}	2.84^{aH}	2.22^{aB}	2.23^{aD}	2.39^{aH}
P $\mu g\ g^{-1}$	29.00^{aA}	21.30^{bD}	24.30^{abG}	24.00^{aA}	12.90^{bE}	19.70^{abG}	11.70^{aB}	9.30^{aE}	10.90^{aH}
K $\mu g\ g^{-1}$	739.90^{aA}	501.90^{bD}	927.50^{aG}	530.60^{aA}	414.20^{aDE}	577.30^{aH}	363.10^{aB}	347.90^{aE}	410.20^{aI}
Ca (meq/100g)	13.01^{aA}	12.31^{aD}	12.35^{aG}	13.13^{aA}	14.06^{aDE}	13.88^{aH}	15.51^{aB}	15.79^{aE}	15.30^{aI}
Mg (meq/100g)	4.67^{aA}	4.06^{aD}	4.21^{aG}	4.73^{aB}	4.83^{aDE}	4.52^{aGH}	5.53^{aB}	5.77^{aE}	5.20^{aH}
pH	6.47^{aA}	6.34^{aD}	6.54^{aG}	6.59^{aA}	6.56^{aDE}	6.68^{aGH}	6.68^{aA}	6.71^{aE}	6.79^{aH}
Poor									
Total N (% D.W.)	$.21^{aA}$	$.13^{bD}$	$.15^{bG}$	$.09^{aB}$	$.12^{bD}$	$.10^{aH}$	$.13^{aB}$	$.09^{bE}$	$.09^{bH}$
Organic Matter (% D.W.)	4.86^{aA}	3.47^{bD}	3.70^{abG}	2.27^{aB}	3.20^{bD}	2.42^{aH}	3.41^{aC}	2.24^{bE}	2.18^{bH}
P $\mu g\ g^{-1}$	42.80^{aA}	25.70^{bD}	22.80^{bG}	14.20^{aB}	22.20^{bD}	15.50^{aH}	23.60^{aC}	11.70^{bE}	10.40^{bI}
K $\mu g\ g^{-1}$	956.00^{aA}	511.80^{bD}	592.80^{bG}	421.50^{aB}	449.80^{aDE}	465.90^{aH}	565.40^{aB}	409.30^{bE}	358.40^{bI}
Ca (meq/100g)	14.60^{aA}	12.23^{bD}	12.59^{bG}	13.00^{aB}	12.95^{abD}	12.03^{bG}	11.91^{aB}	13.13^{bD}	12.52^{abG}
Mg (meq/100g)	4.87^{aA}	4.27^{bD}	4.33^{abG}	4.58^{aA}	4.30^{aD}	4.37^{aG}	3.95^{aB}	4.67^{bD}	4.70^{bG}
pH	6.68^{aA}	6.41^{bD}	6.52^{abG}	6.62^{aA}	6.51^{abD}	6.46^{bGH}	6.56^{aA}	6.63^{aD}	6.56^{aH}

*Similar capital letters denote non-significant differences holding S, I and BG soil zones and condition class constant, but comparing differences with depth.

APPENDIX A

TABLE A-2 Soil chemical characteristics in an *Artemisia tridentata* ssp. *tridentata/Elymus cinereus* habitat type between canopy, interspace and bunchgrass soil zones, at 3 depths for good and poor condition sites. Similar lower case letters indicate non-significant differences ($\alpha = .05$) at a particular soil depth and condition class for comparison of S, I and BG soil chemical values.

	0-10 cm			10-25 cm			> 25 cm		
Good	S	I	BG	S	I	BG	S	I	BG
Total N (% D.W.)	$.23^{aA*}$	$.14^{bD}$	$.15^{bG}$	$.10^{aB}$	$.08^{bE}$	$.09^{bH}$	$.07^{aB}$	$.07^{aE}$	$.07^{aH}$
Organic Matter (% D.W.)	4.96^{aA}	2.59^{bD}	3.24^{bG}	1.86^{aB}	1.51^{aE}	1.62^{aH}	1.00^{aB}	1.14^{aE}	1.12^{aH}
P $\mu g\ g^{-1}$	57.40^{aA}	37.80^{bD}	32.10^{bG}	28.00^{aB}	20.60^{abE}	18.60^{bH}	7.90^{aC}	4.80^{bF}	5.20^{abI}
K $\mu g\ g^{-1}$	1622.20^{aA}	961.20^{bD}	1556.60^{aG}	1414.50^{aA}	1110.40^{bD}	1145.50^{abH}	1059.70^{aB}	986.20^{aD}	938.90^{aH}
Ca (meq/100g)	10.65^{aA}	9.26^{bD}	9.33^{abG}	9.31^{aB}	9.60^{aD}	9.55^{aG}	9.24^{aB}	9.78^{aD}	9.58^{aG}
Mg (meq/100g)	5.12^{aA}	4.62^{aD}	4.70^{aG}	5.05^{aA}	5.41^{bE}	5.37^{bH}	6.32^{aB}	6.60^{aF}	6.58^{aI}
pH	6.50^{aA}	6.60^{abD}	6.70^{bG}	7.09^{aB}	6.86^{bE}	7.12^{aH}	7.25^{aB}	7.22^{aF}	7.29^{aH}
Poor									
Total N (% D.W.)	$.13^{aA}$	$.08^{bD}$	$.12^{aG}$	$.06^{aB}$	$.05^{aE}$	$.06^{aH}$	$.05^{aB}$	$.05^{aE}$	$.05^{aH}$
Organic Matter (% D.W.)	2.85^{aA}	1.44^{bD}	2.29^{aG}	1.08^{aB}	$.94^{aE}$	1.05^{aH}	$.84^{aB}$	$.68^{abE}$	$.63^{bI}$
P $\mu g\ g^{-1}$	42.80^{aA}	25.48^{bD}	21.90^{bG}	17.40^{aB}	14.00^{aE}	13.70^{aH}	6.10^{aC}	5.90^{aF}	5.00^{aI}
K $\mu g\ g^{-1}$	1316.00^{aA}	731.30^{bD}	869.50^{bG}	996.50^{aAB}	729.90^{bD}	825.20^{abG}	615.00^{aB}	568.00^{aD}	555.80^{aH}
Ca (meq/100g)	8.91^{aA}	7.98^{bD}	7.96^{bG}	8.95^{aA}	8.68^{aDE}	8.77^{aG}	9.68^{abA}	9.02^{aE}	10.20^{bH}
Mg (meq/100g)	4.27^{aA}	3.80^{bD}	4.10^{bG}	4.67^{aA}	4.65^{aE}	4.91^{aH}	5.65^{aB}	5.71^{abF}	6.15^{bI}
pH	6.93^{aA}	6.60^{bD}	6.60^{bG}	7.27^{aB}	7.05^{aE}	7.18^{aH}	7.19^{aB}	7.31^{aF}	7.33^{aH}

*Similar capital letters denote non-significant differences holding S, I and BG soil zones and condition class constant, but comparing differences with depth.

APPENDIX A

TABLE A-3 Soil chemical characteristics in an *Artemisia tridentata* ssp. *wyomingensis*/*Stipa thurberiana* habitat type between canopy, interspace and bunchgrass soil zones, at 3 depths for good and poor condition sites. Similar lower case letters indicate non-significant differences ($\alpha = .05$) at a particular soil depth and condition class for comparison of S, I and BG soil chemical values.

	0-10 cm			10-20 cm			> 20 cm		
Good	S	I	BG	S	I	BG	S	I	BG
Total N (% D.W.)	$.16^{aA}$*	$.08^{bD}$	$.10^{bG}$	$.08^{aA}$	$.06^{bDE}$	$.06^{bH}$	$.04^{aA}$	$.04^{aE}$	$.04^{aI}$
Organic Matter (% D.W.)	3.84^{aA}	1.60^{bD}	2.21^{bG}	1.87^{aB}	1.12^{bE}	1.24^{bH}	$.81^{aC}$	$.72^{aF}$	$.61^{aI}$
P $\mu g\ g^{-1}$	45.80^{aA}	20.90^{bD}	23.60^{bG}	22.00^{aB}	10.60^{bE}	10.20^{bH}	6.10^{aC}	4.10^{aF}	4.30^{aI}
K $\mu g\ g^{-1}$	1263.60^{aA}	546.50^{bD}	693.10^{bG}	1032.50^{aA}	599.60^{bD}	553.20^{bH}	478.20^{aB}	515.30^{aD}	452.80^{aH}
Ca (meq/100g)	8.16^{aA}	6.67^{bD}	6.84^{bG}	7.78^{aA}	7.65^{aE}	7.71^{aG}	8.07^{aA}	8.49^{abE}	8.90^{bH}
Mg (meq/100g)	3.91^{aA}	3.51^{aD}	3.61^{aG}	4.23^{aA}	4.94^{bE}	4.63^{abH}	5.68^{aB}	6.40^{bF}	6.00^{abI}
pH	7.03^{aA}	6.85^{bD}	6.82^{abG}	7.44^{aB}	7.36^{aE}	7.31^{aH}	7.48^{aB}	7.66^{aF}	7.60^{aI}
Poor									
Total N (% D.W.)	$.19^{aA}$	$.12^{bD}$	$.12^{bG}$	$.09^{aA}$	$.09^{aDE}$	$.08^{aH}$	$.07^{aB}$	$.07^{aE}$	$.07^{aH}$
Organic Matter (% D.W.)	4.06^{aA}	2.17^{bD}	2.51^{bG}	1.53^{aB}	1.51^{aDE}	1.34^{aH}	1.11^{aB}	1.05^{aE}	$.93^{aH}$
P $\mu g\ g^{-1}$	19.80^{aA}	24.60^{aD}	32.00^{aG}	18.80^{aA}	13.20^{abE}	12.20^{bH}	5.90^{aA}	4.30^{aF}	4.80^{aI}
K $\mu g\ g^{-1}$	1681.10^{aA}	741.50^{bD}	1001.70^{bG}	965.00^{aB}	651.00^{bD}	627.10^{bH}	443.30^{aC}	388.40^{aE}	389.00^{aI}
Ca (meq/100g)	10.28^{aA}	9.12^{aD}	9.17^{aG}	9.81^{aA}	9.55^{aD}	9.75^{aG}	9.99^{aA}	9.75^{aD}	9.68^{aG}
Mg (meq/100g)	4.89^{aA}	4.55^{bD}	4.88^{aG}	5.60^{aB}	5.65^{aE}	6.01^{aH}	6.19^{aC}	6.10^{aF}	6.13^{aH}
pH	7.00^{aA}	6.80^{aD}	6.94^{aG}	7.21^{aA}	7.04^{bE}	7.23^{aH}	7.18^{abA}	7.31^{bE}	7.53^{bI}

*Similar capital letters denote non-significant differences holding S, I and BG soil zones and condition class constant, but comparing differences with depth.

APPENDIX B

Analysis of Variance and mean values for transformed % germination, coefficient of rate of germination, and days to 50% germination for six constant temperatures at the end of a 30 day trial period.

APPENDIX B

TABLE B-1. Analysis of Variance for Total Transformed % Germination, CRG and Days to 50% germination for six constant temperatures at the end of a 30 day trial period.

Source	df	Mean Square Total	Mean Square CRG	Days to 50%
Total	95	151.54	16.71	45.47
Collection	3	1212.91*	79.95*	18.37*
Temperature	5	1208.29*	231.74*	836.29*
Collection x Temperature	15	111.37*	6.19*	.86
Error	72	42.29	1.34	.98

*Significant at α = .05

APPENDIX B

TABLE B-2. Two-way interactions means for total transformated % germination at six constant temperatures. HSD values for 4 and 6 mean comparisons are given.

Temperature	5	10	15	20	25	30
Collection			% Germination			
ARTRW/FEID	55.59^{a*}	76.72^{ab}	72.67^{a}	77.17^{a}	68.90^{a}	60.35^{a}
ARTRV"P"/FEID	51.98^{ab}	84.16^{a}	70.61^{a}	70.47^{ab}	74.10^{a}	53.91^{ab}
ARTRV/FEID	64.93^{b}	73.49^{ab}	77.94^{a}	62.56^{bc}	72.61^{a}	58.23^{ab}
PIPO/FEID	43.26^{c}	71.16^{b}	54.08^{c}	57.35^{c}	51.37^{c}	46.41^{b}

HSD value for 4 means 12.096.

HSD value for 6 means 13.494.

*Similar letters denote non-significant differences between collections at a particular temperature level ($\alpha = .05$).

APPENDIX B

TABLE B-3. Two way interaction means for Coefficient of Rate of Germination (CRG) at 6 constant temperatures. HSD values for 4 and 6 mean comparisons are given.

Temperature	5	10	15	20	25	30
Collection			CRG			
ARTRW/FEID	2.74^{a*}	8.88^{a}	11.19^{ab}	14.47^{a}	13.44^{a}	9.51^{a}
ARTRV"P"/FEID	2.42^{a}	9.72^{a}	10.79^{a}	14.46^{a}	14.44^{a}	8.80^{a}
ARTRV/FEID	3.38^{a}	9.25^{a}	13.08^{b}	12.64^{a}	15.50^{a}	9.28^{a}
PIPO/FEID	1.80^{a}	7.88^{a}	6.68^{c}	9.41^{b}	8.25^{b}	5.56^{b}

HSD value for 4 means 2.153.

HSD value for 6 means 2.402.

*Similar letters denote non-significant differences between collections at a particular temperature level (α = .05).

APPENDIX B

TABLE B-4. Mean number of days to 50% germination for four Idaho fescue collections germinated at 6 constant temperatures.

Temperature	5	10	15	20	25	30	$\overline{X}$
Collection			Days to 50% Germination				
ARTRW/FEID	25.25	10.25	7.75	6.25	6.00	7.50	10.5[a]*
ARTRV"P"/FEID	25.75	10.25	8.00	6.25	6.25	7.50	10.67[a]
ARTRV/FEID	24.00	10.00	7.50	5.75	6.00	8.00	10.21[a]
PIPO/FEID	26.25	11.50	10.00	7.50	7.25	10.50	12.17[b]

*Similar letters denote non-significant differences between collections at a particular temperature level (α = .05).

APPENDIX C

Analysis of Variance and mean values for transformed % germination, coefficient of rate of germination and days to 50% germination for three temperatures and three moisture stress levels at the end of a 30 day trial.

APPENDIX C

TABLE C-1. Analysis of Variance for total transformed % germination, CRG and days to 50% germination for three moisture stress levels at three constant temperatures during a 30 day germination trial.

Source	df	Mean Square Total	Mean Square CRG	Days to 50%
Total	143	272.04	17.54	16.14
A-Collection	3	1677.86	72.10	18.55*
B-Temperature	2	6318.11	78.21	26.22
C-Moisture Stress	2	4187.67	828.86	888.47
AB	6	87.49	2.46	5.32
AC	6	127.53	16.65	3.18
BC	4	1517.36	57.60	19.42*
ABC	12	80.76*	2.70*	2.51
Sampling Error	108	41.92	.93	2.44

*Significant at $\alpha = .05$ level.

APPENDIX C

TABLE C-2. Three way interaction means for total transformed percent germination at three temperatures and three moisture stress levels. HSD value for 3, 4 and 9 mean comparisons are given.

	Temperature								
	15°			20°			25°		
ψw	0	-6	-9	0	-6	-9	0	-6	-9
Collection	% Germination								
ARTRW/FEID	72.67^{a}*	76.15^{a}	64.93^{a}	77.17^{a}	70.82^{ab}	58.90^{a}	68.90^{a}	47.32^{ab}	33.76^{a}
ARTRV"P"/FEID	70.61^{a}	78.90^{a}	68.29^{a}	70.47^{ab}	75.06^{a}	62.35^{a}	74.10^{a}	58.48^{a}	29.95^{a}
ARTRV/FEID	77.94^{a}	67.46^{ab}	69.12^{a}	62.56^{bc}	71.30^{ab}	46.86^{b}	72.61^{a}	39.34^{bc}	27.74^{ab}
PIPO/FEID	54.08^{b}	60.78^{b}	57.52^{a}	57.35^{c}	62.07^{b}	51.98^{ab}	51.37^{b}	35.19^{c}	19.66^{b}

HSD 3 means = 10.92.
HSD 4 means = 11.98.
HSD 9 means = 14.48.

*Similar letters denote non-significant differences between collections at a particular temperature/moisture stress level ($\alpha = .05$).

APPENDIX C

TABLE C-3. Three way interaction means for coefficient of rate of germination (CRG) at three temperatures and three moisture stress levels. HSD values for 3, 4 and 9 mean comparisons are given.

	Temperature								
		15°			20°			25°	
ψw	0	-6	-9	0	-6	-9	0	-6	-9
Collection					CRG				
ARTRW/FEID	11.19^{a}*	8.86^{a}	5.56^{a}	14.47^{a}	9.71^{a}	5.27^{a}	13.44^{a}	5.25^{a}	2.11^{a}
ARTRV"P"/FEID	10.79^{a}	8.93^{a}	5.68^{a}	14.46^{a}	8.92^{a}	5.13^{a}	14.44^{ab}	6.31^{a}	1.57^{a}
ARTRV/FEID	13.08^{b}	8.32^{ab}	5.59^{a}	12.64^{b}	9.33^{a}	3.83^{a}	15.50^{b}	3.34^{b}	1.19^{a}
PIPO/FEID	6.68^{c}	6.79^{b}	4.56^{a}	9.41^{c}	6.81^{b}	4.12^{a}	8.26^{c}	2.40^{b}	.66^{a}

HSD 3 means = 1.62.
HSD 4 means = 1.78.
HSD 9 means = 2.15.

*Similar letters denote non-significant differences between collections at a particular temperature/moisture stress level ($\alpha = .05$).

APPENDIX C

TABLE C-4. Mean number of days to 50% germination for four Idaho fescue collections germinated at six constant temperatures.

	Temperature									
	15°			20°			25°			
ψw	0	-6	-9	0	-6	-9	0	-6	-9	$\overline{X}$
Collection	Days to 50% Germination									
ARTRW/FEID	7.75	10.75	15.50	6.25	9.00	14.75	6.00	10.50	14.50	10.56^{a*}
ARTRV"P"/FEID	8.00	10.75	15.25	6.25	10.75	15.50	6.25	11.75	17.50	11.33^{ab}
ARTRV/FEID	7.50	10.25	15.50	5.75	9.50	13.75	6.00	14.00	17.75	11.11^{a}
PIPO/FEID	10.00	11.00	15.25	7.50	11.75	15.50	7.25	15.25	17.00	12.28^{b}

*Similar letters denote non-significant differences between collections ($\alpha = .05$).