EFFECTS OF BULK DENSITY AND SOIL STRENGTH ON THE GROWTH OF BLUE WILDRYE (*ELYMUS GLAUCUS* BUCKL.)

by

Allison A. Tokunaga

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Approved by the Master's Thesis Committee:

Dr. Susan Edinger-Marshall, Major Professor — Date

Dr. William L. Bigg, Committee Member — Date

Dr. Erik S. Jules, Committee Member — Date

Dr. Gary L. Hendrickson, Coordinator, Natural Resources Graduate Program — Date

Donna E. Schafer, Dean for Research and Graduate Studies — Date

ABSTRACT

Effects of bulk density and soil strength on the growth of
blue wildrye (*Elymus glaucus* Buckl.)

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The effects of soil compaction on plant productivity have frequently been studied in the context of agriculture, but less information exists about this relationship in the context of rangeland resources. Domestic livestock grazing has been cited as contributing to soil compaction and loss of native species on rangelands. This study used a greenhouse experiment to identify the effects of soil compaction on the productivity of seedlings of *Elymus glaucus* Buckl. (blue wildrye), a native perennial grass. Compaction was characterized by bulk density and by soil strength as a function of bulk density and water content. Plants were grown in three levels of bulk density (1.00, 1.25, and 1.55 g cm^{-3}) at three water potentials (-33, -500, and -1500 kPa). Shoot production increased significantly at high water potential and moderate bulk density (ANOVA, $p<0.05$). Root production decreased significantly at high bulk density and low water potential (ANOVA, $p<0.05$). Soil strengths exceeding 3 MPa and 6 MPa were present in treatments producing the greatest shoot and root biomass, respectively. Similar, intermediate levels of production occurred across the range of bulk densities in this study and across a wide range of soil strength, suggesting that no threshold bulk density or soil strength exists that limits *E. glaucus* production. Biomass production was greatest when water was readily available. Negative effects of highly compacted soils were often less severe when water was available. This suggests the importance of water in biomass production as well as in the ability of plants to tolerate compacted soil. In field settings, where water availability

may be highly variable, soil compaction as it affects water availability to plants may be more important in influencing *E. glaucus* establishment than physical impedance itself.

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INTRODUCTION

The Soil Science Society of America defines “soil quality” as “the capacity of a soil to function within ecosystem boundaries to sustain biological productivity, maintain environmental quality, and promote plant and animal health.” (Soil Science Society of America 2005). The topic of soil quality is relevant to the use and management of several natural resources. Productive soil is vital for timber, forage, and crop production. Soil particles bind compounds that can pollute groundwater sources. The ability of a soil to transmit surface water below ground is important for preventing erosion and sedimentation.

The ability of a soil to generate such products or perform such functions may decline with certain land uses. One of the most common land uses in the western United States is grazing. Much of the western U.S. landscape is rangeland. Rangelands are located from the tropics to the arctic and are characterized by vegetation dominated by grass, forbs, and shrub vegetation. According to the Society for Range Management (2005), 40% of the U.S. land mass is classified as rangeland. Due to limitations of soil, water, or terrain, many rangelands are not suitable for intensive cultivation of row crops, and so have often been utilized as grazing lands for domestic livestock.

Grazing has been observed to benefit ecosystems. Edwards (1992) and Hobbs and Huenneke (1992) review some of these benefits, including increased productivity, reduced encroachment of shrubs and trees into open grasslands, improved seed germination, and increased species diversity.

Conversely, grazing has been faulted for many changes that have occurred in western rangelands (Fleischner 1994). In California, the prevailing viewpoint is that what are today annual grasslands were once dominated by perennial bunchgrasses. Such formerly dominant grasses included *Nassella pulchra* (A.S. Hitchc.) Barkworth, *Danthonia californica* Boland., and *Elymus glaucus* Buckl. (Bartolome et al. 1986, Dwire 1988). The role of grazing in this conversion included excessive trampling of plants, consumption of shoot biomass beyond the level at which the plants could recover, and changes in fire regimes. Reduction in vegetation abundance and vigor created areas of bare soil or lesser competition in which exotic plants could establish (Kimball and Schiffman 2003, Hobbs and Huenneke 1992).

The role of soil condition on the persistence of native species in California rangelands has been studied less frequently. Grazing has been cited as a source of soil degradation. One potentially degrading effect on soil condition is that of soil compaction. Because soil is a complex system of biotic and abiotic components, soil compaction affects several properties of soils that may affect rangeland vegetation. These include changes in root growth, availability and movement of air and water, and microbial activity.

Soil compaction is defined as an increase in the oven-dry mass per unit volume of soil particles by application of mechanical force (Soil Science Society of America 2005). It is described by soil dry bulk density (Db), or the mass of dry soil per unit bulk volume (Soil Science Society of America 2005). Bulk density is calculated using only the fine earth fraction of soil (particle diameters less than 2 mm). It is calculated by the following equation:

$$\text{dry bulk density} = (\text{dry mass soil})*(\text{volume soil})^{-1}$$

Bulk density is expressed in units of g cm^{-3}. In grazed rangelands, soil compaction can be affected by stocking rates (Van Haveren 1983, Naeth et al. 1990), soil texture (Orr 1960, Van Haveren 1983), season of grazing (Naeth et al. 1990), and water content and organic matter (Howard et al. 1981).

Soil compaction may affect several physical and biological processes. Physical impedance of roots may limit plant access to water and nutrients by reducing the volume of soil exploited. Compaction may destroy soil structural units and change pore distribution, thereby slowing water infiltration and gaseous diffusion (Taylor and Brar 1991, Orr 1960). Slower infiltration may translate into increased runoff and erosion. Slower gas diffusion may increase carbon dioxide concentrations in soil air, potentially affecting root respiration (Simojoki et al. 1991). Compaction may also slow decomposition, thereby slowing the return of nutrients to the soil (Breland and Hansen 1996).

Soil compaction also increases soil strength, defined as a transient localized soil property that is a combined measure of the adhesive and cohesive qualities of the solid phase of a soil subunit (Soil Science Society of America 2005). Murphy et al. (2000) describe soil strength as “the capacity of soil to resist a force without rupture, fragmentation, or flow.” Compacted soil will not respond as easily to forces acting against it, such as root movement, due to higher frictional forces between particles and less space into which particles can shift. Soil strength is affected by factors including soil structure, soil water content, soil texture, and cementing agents (Mirreh and Ketcheson 1972, Vepraskas 1988). It is also affected management variables including trampling intensity (Bryant et al. 1972), season of use (Chanasyk and Naeth 1995), and grazing regime (Donkor et al. 2002b).

Ecological applications of soil strength generally address soil resistance to root penetration. Measured with a penetrometer, soil strength is measured as penetration resistance. Penetration resistance describes the amount of pressure, in megapascals (MPa), applied to push the penetrometer through a soil profile. Unlike bulk density, penetration resistance attempts to mimic a root growing through soil. However, Whiteley et al. (1981) and Atwell (1993) noted that soil strength as measured with this instrument may exceed that encountered by roots by 2 to 5 times. Reasons for this include preferential growth of roots into spaces or cracks of larger diameter, and higher friction between the penetrometer shaft and soil than between roots and soil (Atwell 1993, Clark et al. 2003).

Soil compaction is measured by bulk density and soil strength. Bulk density directly measures compaction, and generally does not vary with other soil properties because it is most often expressed on a dry soil basis. Soil strength measures soil compaction indirectly. Because soil strength is a function of several variables, including soil water content, it is possible for similar soil strengths to exist at different levels of compaction.

Root-limiting bulk densities and soil strengths have been studied largely in agricultural contexts where farm machinery is the major compactive force. Studies have focused on warm-season crop species, many of which have taproots. Studies of grazing and soil compaction have typically focused on soil physical properties rather than compaction effects on plant production.

Studying sunflowers (species not identified by author) on a range of soil textures, Veihmeyer and Hendrickson (1948) cited root-limiting bulk densities that ranged from 1.46 g cm^{-3} to 1.9 g cm^{-3} for fine- to coarse-textured soils, respectively. The root limiting bulk density was a function of texture.

Zimmerman and Kardos (1961) tested the effect of bulk density on root biomass production of soybeans and Sudan grass (species not identified by authors). Treatment levels included four textures ranging from coarse to fine, and four bulk densities (1.4, 1.6, 1.8, and 2.0 g cm^{-3}). Bulk density was the only significant variable affecting root biomass, with higher bulk densities yielding less. Sudan grass roots penetrated deeper than soybean roots, and bulk densities of 1.8 g cm^{-3} and above excluded almost all roots. Although not rigorously monitored, plant available water was not limiting in this experiment.

While not studying root-excluding bulk densities, Jones (1983) reviewed ten published and unpublished studies describing rooting patterns in different soil textures at field capacity. He found that bulk densities greatly reducing root density varied with soil texture. These critical bulk densities decreased as the percentage of clay and silt increased.

Taylor and Burnett (1964) studied how compaction of a fine sandy loam affects the root production and growth patterns of a variety of crop plants. Bulk densities of 1.73 g cm^{-3} and 1.88 g cm^{-3} were found to be root-limiting. Root-limiting soil strengths at field capacity were 25-30 bars (2.5-3.0 MPa), and there was no difference between plants at these levels. Some penetration occurred at 19 bars (1.9 MPa).

Using cotton planted in a fine sandy loam, Taylor and Gardner (1963) found that soil strength was critical in stopping root growth. They did not find a critical root limiting bulk density because root penetration at each bulk density was affected by soil water content. Root-limiting resistances were reached at lower bulk densities when soils were dry. Higher strength decreased root growth rate. No penetration occurred at 29.6 x 10^6 dynes cm^{-2} (2.96 MPa) whether caused by low water content or bulk density.

In another study on cotton, Taylor et al. (1966) found large differences in soil strength depending on soil texture. Soils with more clay produced higher strength measurements. Root penetration declined rapidly at soil strengths between 3 bars and 15 bars (0.3-1.5 MPa), with no penetration at 25 bars (2.5 MPa) regardless of soil texture.

Taylor et al. (1966) also cited unpublished data in which yields decreased with increasing soil strength. Species studied include switchgrass (*Panicum* sp.). Soil strengths up to 25 bars (2.5 MPa) progressively reduced yields, but further reductions were minimal at higher soil strengths.

Vepraskas (1988) found that the ability of tobacco (*Nicotiana tabacum*) roots to penetrate the soil was a function of bulk density, water content, soil texture, and soil structure. Penetration resistances greater than 3 MPa stopped virtually all root growth.

Penetration resistances of ~1.5 MPa reduced growth such that subsoiling significantly increased root production.

Gerard et al. (1982) developed models describing root growth of cotton in a fine sandy loam (Udic Paleustalf) and a clay loam (Pachic Argiustoll). Root growth was a function of soil strength, water content, voids, and clay content. The critical strength at which root elongation stopped was a function of clay content, and ranged from 60-70 bars (6-7 MPa) in coarse soils to 25 bars (2.5 MPa) in finer soils. These strengths occurred over a range of bulk densities (1.5-1.7 g cm^{-3}) and gravimetric water contents (3.5-20%).

Chanasyk and Naeth (1995) found that grazing increased bulk density and soil strength, with potentially root-limiting penetration resistances occurring between 10 and 30 cm. Donkor et al. (2002b) and Daniel et al. (2002) also found that grazing increased bulk density and soil strength, with the most pronounced effect in the top 10 cm. Orr (1960) found an increase in bulk density with grazing at a shallower depth of 0-5 cm.

The impacts of grazing on soil conditions at shallow depths and of compaction on rooting ability suggest that compaction may have a considerable effect on establishment of native perennial grass seedlings. In an ecosystem grazed by large herbivores, the ability of a species to take root in compacted soils may play an important role in maintaining that species in the plant community.

The impacts of grazing on soil compaction and consequent effects on the native grass *Elymus glaucus* were to be studied on Nixon Ridge, a lightly grazed coastal prairie (Heady et al. 1988) in Humboldt County, California (40° 56' 14"N latitude, 123° 47'

36"W longitude, NAD83). *Elymus glaucus* is a native, perennial, cool-season grass distributed in patches at this location on varying slope positions and aspects. However, preliminary sampling of bulk density and soil strength on Nixon Ridge showed high variability in soil compaction over short distances, consistent with the experiences of Sojka et al. (2001). Bulk density was measured using a core sampler. Soil strength was measured in terms of penetration resistance using a Field Scout SC-900 Soil Compaction Meter, henceforth referred to as "penetrometer." Bulk densities ranged from less than 1.0 g cm^{-3} to 1.26 g cm^{-3} after being corrected for rock fragment content. Penetration resistances ranged from 0.03-3.9 MPa in the top 10 cm.

Low water content and high rock fragment content reduced the accuracy of measuring soil compaction with the core sampler and penetrometer methods. In addition, studying the effects of soil compaction on plants was difficult because these methods necessarily disturb the soil, making a site unsuitable for planting seeds. Because of this, a greenhouse experiment was necessary for isolating and understanding the effects of soil compaction on *E. glaucus* establishment and growth. The greenhouse experiment had a more controlled growing environment in which bulk densities and water contents were known and replicable.

The objectives of this study were to determine

(1) what are, if any, the root-limiting bulk densities and penetration resistances for first year *E.glaucus* plants.

(2) what is the difference in shoot and root production over a range of soil strength as a function of bulk density and water content.

Other factors important to *E. glaucus* seedling establishment and growth, while important in a natural field setting, were not addressed in this greenhouse study. These factors would likely include coarse fragment content, surface plant litter, seed predation and biomass consumption by rodents and insects, ectomycorrhizal infection, microbial pathogens, site modification by or resource competition from adjacent plants, and fluctuations in soil and air moisture and temperature.

MATERIALS AND METHODS

Soil for this experiment was collected from Nixon Ridge in Humboldt County, California. Soil was collected from a depth of 0-20 cm. Appendix A presents a more detailed description of the soil at this site. Soil was crushed and sieved through a 2 mm mesh. Only the fine earth fraction was used in this experiment. The soil was a loam with an organic matter content of approximately 11% (weight loss on ignition, 16 hours at 375° C). The soil was not sterilized.

Three compaction levels were studied. These were bulk densities of 1.00 g cm^{-3}, 1.25 g cm^{-3}, and 1.55 g cm^{-3}. Values of 1.00 g cm^{-3} and 1.25 g cm^{-3} were chosen based on observed field conditions on Nixon Ridge. The high density value was chosen based on published values for observed levels of compaction on other rangeland or pasture systems (e.g. Stephenson and Veigel 1987).

Because soil strength is a function of water content, three levels of water content were chosen to provide a range of soil strengths at each bulk density, creating nine bulk density-water content treatments. Water content was measured gravimetrically, but the three levels were chosen based on soil water potential. Water potential gauges the ease with which plants can access soil water, and is a more precise descriptor of water availability to plants than is gravimetric water content.

Soil water potential (Ψ) is defined as "the amount of work that must be done per unit of a specified quantity of pure water in order to transport reversibly and isothermally an infinitesimal quantity of water from a specified source to a specified destination" (Soil Science Society of America 2005). Matric potential, defined as "the portion of the total soil water potential due to the attractive forces between water and soil solids as represented through adsorption and capillarity" (Brady and Weil 2002), is generally the most important component of total soil water potential.

The water potentials chosen were -33 kPa, -500 kPa, and -1500 kPa. The high and low potentials were selected based on their use as standard values for field capacity (-33 kPa) and permanent wilting point (-1500 kPa), respectively. Field capacity describes the content of water, on a mass or volume basis, remaining in a soil two or three days after having been saturated with water and after free drainage is negligible (Soil Science Society of America 2005). Permanent wilting point is the largest water content of a soil at which indicator plants, growing in that soil, wilt and fail to recover when placed in a humid chamber (Soil Science Society of America 2005). Field capacity would occur during the wet season on Nixon Ridge, when water is abundant but has drained out of soil macropores, and permanent wilting point would occur in the summer dry season. The intermediate potential was chosen somewhat arbitrarily as a point between two extremes, but it is referenced in Fitter and Hay (2002) as being a moderate stress level for mesophytic plants. Treatments will be henceforth referred to by their bulk densities and water potentials. Table 1 summarizes treatments and descriptive terms.

Water potentials of -33 kPa, -500 kPa, and -1500 kPa correspond to gravimetric water contents of 30%, 20%, and 15%, respectively, for this soil. The gravimetric water content associated with each water potential was obtained from a water retention curve derived by the United States Department of Agriculture (USDA) Natural Resources

Table 1. Summary of nine treatments and descriptive terms.

Bulk density (Db)		Water potential (Ψ) Wet (high potential) Ψ = -33 kPa θ_g = 30%	Moist (moderate potential) Ψ = -500 kPa θ_g = 20%	Dry (low potential) Ψ = -1500 kPa θ_g = 15%
Loose (low)	1.00 g cm^{-3}	loose-wet	loose-moist	loose-dry
Medium	1.25 g cm^{-3}	medium-wet	medium-moist	medium-dry
Dense (high)	1.55 g cm^{-3}	dense-wet	dense-moist	dense-dry

Conservation Service (NRCS) National Soil Survey Center (Lincoln, Nebraska). The Relationship between soil water content and soil water potential is graphed in Figure 1.

Soil was compacted into pots made from 4-inch diameter ABS sewer pipe. Pots were closed at the bottom using ABS test caps with a ¼-inch hole drilled in the center to allow drainage. Based on a 10% sample of all pots and all lids, the inside dimensions of a pot with a lid averaged 10.1 cm in diameter, 10.2 cm in height, and 816 g cm^{-3} in volume. This volume was used in all bulk density calculations.

American Standard Testing Methods (ASTM) are protocols widely used in geotechnical and soil testing laboratories. American Standard Testing Method D698-00ae1 (ASTM 698) was used to prepare 1.25 g cm^{-3} treatments. American Standard Testing Method D1557-02e1 (ASTM 1557) was used to prepare 1.55 g cm^{-3} treatments (American Society for Testing and Materials International 2001).

In ASTM 1557, soil with a water content of 16% was compacted into each pot in 5 layers. A 10-pound compaction hammer was allowed to freefall from a height of 18 inches, and was repeated 25 times per layer. For this soil, a soil moisture density curve was derived. From this curve it was determined that soil with a water content of 16% would compact to a dry bulk density of approximately 1.55 g cm^{-3} using ASTM 1557 (Appendices B-C). Actual dry bulk densities ranged from 1.49 g cm^{-3} to 1.63 g cm^{-3}. acted into each pot in three layers. A 5.5-pound compaction hammer was allowed to freefall to the soil surface from a height of 12 inches, and was repeated 25 times per layer. The air-dry water content of the soil (5-8%) was appropriate for compacting soils to 1.25 g cm^{-3}. For this reason, a soil moisture density curve was not derived for this soil for

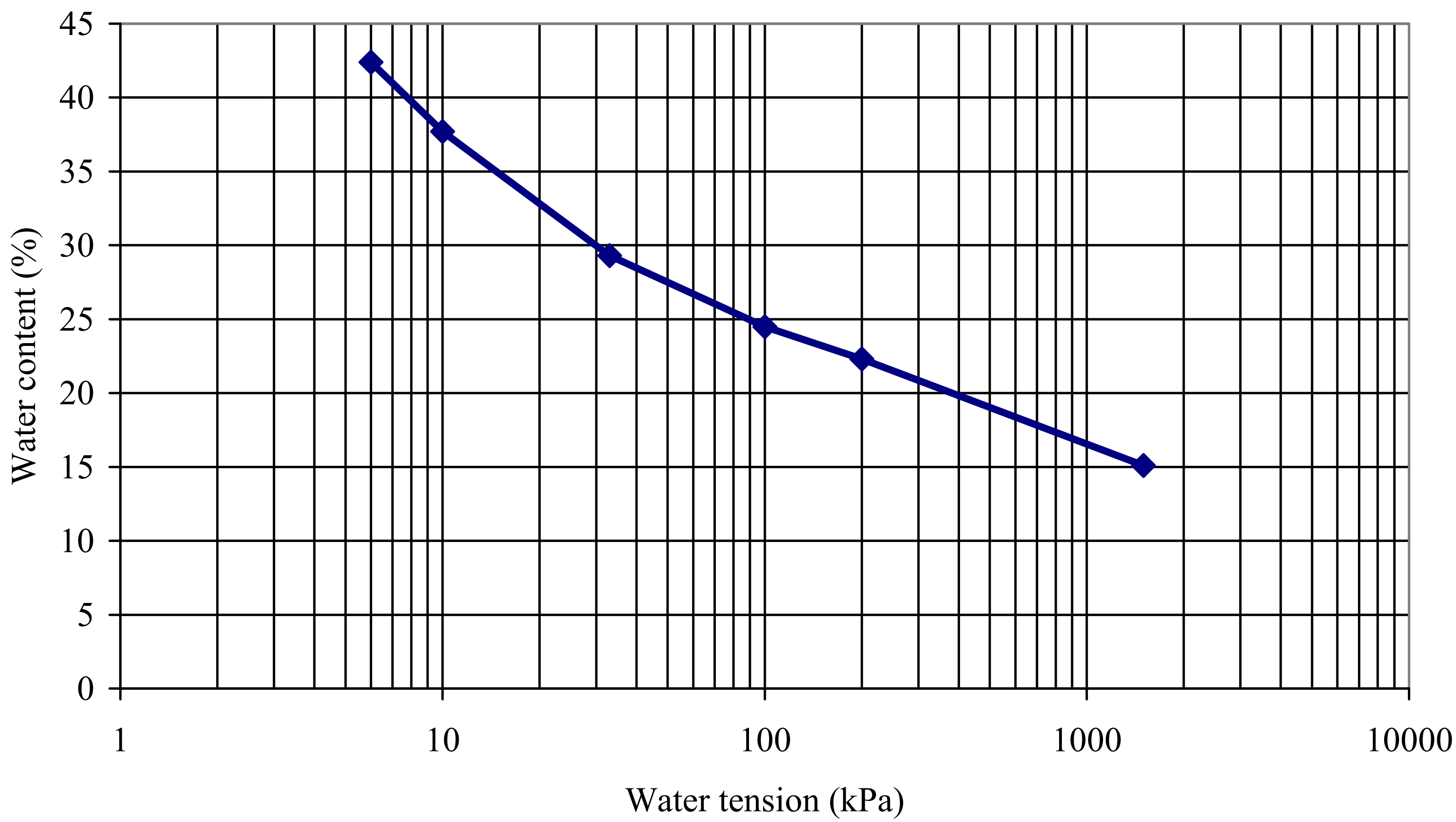

Figure 1. Water retention curve for the study soil collected from Nixon Ridge. Only the fraction of soil with particle diameters less than 2 mm was used to derive the curve. Water tension is the negative of water potential, and it describes how tightly water is held to soil rather than how easily it will move. This curve was derived by the USDA-NRCS National Soil Survey Center Soil Survey Laboratory in Lincoln, Nebraska (Project ID I2005USNL046).

ASTM 698. Air-dry water content was sampled after every fifth pot was compacted. The water content of this sample was assigned to the five pots compacted following that sample. Actual dry bulk densities of each pot ranged from 1.22 g cm^{-3} to 1.32 g cm^{-3}.

Low bulk density treatments were made with air-dry loose soil. Based on the range of water contents observed while preparing 1.25 g cm^{-3} treatments, an air-dry water content of 6% was assumed. Approximately 865 g of air-dried soil was added to each pot to get a dry bulk density of 1.00 g cm^{-3}. The pot was tapped to hasten settling of the soil so that the soil was flush with the pot rim. Actual dry bulk densities ranged from 0.99 g cm^{-3} to 1.02 g cm^{-3}.

Seventy-five pots of each bulk density were prepared, for a total of 225 pots. Within each bulk density, 25 pots were assigned to each of the three water potential treatments. Before planting, each pot was raised to -33 kPa (field capacity) by placing them in saucers filled with tap water.

Seeds were planted at field capacity during the third week of January 2005 with seed stock from Tehama County, California, purchased from Hedgerow Farms in Winters, California. Although seed collected from Nixon Ridge would have been the ideal stock, Hedgerow Farms provided a quantity and quality of seed that could not be obtained from the field at the time of the experiment setup. Each pot was sprinkled with 0.38-0.40 g of *E. glaucus* seed. The amount of seeds needed to be large enough to produce measurable biomass within the time span of the experiment, but small enough to allow good seed-soil contact. Ten grams of soil were sprinkled over the seeds in each pot to increase seed-soil contact and facilitate germination. A spray bottle was used to mist the seeds once a day during this time. Most seeds germinated within two weeks.

After germination, pots were randomized into 25 blocks containing one pot of each treatment. Each block was arranged in a 3 pot by 3 pot square, and blocks were arranged two deep on the greenhouse benches. Treatments were randomly assigned positions within each block.

Following randomization, each pot was allowed to dry down to a target total weight. The total target weight was the sum of the following weights, measured in grams:

- oven dry soil
- water needed to raise soil to 15%, 20%, or 30% water content
- pot
- test cap
- 0.38 g seeds
- 10 g cover soil

Maintenance of water potentials began when a pot reached its target water content, and therefore began at different times for each pot. All had reached target moisture within 3 weeks of randomization. Treatments were maintained at that target by watering on Monday, Wednesday, and Friday of each week. Each pot was weighed individually to the nearest gram. Tap water was added using a spray bottle and a pipette to raise the total weight to its target. Each pot was overwatered by 10-15 g in an attempt to keep the target weight bracketed by higher and lower values. Mass added by root and shoot growth was assumed to be negligible.

The entire watering process took approximately six to eight hours. Weight before ("initial") and after ("final") watering was recorded at every watering until harvest began 15 April 2005. High and medium density treatments had slow infiltration rates. These treatments were watered until water ponded at the surface. More water was added as the ponding diminished. Treatments with low water contents exhibited water movement at the soil-pot boundary. Drying of the soil from field capacity to the appropriate water content caused some shrinkage in the volume of the soils. This created a gap between the pot and soil core that allowed rapid movement of water toward the bottom of the pot. As no water drained out of the bottom, it was assumed that the water eventually equilibrated throughout the volume of soil.

Plants were grown in the Natural Resources greenhouse on the Humboldt State University campus until harvest. Greenhouse conditions offered no control over relative humidity, temperature, or the amount of light to which plants were exposed.

At every watering, blocks were rotated from west to east, and from the front of the bench to the back. Treatments were re-randomized within each block every week. Weeds were clipped at the soil surface. One block was chosen to observe differences between treatments using photography, and photographs were taken once a week.

Shoot biomass harvest

Shoot harvest occurred from 15 April to 20 May 2005. Harvest and soil strength measurements were done two to three blocks at a time. The night before harvest, each pot was raised to its target weight in the evening. This minimized water loss by evapotranspiration, and allowed a minimum of 8 hours for water to equilibrate throughout the pot. Biomass harvest and soil strength measurements were done at sunrise before evapotranspiration began to increase. Shoots were cut at the soil surface and dried for 24 hours at 65°C to obtain dry shoot biomass. Shoots were harvested from all treatments in all 25 blocks.

Soil strength

Penetration resistance measurements were taken in the center of each pot on 21 blocks using the Field Scout penetrometer. Penetration resistance was recorded at every 2.54 cm from 0-10.16 cm. The measurement at 10.16 cm was discarded because the test cap interfered with the penetrometer. The highest, the lowest, and the average of the remaining four values were used in multiple regression analysis.

Due to difficulties in obtaining measurements on high density treatments, four blocks were measured using a Tinius Olsen hydraulic press (“hydraulic press”) at SHN Consulting Engineers & Geologists, Inc., Eureka, California. A custom “penetrometer” for the press was fashioned using a replacement cone for the Field Scout penetrometer. A cylindrical metal plate approximately 5 cm in diameter was placed on the opposite end of the shaft to provide a larger, more stable surface onto which pressure was applied, and helped ensure that the penetrometer was being inserted vertically. Measurements were in pounds-force and were converted to psi by dividing by the basal area of the cone (0.2 in^2).

Root length examination

Soil cores were extracted from pots mechanically using a hydraulic press with a 4-inch diameter piston. This was done at SHN Consulting Engineers and Geologists, Inc., Eureka, California. Most cores stayed intact, but some crumbled on extraction or were broken in order to remove the custom penetrometer. Once extracted, cores were examined for maximum root depth and root biomass production. When cores were shattered, the maximum rooting depth was estimated if possible. Intact cores were split in half using a hammer and a 6-inch stainless steel broad knife. Maximum rooting depth was measured to the nearest centimeter. Root depth was determined by breaking a half-core vertically into two quarters by hand. One could then see the location at which roots broke apart or where they were still connecting the halves. Measurements were taken from the surface to the deepest root observed by this process.

Root biomass harvest

Roots were washed over sieves of mesh sizes 2.0, 0.42, and 0.25 mm (0.0787, 0.0165, and 0.0098 inches, respectively), according to Livesley et al. (1999) who found that 93-96% of *Zea mays* L. root biomass was collected on sieve sizes greater than 0.5 mm. For *E. glaucus* roots, a soil core was first soaked in water until the core was saturated. Loose soil was shaken out of the core, and the root mass was washed over the sieves using the shower spray setting on a garden hose nozzle. The main root mass was then placed in an empty 5-quart bucket and sprayed with a high-pressure stream of water to remove most remaining soil particles. Soil particles settled to the bottom of the bucket, and the floating root mass was collected. Water was then strained through the smallest mesh to collect any root pieces remaining in the water. This mass was stored separately from other soil organic material collected as described below.

The remaining soil went through a process of agitation and decanting to collect smaller pieces of organic matter. Water was added to the soil, and the soil was agitated. Larger mineral soil particles were allowed to settle briefly. The water was then strained through the three sieves to collect organic matter. This process was repeated until no appreciable amount of organic matter remained floating in the water. This process was repeated for materials on each sieve. This helped to ensure that organic matter of all sizes was separated from soil particles of similar size.

Eight blocks of nine pots each were harvested for analysis. One block took approximately seven to eight hours to wash, and roots were placed in a drying oven within three days of harvest. Because of the time involved in root washing and the lack of facilities to preserve roots without the shoots, blocks were harvested in groups of two or three over a three week period (26 April to 20 May). Roots were harvested for only eight blocks in order to harvest shoots as close together as possible.

Statistical analysis

Number Cruncher Statistical Systems (NCSS) (Hintze 2004) was used to screen data and to perform statistical analyses. Each treatment was defined by a level of bulk density and of water potential. For each combination, shoot biomass and root biomass were examined for outliers using the NCSS data screening tool. Penetration resistance measurements were examined for outliers per treatment at each depth at which a measurement was recorded. For each treatment, the data screening procedure was run once each for shoot biomass, root biomass, and penetration resistance. Values identified as outliers were compared for agreement with stem-leaf plots identifying extreme high and low values. All shoot data were used. For each treatment, there were 25 shoot biomass measurements. Nine root biomass values were missing due to loss of samples. Because of this, the number of root biomass measurements for each treatment ranged from five to eight. Twenty-one penetration resistance values identified as outliers were removed from the analysis.

ANOVA was used to analyze the effects of bulk density and water potential on shoot and root biomass. All shoot and all root biomass were analyzed together. Penetration resistance was also analyzed using ANOVA, using independent variables bulk density, water potential, and depth. Penetration resistance data was separated by the method of measurement before being analyzed. No statistical analysis was performed on root depth because the depth of root growth was limited to 10 cm.

Multiple regression analysis was used to understand factors affecting biomass production. To find the best relationship, three analyses were run for shoot biomass production and for root biomass production. Independent variables for each equation included bulk density, water potential, and one of the penetration resistance values defined as follows: Maximum penetration resistance is the largest penetration resistance value in a pot from 0-7.62 cm. Minimum penetration resistance is the lowest penetration resistance value in a pot from 0-7.62 cm. Average penetration resistance is the average of all penetration resistance values in a pot from 0-7.62 cm. Soil strength data collected by each method, with its associated biomass data, were analyzed separately.

RESULTS

An ANOVA on shoot biomass production showed that bulk density, water potential, and their interaction were significant terms in accounting for differences in biomass production between treatments ($p<0.01$ for all terms). The most biomass was produced in the medium-wet treatment. The lowest biomass was produced in the dense-dry treatment. For each bulk density, the most biomass was produced under the wettest condition (Figures 2-4). Biomass production response to bulk density differed between the dry condition and the two wetter conditions. Under wet and moist conditions, biomass production peaked at 1.25 g cm^{-3}. In dry conditions, biomass production peaked at 1.00 g cm^{-3}.

Analysis of the nine treatments using the Tukey-Kramer multiple comparison test showed that several treatments with highly contrasting growing conditions did not differ significantly in their production. Treatments with the lowest and highest production, dense-dry and medium-wet, respectively, were significantly different from all other groups. Figure 5 shows differences in production, grouped by bulk density.

An ANOVA on root biomass production showed that bulk density ($p<0.01$) and water potential ($p<0.01$) were significant terms in accounting for differences in root biomass production. However, there was no significant interaction between them ($p>0.05$). Root biomass production showed a similar trend to shoot production with respect to bulk density, but a different trend with respect to water potential. Unlike shoot biomass, root biomass at each bulk density peaked under moist conditions (Figure 6).

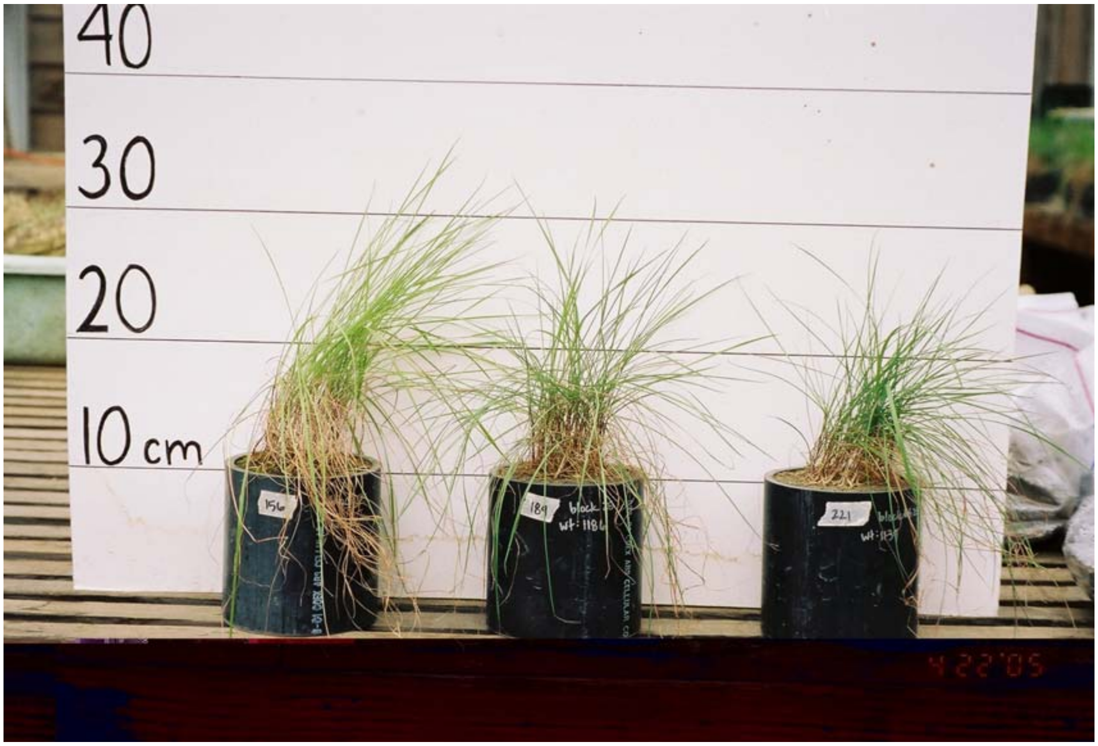

Figure 2. Plants before harvest. Plants are growing in low bulk density pots (1.00 g cm^{-3}). Wettest growing conditions are on the left, driest on the right.

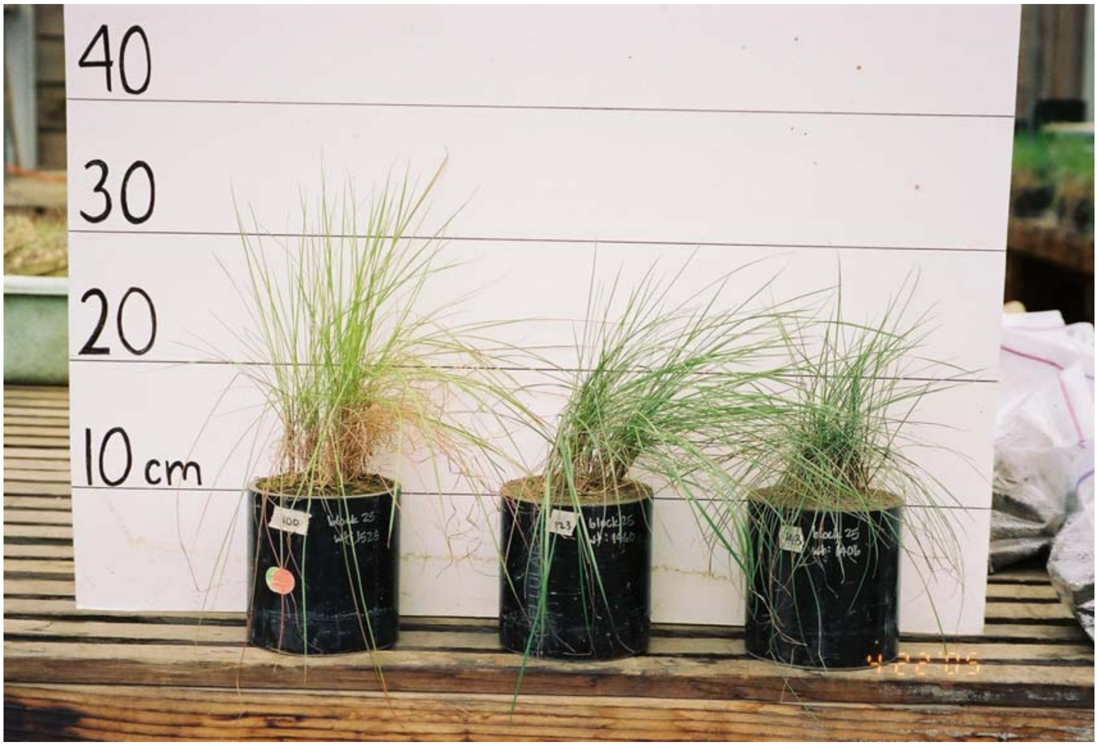

Figure 3. Plants before harvest. Plants are growing in medium bulk density ($1.25\ g\ cm^{-3}$) pots. The wettest growing conditions are on the left, driest on the right.

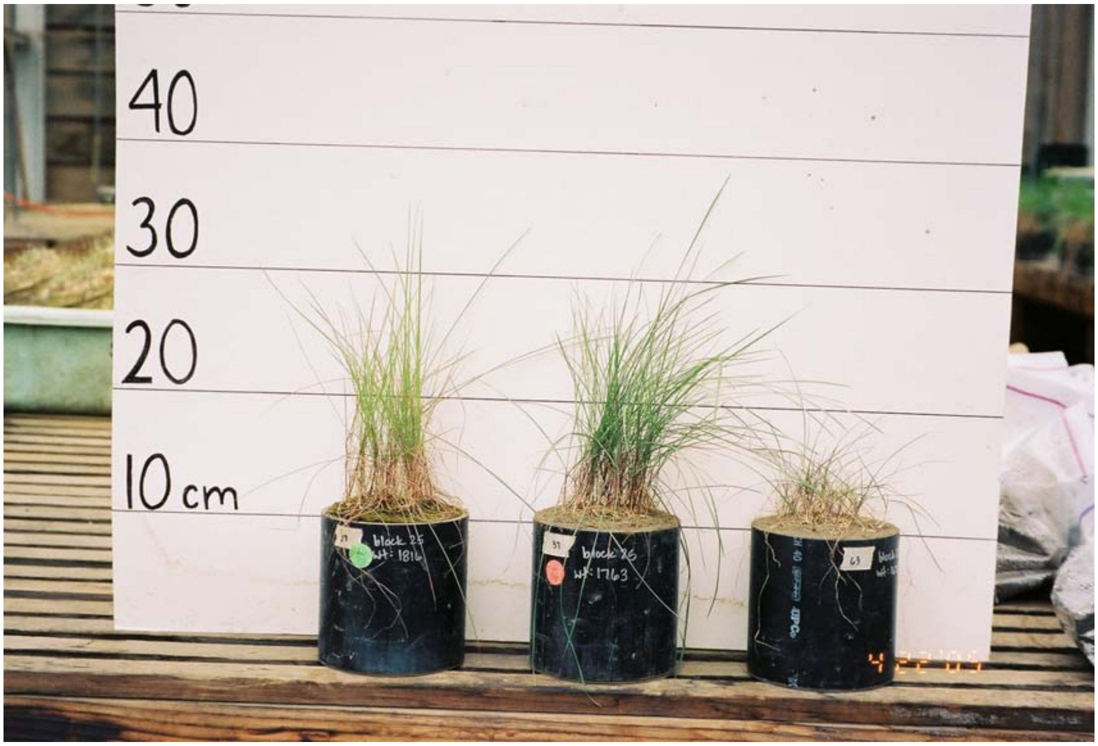

Figure 4. Plants before harvest. Plants are growing in high bulk density ($1.55\ g\ cm^{-3}$) pots. The wettest growing conditions are on the left, driest on the right.

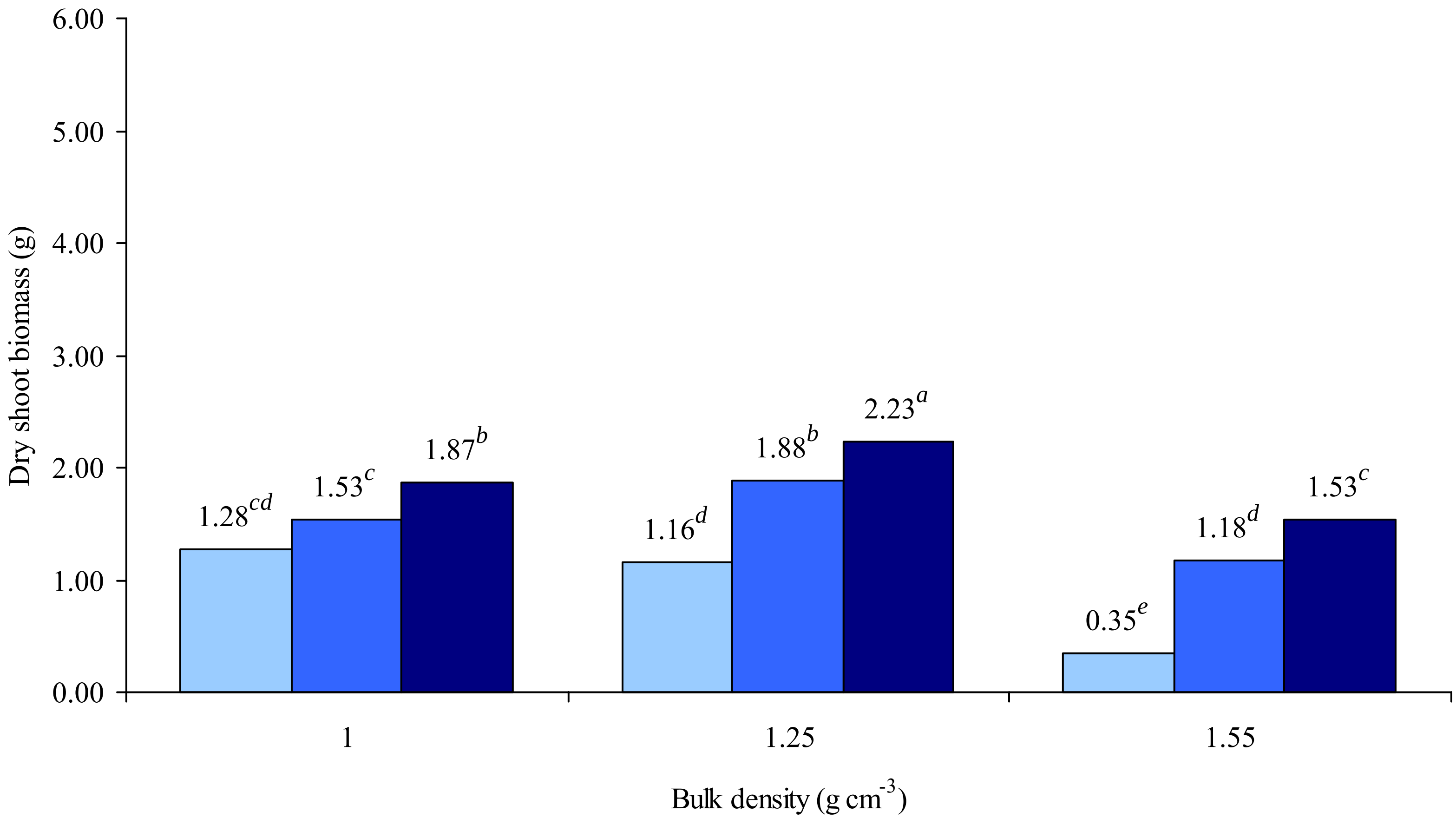

Figure 5. Average shoot biomass production by treatment. Letters indicate significant differences between treatments by the Tukey-Kramer multiple comparison test (α=0.05). n=25 for all treatments. ■-1500 kPa ■-500 kPa ■-33 kPa

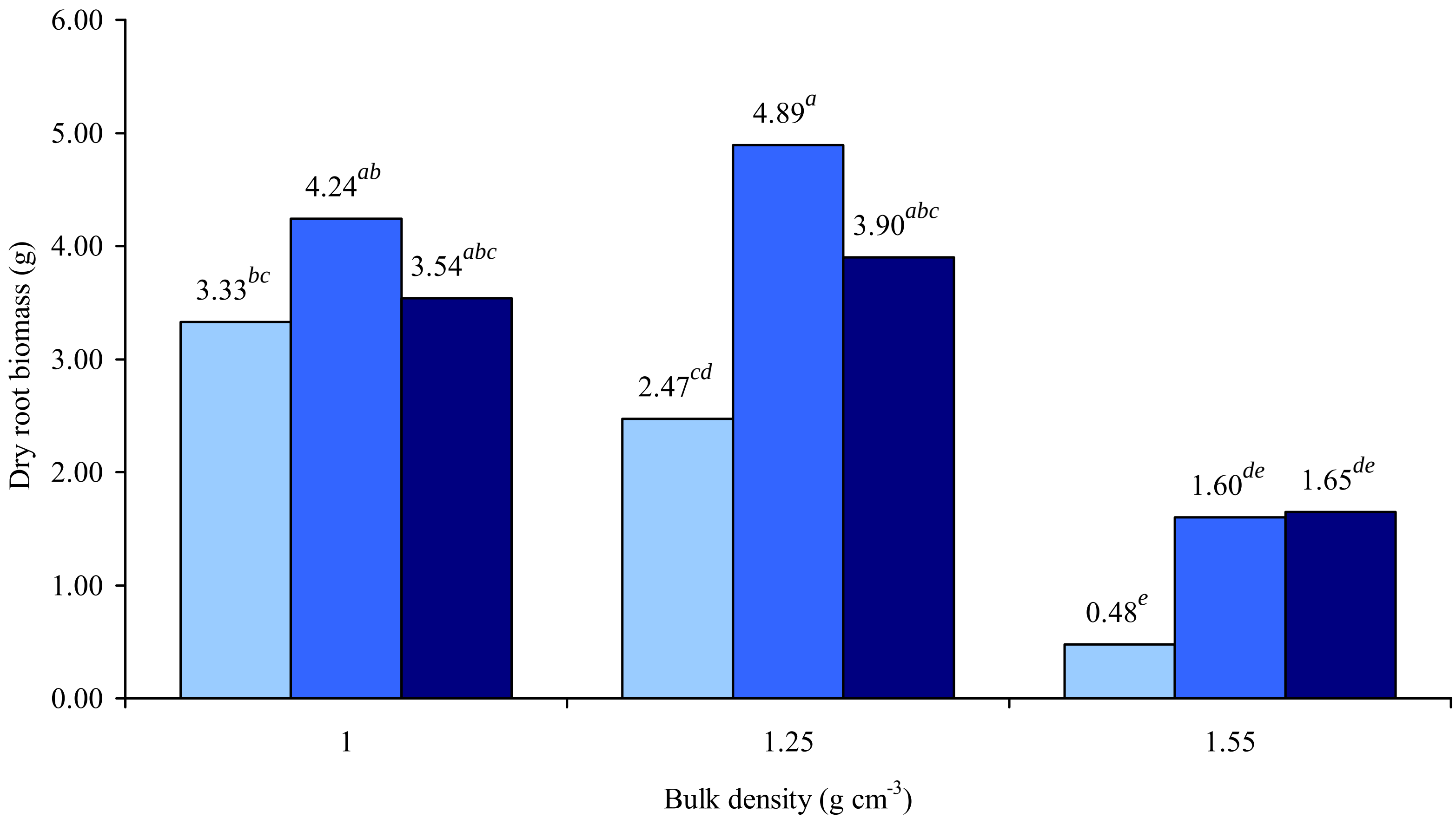

Figure 6. Average root biomass production by treatment. Letters indicate significant differences between treatments by the Tukey-Kramer multiple comparison test (α=0.05). n=5 to 8. ■-1500 kPa ■-500 kPa ■-33 kPa

Root biomass production was greatest in the medium-moist treatment. The dense-dry treatment produced the least overall. As with shoots, the Tukey-Kramer multiple comparison test showed several treatments produced similar levels of biomass production despite highly contrasting growing conditions. No treatment was significantly different from all others.

Root-shoot ratios were calculated for each treatment using data from the nine blocks from which roots were harvested. An ANOVA on the root-shoot ratios showed that bulk density and water potential were significant factors in accounting for differences between treatments ($p<0.01$ and $p<0.05$, respectively). There was no significant interaction between terms ($p>0.05$). Evaluating all nine treatments individually showed that root-shoot ratios for high bulk density treatments decreased with increasing water potential (Figure 7). For low and medium bulk density treatments, root-shoot ratios peaked at moderate water potential and were lowest under wet conditions.

Penetration resistances increased with increasing bulk density, decreasing water potential, and increasing depth (Figure 8). Each factor was found to be significant in accounting for differences in penetration resistance ($p<0.01$ for each factor). The only significant interaction term was that between bulk density and water potential ($p<0.01$). Averaged over all depths, the highest penetration resistance at low bulk density occurred at moderate potential. The highest penetration resistance at medium bulk density occurred at the lowest potential.

Increases in penetration resistance were gradual over all treatments and depths, and penetration resistances ranged from 0.63 to 3.14 MPa (Table 2). No penetration

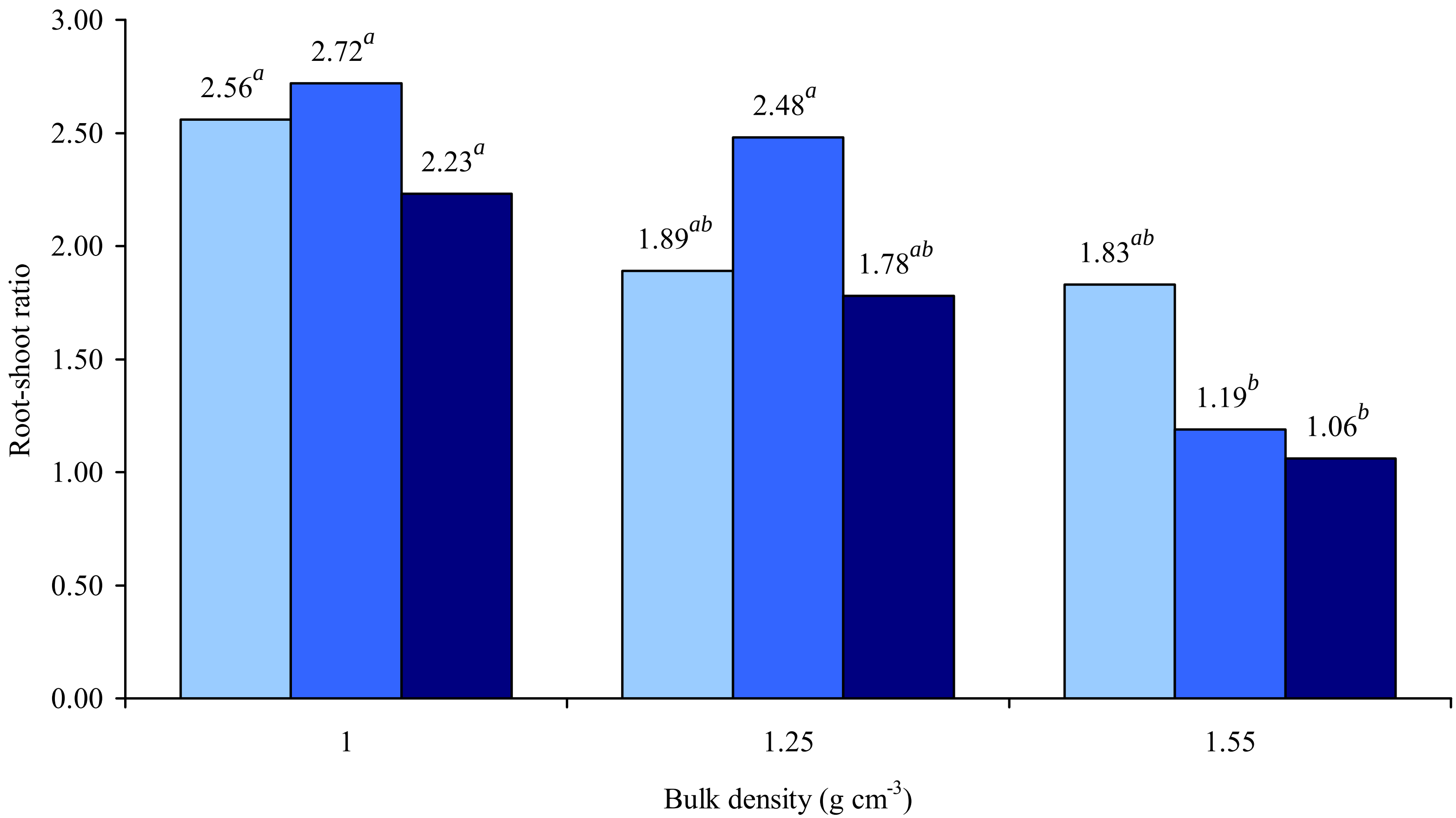

Figure 7. Root-shoot ratios by treatment. Letters indicate significant differences between treatments by the Tukey-Kramer multiple comparison test (α=0.05). n=5 to 8. ■-1500 kPa ■-500 kPa ■-33 kPa

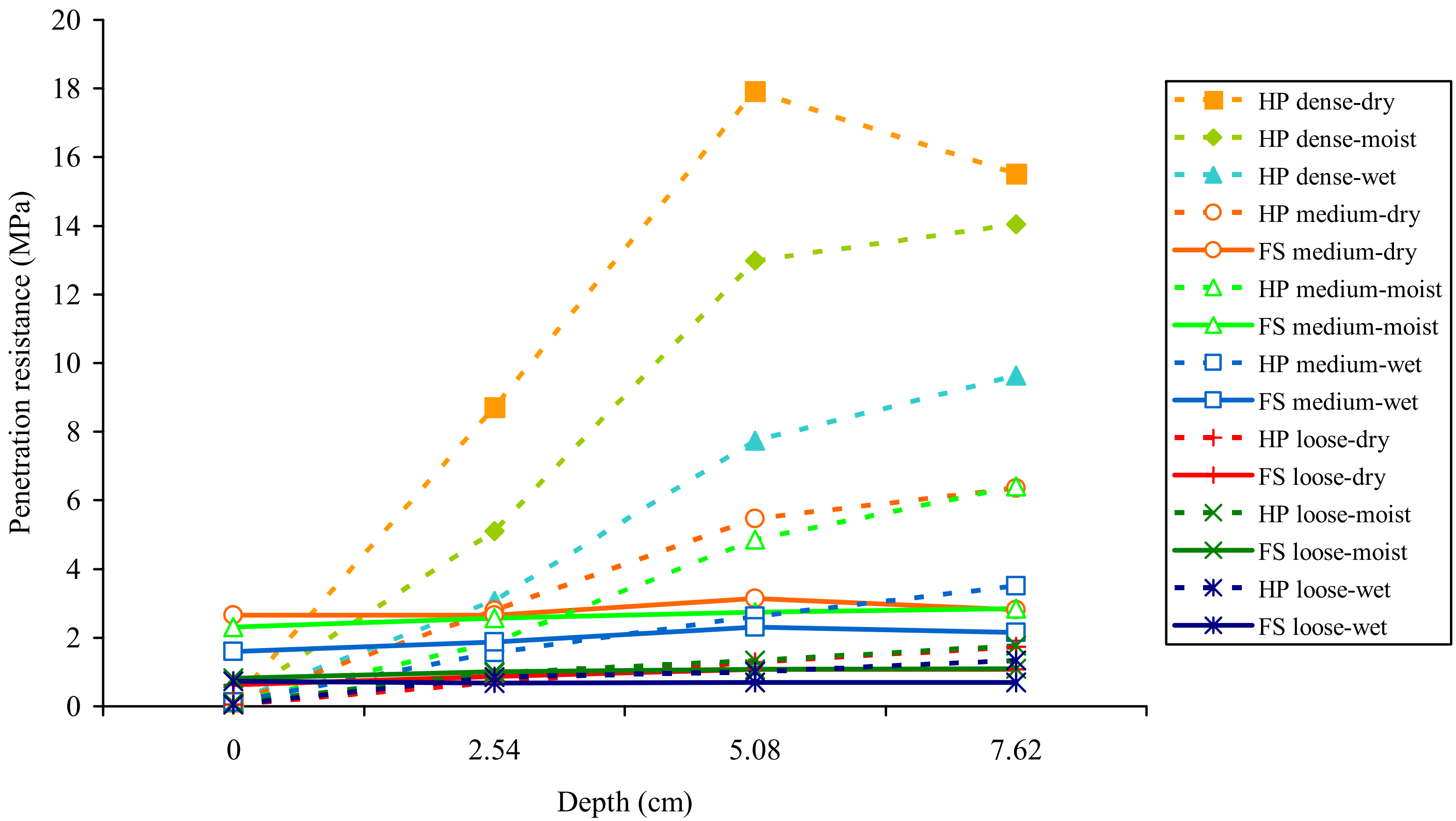

Figure 8. Trends in penetration resistance with depth as measured by the Tinius Olsen hydraulic press (HP) and the Field Scout penetrometer (FS).

resistance measurements for Db=1.55 g cm^{-3} were obtained using the Field Scout penetrometer due to physical limitations of the researcher and the apparatus. Because of this, supplemental data were collected using the Tinius Olsen hydraulic press so that penetration resistance measurements for high bulk density treatments could be obtained. The data were collected on four blocks, and showed that increases in penetration resistance followed the same trends as with the Field Scout penetrometer. All factors and all interactions were found to be significant through ANOVA ($p<0.01$ for all factors and interactions).

As measured by this method, penetration resistance for each treatment followed two general patterns. Penetration resistances of low density treatments increased gradually with depth. Penetration resistances of high density treatments increased rapidly with depth. Medium density treatments had patterns intermediate to these.

The range of penetration resistances collected by the Field Scout method was much smaller than those collected for corresponding treatments using the hydraulic press method. Over all treatments measured with the Field Scout penetrometer, the range was 0.63-3.14 MPa. Over all corresponding treatments measured with the hydraulic press, penetration resistances ranged from 0.06 to 6.40 MPa. Averaged over all depths, significant differences in penetration resistance between the methods occurred for medium-dry treatments ($p<0.01$) (Tables 2 and 3).

Before multiple regression analysis was performed, shoot biomass was separated by the method with which penetration resistance was measured. Multiple regression analysis was used to relate shoot biomass production in relation to water potential, bulk

Table 2. Summary of Field Scout penetration resistance measurements and maximum root depth. The last three lines of the table summarize the penetration resistance variables used in multiple regression analysis. Values are averages (standard error of the mean in parentheses). Units for penetration resistance are MPa. For penetration resistance, n=21 unless otherwise specified. Units for depth are cm. For depth, n=22 to 24. na=data not available.

Depth (cm)	Dense-wet	Dense-moist	Dense-dry	Medium-wet	Medium-moist	Medium-dry	Loose-wet	Loose-moist	Loose-dry
0	na	na	na	1.60 (0.14) n=20	2.31 (0.16) n=18	2.66 (0.18) n=19	0.73 (0.04) n=19	0.81 (0.09)	0.63 (0.07)
2.54	na	na	na	1.88 (0.12) n=19	2.57 (0.19) n=18	2.65 (0.22) n=20	0.68 (0.05) n=20	1.00 (0.05) n=20	0.86 (0.05) n=19
5.08	na	na	na	2.31 (0.06) n=19	2.75 (0.16) n=19	3.14 (0.25) n=20	0.69 (0.04) n=20	1.07 (0.05) n=20	1.07 (0.05) n=20
7.62	na	na	na	2.16 (0.09) n=20	2.84 (0.11) n=19	2.81 (0.15) n=20	0.69 (0.04) n=20	1.09 (0.07) n=20	1.07 (0.05) n=20
Maximum root depth	2 (0.2)	2 (0.2)	1 (0.1)	10 (0)	8 (0.4)	6 (0.3)	10 (0)	10 (0)	10 (0)
Average penetration resistance	na	na	na	1.94 (0.10)	2.58 (0.11) n=20	2.73 (0.14)	0.67 (0.04)	0.99 (0.05)	0.88 (0.05)
Minimum penetration resistance	na	na	na	1.60 (0.13)	2.00 (0.14) n=20	1.83 (0.15)	0.59 (0.05)	0.75 (0.08)	0.63 (0.07)
Maximum penetration resistance	na	na	na	2.31 (0.08)	3.11 (0.14) n=20	3.46 (0.21)	0.77 (0.04)	1.19 (0.06)	1.12 (0.05)

Table 3. Summary of Tinius Olsen hydraulic press penetration resistance measurements and maximum root depth. The last three lines of the table summarize the penetration resistance variables used in multiple regression analysis. Values are averages (standard error of the mean in parentheses). Units for penetration resistance are MPa. For penetration resistance, n=4 unless otherwise specified. Units for depth are cm. For depth, n=22 to 24.

Depth (cm)	Dense-wet	Dense-moist	Dense-dry	Medium-wet	Medium-moist	Medium-dry	Loose-wet	Loose-moist	Loose-dry
0	0.14 (0.01)	0.16 (0.02) n=5	0.12 (0.02) n=5	0.12 (0.02)	0.13 (0.04)	0.10 (0.03)	0.06 (0.01)	0.10 (0.03)	0.06 (0.02)
2.54	3.08 (0.33)	5.11 (0.36) n=5	8.72 (0.62) n=5	1.56 (0.10)	1.86 (0.45)	2.79 (0.25)	0.85 (0.08)	0.97 (0.09)	0.69 (0.09)
5.08	7.74 (0.63)	12.99 (0.68) n=5	17.91 (0.99) n=5	2.62 (0.13)	4.86 (0.17)	5.47 (0.14)	1.00 (0.10)	1.34 (0.09)	1.28 (0.13)
7.62	9.63 (0.52)	14.04 (1.15) n=5	15.52 (0.41) n=5	3.50 (0.21)	6.40 (0.31)	6.36 (0.32)	1.33 (0.13)	1.77 (0.17)	1.74 (0.11)
Maximum root depth	2 (0.2)	2 (0.2)	1 (0.1)	10 (0)	8 (0.4)	6 (0.3)	10 (0)	10 (0)	10 (0)
Average penetration resistance	5.15 (0.28)	8.07 (0.44) n=5	10.57 (0.32) n=5	1.95 (0.11)	3.31 (0.19)	3.68 (0.13)	0.81 (0.08)	1.05 (0.08)	0.94 (0.08)
Minimum penetration resistance	0.14 (0.01)	0.16 (0.02) n=5	0.12 (0.02) n=5	0.12 (0.02)	0.13 (0.04)	0.10 (0.03)	0.06 (0.01)	0.10 (0.03)	0.06 (0.02)
Maximum penetration resistance	9.63 (0.52)	14.24 (1.02) n=5	18.11 (0.85) n=5	3.50 (0.21)	6.40 (0.31)	6.36 (0.31)	1.33 (0.13)	1.77 (0.17)	1.74 (0.11)

Table 4. Best fit multiple regression models for predicting shoot biomass in grams. PR=penetration resistance. Units for penetration resistance are MPa.

	Method	
Water potential	Field Scout penetrometer	Tinius Olsen hydraulic press
-1500 kPa	1.05 + 0.12*(minimum PR)	1.43 – 0.084*(average PR)
-500 kPa	1.52 + 0.12*(minimum PR)	1.91 – 0.084*(average PR)
-33 kPa	1.90 + 0.12*(minimum PR)	2.25 – 0.084*(average PR)

density, and soil strength. Results of the analysis are summarized in Table 4. Using Field Scout penetrometer measurements, the best model describing biomass production included minimum penetration resistance and water potential as significant factors explaining variation in biomass production. Water potential accounted for most of the variation. Adding minimum penetration resistance to the model increased the adjusted R^2 only slightly from 0.51 to 0.55. The multiple regression analysis of hydraulic press data shows that water potential and average penetration resistance contribute significantly to the model. The model has an adjusted R^2 value of 0.63.

A multiple regression analysis of roots was run using seven blocks measured with the Field Scout penetrometer; no analysis was done using hydraulic press data (one block). The multiple regression showed that the variables measured in this experiment are not good predictors of root growth, with only water potential contributing significantly. The adjusted R^2 for this model was 0.20.

Observations of root depths showed that the roots of several treatments reached the bottom of the pot. Because of the truncated depth values, statistical analysis was not performed. The roots of all low density treatments grew to the full depth of the pot. High and medium density treatments decreased in rooting depth with more negative water potentials. High density rooting depths ranged from 1 to 3 cm, and medium density rooting depths ranged from 6 to 10 cm (Table 2 and Table3).

DISCUSSION

Highest shoot and root production occurred in the medium bulk density when water was not scarce. As a main requirement of photosynthesis, abundant water would be important for the establishment and growth of *E. glaucus* seedlings. Although shoot production was greatest under wet conditions, higher root production under the moist condition may have been facilitated by better aeration. Based on approximate calculations of porosity, near ideal conditions of air- and water-filled porosity for root growth existed for the medium-moist treatment. Ideal conditions for root growth with respect to soil porosity are 50% soil, 25% air-filled pores, and 25% water-filled pores (Brady and Weil 2002).

Additional characteristics of medium bulk density soils may have facilitated high biomass production. Compared to low and high bulk densities, the medium bulk density may provide longer retention of water in the soil and increase plant available water due to the higher proportion of mesopores. Uptake of water and nutrients may also be improved by better root-soil contact (Bengough 2003).

Although the medium-wet treatment produced the highest shoot biomass, the later stages of the experiment did not suggest that this treatment provided any advantage over the loose-wet and dense-wet treatments with respect to water availability (Appendix D-E). Between watering days, the average water content of the medium-wet treatment dropped below the average water contents of the loose-wet and dense-wet treatments. However, different conditions may have existed at earlier stages of the experiment. Access to water may have been better when seedlings were first germinating. In combination with improved water uptake, this may have allowed for good seedling establishment. As plants grew and evapotranspiration increased, more water-limiting conditions began to develop.

The possible relationships between changing resource availability over time, plant resource needs at different life stages, and factors affecting a plant's ability to meet those needs were not studied in this experiment. Further study of these subjects may identify the most important factors affecting survival and establishment of seedlings. Such information may be useful in developing management options for improving the native perennial grass component of a rangeland.

Relating maximum biomass production to soil strength was complicated by having two soil strength data sets. According to penetrometer data, maximum shoot production occurred when penetration resistances in the soil environment were less than 3.0 MPa. According to the hydraulic press data, penetration resistances approached 3.5 MPa. The discrepancy between methods was even more pronounced for the medium-moist treatment, which produced the most root biomass. Penetrometer data showed that penetration resistances were less than 3.0 MPa, but the hydraulic press data showed that penetration resistances greater than 6.0 MPa existed in the medium-moist treatment. Despite these differences, data from both methods suggest that *E. glaucus* can produce high biomass and penetrate soils at levels of compaction and soil strength previously reported as limiting or reducing biomass production and root elongation (e.g. 2.5 MPa in Taylor et al. 1966, 1.5-3.0 MPa in Vepraskas 1988). Because these limiting bulk density and soil strength values were typically studied on taprooted species, a similar side by side experiment with several taprooted and fibrous rooted species may offer insight into whether one type of plant is more affected than the other.

Despite having the highest root production, observations of the medium-moist treatment implied that root-limiting conditions existed. Roots in the medium-moist treatment did not penetrate the entire depth of the pot, even though roots overcame penetration resistances greater than 6.0 MPa. Other treatments of similar production showed no limitations to root penetration. The observed rooting depth of the medium-moist treatment may not have resulted from root-limiting soil strengths, but rather that the soil strength reduced the growth rate (e.g. Taylor et al. 1966, Gerard et al. 1982) such that roots did not reach the bottom of the pot during the time span of the experiment. A deeper growing environment, a longer growing period, and periodic destructive sampling to analyze root growth rate may have helped better understand this issue. The root depth may also have resulted from the experimental method. Pots were watered from the top, and water was assumed to have equilibrated throughout the core. Although no gradients in soil moisture were visible within pots, data were not collected to confirm this. Drier or wetter conditions near the bottom may have slowed root growth into that area.

Intermediate root and shoot production levels not significantly different from each other occurred in treatments with highly contrasting levels of bulk density, water potential, and soil strength. This suggests that effects of increasing bulk density and soil strength on root and shoot production can be compensated for provided that access to other resources, such as water and nutrients, are available. Clarke et al. (2003) found that breaking up a subsoil pan increased shoot yields of wheat by 20% from a compacted condition when water was limiting. When water was not limiting, breaking up the pan increased shoot yields by only 1%. However, this study on *E. glaucus* was not conducted on closely spaced intervals of water potential or bulk density, and the levels at which these combined factors may become limiting could not be determined.

Compensating for different stresses may have played a role in different responses of dry treatments compared with moist and wet treatments. Dry treatment biomass peaked at low bulk density rather than medium bulk density as in moist and wet treatments. With the highest root and second highest shoot production, the medium-moist treatment indicates little restriction to production as a result of higher penetration resistances. In each soil strength data set, a similar range of soil strengths was recorded for the medium-dry treatment as occurred in the medium-moist. In addition to restrictions placed on photosynthetic and other metabolic processes, water stress restricts roots from elongating throughout the soil matrix due to low cell turgor pressure (Gregory 1987). One effect of this may be to limit a plant's ability to find water. Although more water in absolute terms may be present in the medium-dry treatment compared with the loose-dry treatment, the ability of the plants to access that water may be limited by the inability of roots to expand throughout the matrix. Under extreme water stress, the roots more easily penetrated the loose-dry treatment, as supported by the observed root depth. More macropores allowed root penetration, and soil particles were more easily pushed aside in the loose treatment due to higher porosity, possibly providing greater access to the little water available and promoting production as a result.

Although *E. glaucus* appeared to compensate for compaction stresses in terms of its root and shoot production, production may not have been the most appropriate variable to study. Atwell (1993) reported that total root mass of lupine is not necessarily reduced by mechanical impedance. Murphy et al. (2000) noted that root length is more consistently affected by compaction than is root biomass, with extension throughout the soil profile decreasing with increasing compaction.

Both root quantity and distribution allow a plant to find and utilize heterogeneously distributed resources in the soil. The root biomass per unit of soil volume has been noted to increase in nutrient-rich areas (Aanderud et al. 2003). Deep roots allow access to water unavailable to plants with shorter root systems. Accessing water is particularly important for herbaceous perennial species in a Mediterranean climate in which there is an extended dry season. Holmes and Rice (1996) studied changes in water availability as related to invasion of exotic annual grasses. Annual grasses, due to their short life cycle, have a relatively small root system, and utilize water in surface horizons. The ability of perennial seedlings to grow roots into deeper horizons may become vital for surviving the dry season. Belowground competition with shallow-rooted annuals for resources other than water may also be reduced. Thus, despite similar root biomass production levels, growing conditions that permit deep root movement may be more important to *E. glaucus* survival, particularly in the presence of annual competitors.

The importance of water was seen in the multiple regression models relating biomass production to bulk density and soil strength. The most important variable in the penetrometer model for shoot production was water potential. Minimum penetration resistance is also included but contributes little to the model. This indicates soil strength has a small effect on *E. glaucus* shoot production at low to medium bulk densities and at penetration resistances of approximately 3 MPa and lower.

For hydraulic press data, water potential and average penetration resistance was important to the model explaining variation in biomass production. Average penetration resistance takes into account the higher soil strength values collected by this method. The wider range of data likely accounted for differences observed in the contribution of variables to their respective models. Water potential alone accounted for more variation than average penetration resistance alone. However, water potential alone accounted for less variation (adjusted R^2=0.44) in the hydraulic press model than in the penetrometer model (adjusted R^2=0.51). This suggests that although water remains important, soil strength plays a greater role at higher soil strengths.

The multiple regression model for root biomass contains only water potential as a significant variable, suggesting that soil strength is not significant in root biomass production at low to medium bulk densities. For plants of this age, water potential appears to be more important in its effects on plant physiological processes than on its effects on soil strength. However, the model in general is a poor predictor of root biomass production.

The importance of water potential, bulk density, and soil strength over all treatment groups could not be examined for root biomass. As seen in the root biomass data, high bulk densities significantly reduced production. A data set including penetration resistance data for all treatments may have shown stronger relationships between variables.

To summarize, water content is independent of soil strength and bulk density under normal environmental conditions, but soil strength is dependent on water potential and bulk density. Limiting factors to plant production vary among these parameters as conditions change. Soil water fulfills a physiological need, but also reduces friction between the soil and penetrometer. Friction between roots and soil are also reduced by water content, as well as by root exudates.

How do the results of this greenhouse experiment relate to the field? The importance of water for biomass production was evident, but water in this experiment was maintained at specific levels. In the field, compaction may be less important in terms of physical impedance itself, but more important in terms of how that impedance and reduced porosity affects water relations. Compaction may physically reduce root penetration, thereby limiting a plant's ability to exploit water resources in a larger volume of soil. In addition, compaction may also lower infiltration and slow percolation, reducing available water in the soil and decreasing rooting depths depending on a site's soil water budget. This effect may be more acute in semi-arid rangelands where water that does not penetrate as deeply in the profile is more susceptible to evaporative loss.

Under such conditions where water may become limiting, a plant's ability to reallocate resources is an important adaptation enabling its survival (Simanton and Jordan 1986). The ratio of root biomass to shoot biomass varies by species, age, and environmental conditions. Various authors have reported a wide range of root-shoot ratios for grasses approximately 15 weeks old. In pot experiments in which no environmental stresses were imposed, ratios have ranged from 0.33-0.46 for annual and cultivated species (El-Shatnawi and Makhadmeh 2002) to 2.0-4.9 for perennial, warm season grasses (Dalrymple and Dwyer 1967). The root-shoot ratios of several treatments in this experiment are closest to those of Dalrymple and Dwyer (1967), although no environmental stresses were imposed in their study.

Published studies that measured root-shoot ratios have generally occurred in a timber harvest or agricultural context, and they have not produced a general trend in response to compaction or water stress. In pot experiments, the root-shoot ratios of grasses were shown to both increase (Donkor et al. 2002a) and decrease (Gales 1979) in response to increased moisture stress. In a field experiment, the ratio did not change with increased moisture stress (Greco and Cavagnaro 2002). In a pot experiment, Houlbrooke et al. (1997) found no trend in root-shoot ratios for *Lolium perenne* L. as bulk density increased.

Root and shoot production in this experiment did not vary in a similar way between treatments, causing variation in the root-shoot ratio. The trends observed in this experiment were not similar to those of previous research involving grasses, possibly because these studies did not consider both factors studied in the *E. glaucus* experiment. The highest ratios occurred under moderate water stress. High bulk density appeared to have a strong effect on root-shoot ratios, with these treatments having the three lowest ratios. The restrictions to root penetration throughout a larger volume of soil and resulting space competition likely contributed to low root production at higher bulk densities.

As previously stated, root length may be more important in the establishment and survival of *E. glaucus*. As such, root-shoot mass ratios may not have been as useful a measurement as one that incorporated both root length and root mass. Root length as observed in this experiment was often truncated due to the limited depth of the pots. The effects of soil compaction on *E. glaucus* can be further understood by examining how changes in bulk density and soil strength affect rooting behavior and distribution as well as how that growth pattern affects the plant's ability to access resources in quantity and over time.

CONCLUSION

The first objective of this study was to determine root-limiting bulk densities and penetration resistances for *E. glaucus*. Overall, given a growing environment in which soil properties that are important contributors to soil strength were relatively well-controlled, a comparison between ANOVA and soil strength observations suggests that the relationship between bulk density and soil strength and biomass production was not as strong as suggested by some studies (e.g. Vepraskas 1988). The results suggest that there is no specific threshold bulk density or soil strength that limits biomass production of *E. glaucus*. Results of this study are more consistent with studies suggesting that the relationship of plant responses to compaction covary with other factors (e.g. Gerard et al. 1982).

Bulk density is a convenient measurement of soil compaction. However, it is commonly reported on a dry soil basis, and does not reflect the natural variation in soil moisture. As observed in this study, soil moisture reduced soil strength through its lubricating effect, or moderated effects of compaction on biomass production. While penetration resistance accounts for some effects of soil moisture and tries to mimic root growth, this experiment also showed limitations to measuring it, particularly at high levels. Portable instruments such as the Field Scout penetrometer were of minimal value at high bulk densities and soil strengths. Although the Tinius Olsen hydraulic press was able to penetrate strong soils, such an instrument would likely not be readily available to land managers nor would it have much practical field use. In addition, penetration resistance measurements may not accurately reflect what a grass root must overcome in order to grow and supply resources to shoots. The resistance actually encountered by roots may be greatly reduced due to the small diameter of roots, tortuous growth patterns, and production of exudates that reduce friction with the soil.

The interpretation of penetration resistance was complicated by having collected data using two methods. Both data sets suggested that *E. glaucus* produced high root and shoot biomass under conditions previously reported as reducing production. However, the range of strengths under which high biomass production occurred was twice as large based on hydraulic press data compared to penetrometer data. Reduced production became more pronounced at higher soil strengths. Because of this, it would seem more important to be able to characterize soil compaction at these higher levels than at lower levels where biomass production is little affected. However, the divergence in penetration resistance measurements between the penetrometer and hydraulic press at these higher strengths suggests that penetration resistance, above a certain level, may not be a useful measurement in understanding what compaction levels are present.

The second objective of this study was to determine the differences in biomass production as a function of bulk density and soil strength. The results summarized in Figure 5 and Figure 6 show that high bulk density and soil strength generally reduced production of shoots and more noticeably of roots, but these production levels were not unique to these conditions. Negative effects appeared to be moderated by an abundant water supply, while benefits of lower bulk densities and strengths were reduced by water stress. Additional research is needed to understand the extent to which production can be reduced while still allowing for seedling survival and growth.

This experiment offered a glimpse into how *E. glaucus* seedlings respond to compacted soil under relatively constant environmental conditions. This experiment also exposed potential shortcomings of using bulk density and soil strength in managing soil quality on rangelands. To better understand the relative importance of compaction in a coastal prairie, several variables need to be incorporated into future research. These variables include changing water availability, wider temperature fluctuations, the presence of plant competitors, biomass consumption by herbivores, and bioturbation of soils. Understanding how these variables interact and under what circumstances each variable exerts the greatest influence on biomass production may provide insight into how bulk density and soil strength can be best used as an indicator of rangeland health.

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APPENDIX A

Pedon description for the soil pit dug on Nixon Ridge on May 26, 2005. The pit was dug on a west-facing slope of 12% slope. The slope shape is slightly concave perpendicular to the contour and linear with the contour. Weather conditions on the observation date were sunny and clear. All data was collected in the field. pH was tested using a LaMotte pH test kit.

A1 – 0 to 16 cm; very dark grayish brown (10 YR 3/2) gravelly loam, grayish brown (10 YR 5/2), dry; 25 percent gravels by volume; moderate medium granular structure and moderate medium subangular blocky structure; slightly sticky, moderately plastic, very friable; common very fine roots throughout and few medium roots throughout and between peds; few medium tubular pores; pH 6.2; clear smooth boundary.

A2 – 16 to 35 cm; very dark grayish brown (10 YR 3/2) gravelly loam, grayish brown (10 YR 5/2), dry; 15 percent gravels by volume; weak medium granular structure and weak medium subangular blocky structure; slightly sticky, moderately plastic, very friable; common very fine roots throughout; few medium tubular pores; pH 5.6; gradual smooth boundary.

AB – 35 to 65 cm; very dark grayish brown (10 YR 3/2) gravelly loam, brown (10 YR 5/3), dry; 14 percent gravels by volume; weak fine and weak medium subangular blocky structure and weak medium granular structure; slightly sticky, moderately plastic, very friable; common very fine roots throughout; few medium tubular pores; pH 5.4; gradual smooth boundary.

ABt – 65 to 84 cm; dark brown (10 YR 3/3) gravelly loam, light brownish gray (10 YR 6/2), dry; 18 percent gravels by volume; weak medium subangular blocky structure; slightly sticky, moderately plastic, very friable; few very fine roots throughout; few medium tubular and irregular pores; few dark prominent organoargillans on pore surfaces; pH 5.4; gradual smooth boundary.

B1 – 84 to 109 cm; brown (10 YR 4/3) gravelly loam, light yellowish brown (2.5 Y 6/3), dry; 25 percent gravels by volume; weak medium subangular blocky structure; slightly sticky, moderately plastic, very friable; few very fine roots throughout; few medium tubular and irregular pores; earthworm channels filled with darker A horizon material; pH 5.4; gradual smooth boundary.

B2 – 109 to 126 cm; yellowish brown (10 YR 5/4) gravelly loam, light brownish gray (2.5 Y 6/2), dry; 30 percent gravels by volume; weak medium subangular blocky structure; slightly sticky, moderately plastic, very friable; few very fine roots throughout; few earthworm channels filled with darker A horizon material; pH 5.2

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APPENDIX B

Derivation of a soil moisture density curve.

The degree of soil compaction will vary depending on the water content of the soil. In order to identify the water content at which a dry bulk density of 1.55 g cm^{-3} would be produced by ASTM 1557, a soil moisture density curve was derived with assistance from the SHN Consulting Engineers and Geologists, Inc., Materials Testing Lab (Eureka, California). The gravimetric water content (θ_g), expressed as a percentage, for a soil sample is described by the following equation:

$$\theta_g = [(\text{grams of soil } H_2O)/(\text{grams of oven-dried soil})]*100 \qquad (1)$$

Soil samples with gravimetric water contents ranging from 12-21% were mixed and allowed to equilibrate for a minimum of eight hours. Samples were compacted using ASTM 1557 protocol. Oven-dried soil masses were calculated using the following formula:

$$\text{Oven-dried soil mass} = \text{moist soil mass}/(1 + \theta_g) \qquad (2)$$

with θ_g expressed as a decimal fraction.

Dry bulk densities were plotted versus water content (Appendix C). A θ_g value of 0.16 or 16% was inferred from the graph as the water content at which 1.55 g cm^{-3} would be produced by ASTM 1557.

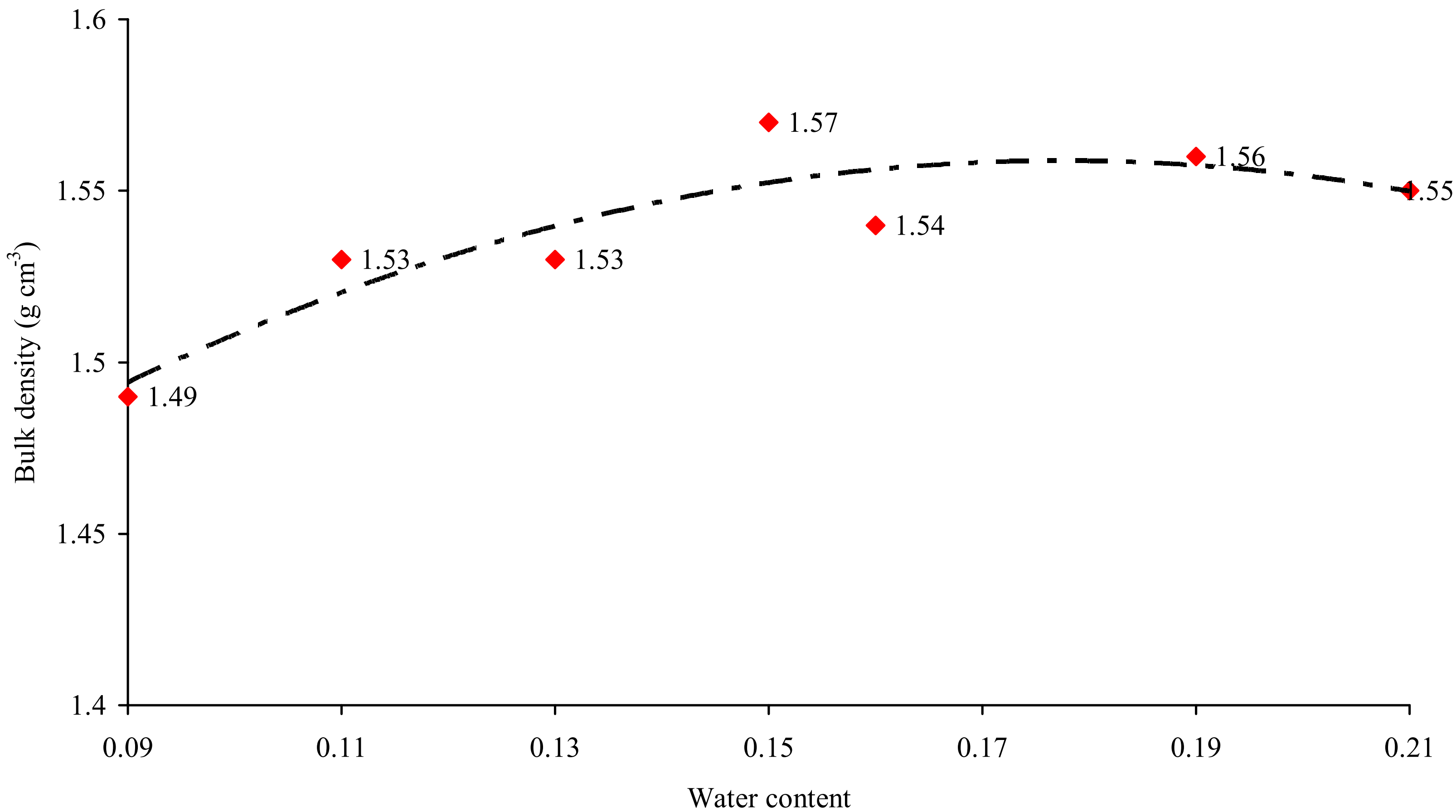
To prepare soil with 16% water content, an air-dried soil moisture sample was dried for 48 hours at 105° C to determine its water content. Approximately 2000 g of air-dried soil was placed in 1-gallon plastic sealable bags. The oven-dried soil weights were calculated by equation (2) based on the results of the soil moisture sample. Based on the

APPENDIX B. Derivation of a soil moisture density curve (continued)

amount of oven-dried soil in the bag, the weight of moist soil with 16% water content was calculated. Water was added to the air-dried soil until this weight was reached. The soil and water were mixed and allowed to equilibrate for at least eight hours before compacting.

Following compaction using ASTM 1557, the weight of the wet soil in each pot was calculated. Dry soil weight was calculated using equation (2). The acutal dry bulk density was calculated by dividing the dry soil weight by 816 g cm^{-3}.

Because the water content of air-dried soil (5-8%) was appropriate for compacting soils to 1.25 g cm^{-3} using ASTM 698, a soil moisture density curve was not derived for this method. Dry bulk densities for 1.25 g cm^{-3} and 1.00 g cm^{-3} were calculated as described for 1.55 g cm^{-3}.



APPENDIX C. Soil compaction moisture density curve for the study soil. Water content is expressed as a decimal fraction. The trendline shows peak bulk density occurring at a water content of approximately 0.16, or 16%. This curve was derived with assistance from SHN Consulting Engineers & Geologists, Inc., Eureka, California.

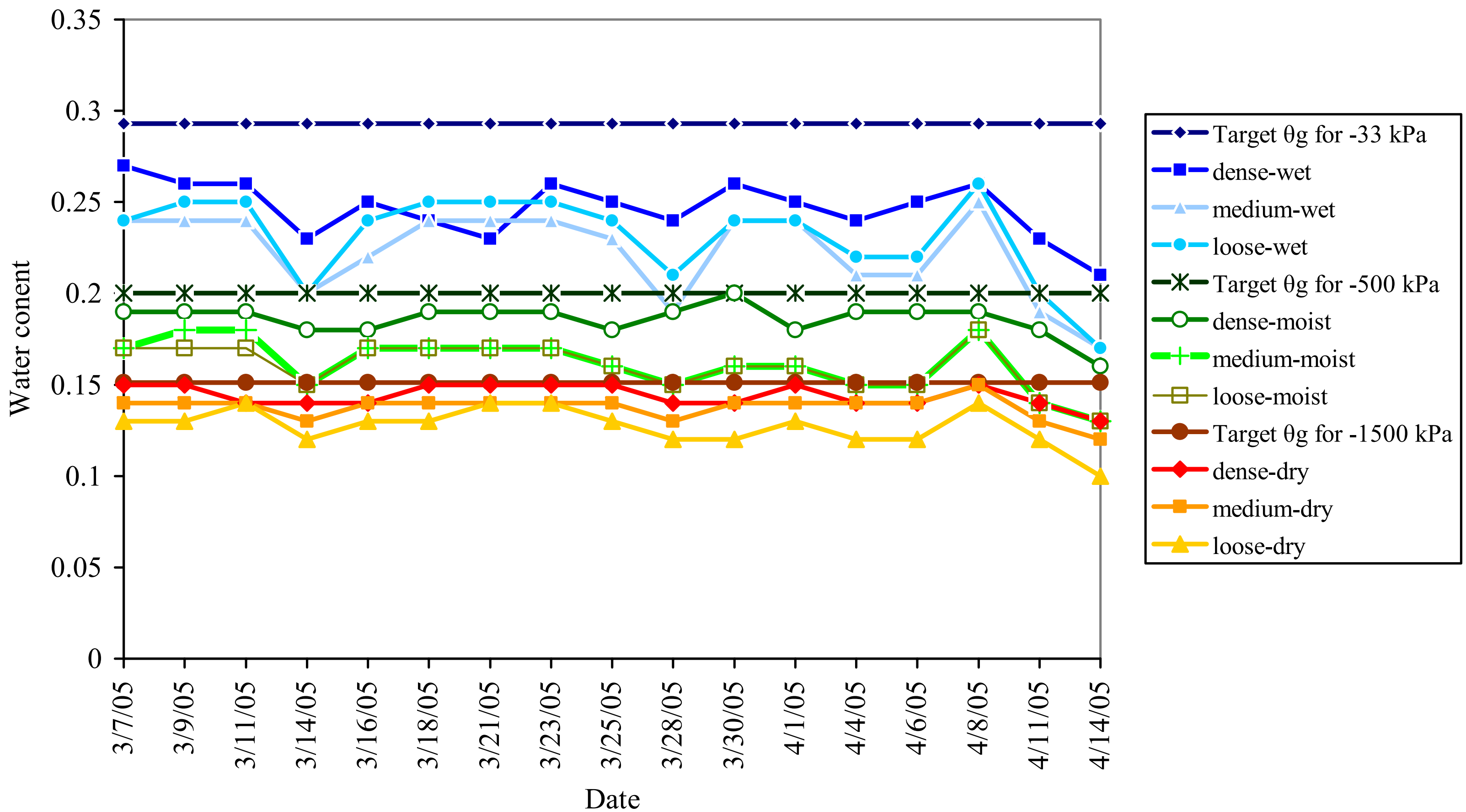
APPENDIX D

Discussion of watering methodology

Observations of the watering schedule and the success with which target water potentials were maintained were made based on the six week period prior to the beginning of harvest (7 March to 14 April 2005). The different rates at which plants reached their target weights, and adjustments to methodology made due to slow infiltration rates prevented collection of complete data before this time period.

The watering scheme generally kept all treatments from overlapping. On only a few days did a treatment dry to the level of the next drier potential. The weather on any given day was important to how much evapotranspiration occurred, with less occurring on foggy or rainy days than on sunny ones. However, because weather varied by day and water measurements were not made daily, water loss under different weather conditions could not be determined.

For each water potential, the dense treatments stayed closer to the target water potential than the medium or loose treatments. More soil particles provide more surface area to which water can bind, and fewer macropores exist from which water can be easily removed. These conditions and low biomass production acted against water loss by evapotranspiration. High water potential treatments showed the greatest fluctuations because water at high potential is easily removed from the soil by plants or evaporation.



APPENDIX E. Trends in water fluctuations between treatments.