Bot. Gaz. 147(1):71–77. 1986.

0006-8071/86/4701-0008$02.00

291

COMPARATIVE WATER RELATIONS OF CAREX GEYERI AND CALAMAGROSTIS RUBESCENS

TONY SVEJCAR[1]

Eastern Oregon Agricultural Research Center, Union, Oregon 97883

Two rhizomatous codominant understory species, an overwintering dryland sedge, *Carex geyeri*, and a deciduous grass, *Calamagrostis rubescens*, were studied in the field for diurnal and seasonal trends in water relations. Diurnal trends in leaf xylem potential (ψ_l) showed that *C. geyeri* had minimum daily values of 0.40–0.71 MPa more negative than *C. rubescens*. Rhizome xylem potential (ψ_r) was more negative for *C. rubescens*, but, in both species, ψ_r was much less negative (1.8–2.3 MPa) than ψ_l. During the growing season, osmotic potentials (π's) of both species were similar when measured with the freeze-and-thaw dewpoint (DP) technique, but π at incipient plasmolysis, using the pressure/volume (P/V) technique, was 0.25–0.77 MPa more negative for *C. geyeri*. Using DP values, I found estimates of minimum daily turgor were consistently negative (< -0.30 MPa) but that, using P/V values, they were seldom more negative than -0.10 MPa. Apparently differences in bound water content make the DP technique inappropriate for comparative studies of these two species.

Introduction

The adaptive advantages and ecological consequences of an evergreen growth habit have been investigated in a number of vegetation types. MONK (1966) studied forest stands in the southeastern United States and concluded that evergreens were better adapted to dry, infertile sites than deciduous species. REGEHR and BAZZAZ (1976) and NOWAK and CALDWELL (1984) studied photosynthetic characteristics of overwintering leaves of winter annuals and bunchgrasses, respectively. They suggested that carbon uptake during winter helps to offset the respiratory costs of maintaining leaves during winter and that overwintering plants then take advantage of earlier growth in the spring when conditions are favorable. This adaptation appears to be successful in winter annuals. NOWAK and CALDWELL, however, emphasized that it has not yet been clearly established that earlier growth can fully compensate for winter respiratory losses of carbon.

In eastern Oregon, the evergreen sedge *Carex geyeri* Boott and the deciduous grass *Calamagrostis rubescens* Buckl. are common understory codominants in open stands of *Pinus ponderosa* Laws (FRANKLIN and DYRNESS 1973). Both species survive relatively dry soil moisture conditions, and *C. geyeri* has been classified as one of the most drought-resistant species of *Carex* (SAMPSON 1917). These species are also similar in that both form thick rhizome sods and are thought to reproduce vegetatively on undisturbed sites (USDA-FOREST SERVICE 1937). However, the different growth habits of these species influence their distribution. KNIGHT et al. (1977) found that cover of *C. geyeri* declined in high-elevation understory communities where snow persisted into late June, suggesting that the respiratory cost of maintaining leaves during very long periods of snow cover was too high.

Carex geyeri and *C. rubescens* have different wintering habits, but it is unclear how this factor influences their respective physiologies during the growing season. The objectives of this study were (1) to make intraspecific comparisons of leaf and rhizome water potentials and of osmotic potentials during active growth, and (2) to assess how these species respond to the summer drought characteristics of the interior Pacific Northwest.

Material and methods

STUDY SITE

The area, ca. 19 km southeast of Union, Union County, Oregon, is in the foothills of the northeastern portion of the state at an elevation of ca. 1,200 m. The community dominating the site resembles the mixed conifer–*Calamagrostis rubescens*, ash soils habitat type (HALL 1973). Overstory vegetation was primarily *Pinus ponderosa* Laws but also contained *Pseudotsuga menziesii* (Mirb.) Franco and *Larex occidentalis* Nutt. There was limited tree regeneration on the site. The understory vegetation was dominated by *Carex geyeri*, *C. rubescens*, and *Arnica cordifolia* Hook.

Soils on the study site were silt loam Typic Vitrandepts belonging to the Tolo series. The top 10 cm of soil averaged 22% clay, 55% silt, and 23% sand. This series is formed from volcanic ash over buried soil and is generally deep (100–150 cm) and well drained. The aspect of the site faced north with 15%–20% slope.

The study area normally receives most of its precipitation during the winter and spring. Summers are typically hot and dry with daytime temperatures often reaching 32–35 C. Precipitation data

---

[1] Current address: Forage and Livestock Research Laboratory, P.O. Box 1199, El Reno, Oklahoma 73036.

Manuscript received March 1985; revised manuscript received August 1985.

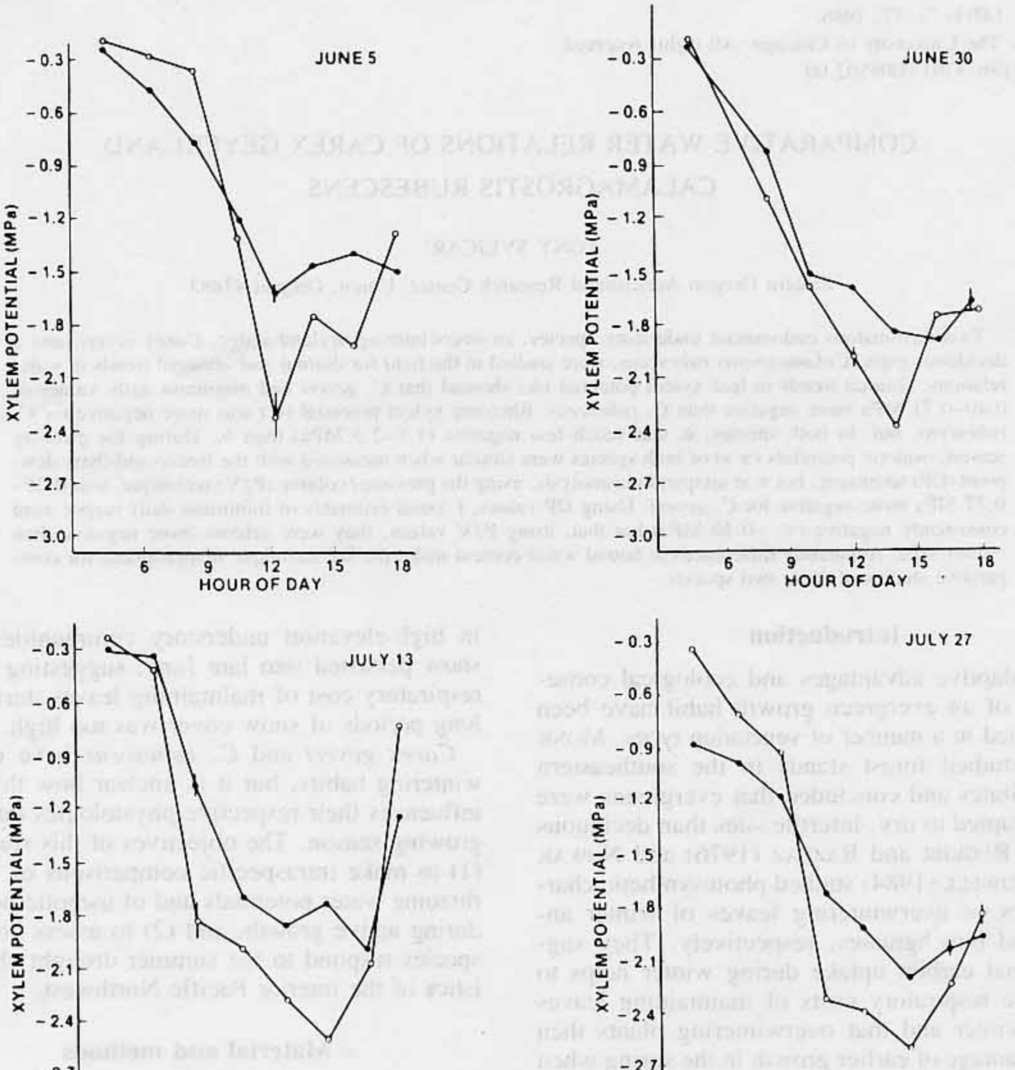

FIG. 1.—Diurnal variation in xylem potential of *Carex geyeri* (open circles) and *Calamagrostis rubescens* (closed circles). Initial points for each line are predawn values. Vertical lines represent maximum variability (±1 SE) around each line.

were collected at a weather station ca. 1.6 km from the study site. The average precipitation for 1971–1981 was 61.0 cm; for 1981, 65.3 cm. During 1981, precipitation totaled 7.1, 7.4, 2.5, and 2.5 cm for May, June, July, and August, respectively.

PLANT WATER POTENTIALS

Diurnal variation in leaf xylem potential (ψ_l) of *C. geyeri* and *C. rubescens* was measured on 6 cloudless days during summer 1981. Measurements were taken at 2-h intervals from predawn to ca. 1800 hours PDT with a pressure chamber (PMS, Corvallis, Oreg.). Four arbitrarily selected samples of the most recently expanded leaf blades were measured at each sampling time. Leaves were enclosed in moist toweling prior to collection to limit water loss. Rhizome xylem potential (ψ_r) was measured with a pressure bomb at 4-h intervals on four sampling dates. Three subsamples for each species were measured at each sampling time. Each sample was a 6–8-cm rhizome segment including the crown region. Roots and aboveground plant parts were removed from the rhizome.

Four leaf-blade samples of each species were collected at midafternoon on each sampling date, frozen on dry ice, transported to a freezer, and stored at −20 C. Osmotic potential (π) was measured on thawed leaf blades with C-52 sample chamber hygrometers (Wescor, Logan, Utah) in conjunction with a Wescor HR-33T microvoltmeter.

Four times during the sampling season, pressure-volume (P/V) curves were determined for each species. Entire tillers of the two species were collected in the field and rehydrated overnight for P/V measurements the following day. On each date, four P/V graphs for each species were constructed using the technique of WILSON et al. (1979). A pressurization rate of ca. 0.01 MPa s^{-1} was used. The π at incipient plasmolysis (π°) was derived from P/V graphs using least-squares analysis.

SOIL WATER POTENTIAL

Soil moisture content was determined gravimetrically on seven dates during late spring and summer 1981. A 4-cm soil corer was used to collect samples at depths of 0–10 and 10–30 cm. Four subsamples were taken on each date. Soil moisture release curves were constructed on soil from the study site with soil moisture extractors (Soilmoisture Equipment Corp., Santa Barbara, Calif.), and gravimetric soil moisture content was converted to soil water potential.

Results

XYLEM POTENTIALS

During the first five measurement dates both species exhibited typical diurnal patterns in ψ_l (fig. 1); i.e., values were highest at predawn, declined throughout the day, and recovered by evening. Predawn ψ_l was high and similar to soil moisture (table 1) on the first three dates. Soil moisture declined during mid- to late July, and the two species responded differently in that *Carex geyeri* maintained a significantly higher ($P < .01$) predawn ψ_l than *Calamagrostis rubescens*. Soil moisture continued to decline into August. By August 10, predawn ψ_l of both species was similar to soil moisture potential (−1.5 MPa).

TABLE 1

SOIL MOISTURE POTENTIAL (MPa) AT VARIOUS DATES DURING 1981

DATE	DEPTH (cm) 0–10	DEPTH (cm) 10–30
May 18	−.01	−.03
June 5	−.01	−.03
June 30	−.03	−.09
July 13	−.02	−.07
July 27	−.23	−.85
August 10	−1.50	−1.40
August 26	−1.43	−1.50

On the first five dates *C. geyeri* had more negative afternoon ψ_l than *C. rubescens*. The difference in afternoon ψ_l values for the two species ranged from 0.7 MPa on June 5 to 0.4 MPa on August 10. The trends, however, were similar with a highly significant ($P < .01$) correlation between the two species ($r = .96$). The general tendency was for *C. geyeri* to have a more rapid decline in ψ_l from predawn to noon but to recover to levels equal to or greater than those of *C. rubescens* by evening. On August 26 the two species no longer displayed typical diurnal trends in ψ_l, which varied diurnally by less than 0.3 MPa. Values were nearly twice as negative as soil moisture potential (ca. −2.8 MPa and −1.5 MPa for plant and soil water potential, respectively).

The water status of rhizomes differed from that of leaf blades both in actual values and diurnal trends (table 2). The ψ_r was less negative than ψ_l for both species on all sampling dates. Diurnal changes in ψ_r were significant ($P < .05$) only on July 27, and species differences were significant ($P < .01$) on July 27 and August 26, with *C. rubescens* having more negative values.

OSMOTIC POTENTIALS

When π was measured with the dew-point (DP) technique, the largest difference between species was 0.22 MPa in early September (fig. 2), after the growing season. Prior to late August the difference between species was less than 0.15 MPa on all dates. The trend in π was similar to that of soil moisture; i.e., levels were high until mid-July and then declined rapidly.

TABLE 2

DIURNAL VARIATION IN ψ_l($-$MPa) FOR CALAMAGROSTIS RUBESCENS AND CAREX GEYERI

DATE AND SPECIES	TIME OF DAY 0630	1030	1430	1830
June 5:				
C. rubescens ...	.12 ± .03[a]	.15 ± .04	.13 ± .03	.14 + .05
C. geyeri	.09 ± .04	.10± .03	.12 ± .06	.12 ± .02
June 30:				
C. rubescens ...	.10 ± .03	.09 ± .05	.14 ± .05	.12 ± .01
C. geyeri	.12 ± .06	.10 + .03	.10 ± .04	.13 ± .04
July 13:				
C. rubescens ...	.08 ± .02	.13 ± .05	.14 ± .04	.12 ± .05
C. geyeri	.08 ± .01	.10 ± .04	.14 ± .07	.13 ± .07
July 27:				
C. rubescens ...	.12 ± .06	.33 ± .11	.34 ± .12	.30 ± .15
C. geyeri	.10 ± .04	.15 ± .08	.19 ± .10	.21 ± .08
August 10:				
C. rubescens ...	.65 ± .26	.52 ± .07	.55 ± .35	.78 ± .40
C. geyeri	.52 ± .10	.45 ± .22	.64 ± .21	.67 ± .29
August 26:				
C. rubescens ...	.73 ± .35	.73 ± .16	.60 ± .18	.62 ± .08
C. geyeri	.47 ± .30	.28 ± .06	.30 ± .07	.29 ± .08

[a] Mean ± 1 SE.

Species differences in π were significant ($P <$ .01) when measured with the P/V technique (fig. 3). On all sampling dates *C. geyeri* had more negative π° values; the difference between species ranged from 0.25 to 0.77 MPa. In late August, neither species exhibited typical P/V relationships. The plots for *C. rubescens* were linear from the first point, whereas a clearly linear phase was difficult to detect for *C. geyeri*.

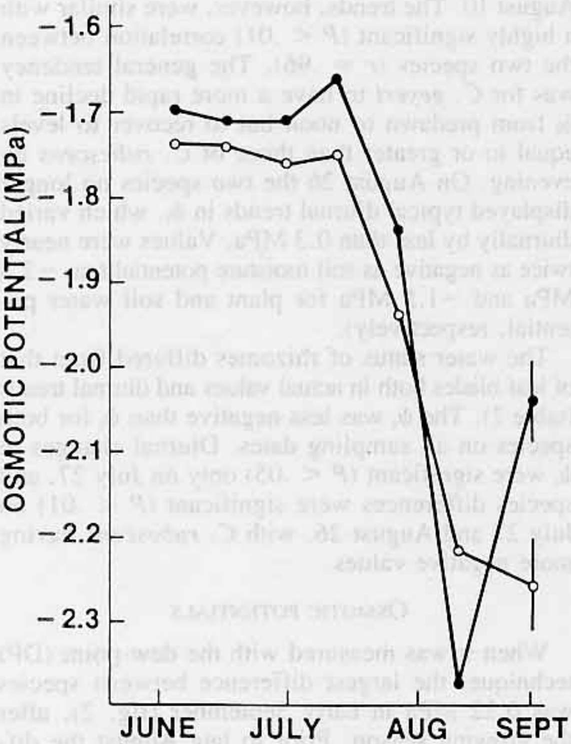

FIG. 2.—Seasonal changes in π of *Carex geyeri* (open circles) and *Calamagrostis rubescens* (closed circles) as determined by the DP technique. Vertical lines represent maximum variability (±1 SE) around each line.

The π's determined by the DP and P/V techniques were subtracted from minimum daily ψ_l to obtain an estimate of minimum daily turgor (table 3). Values derived from the P/V technique are π° and those obtained with DP analysis are π at the total water potential of the tissue sample. However, in this case, samples used in the DP analysis were collected when ψ_l approached incipient plasmolysis; thus, the two techniques should have yielded comparable values and resulted in similar estimates of minimum daily turgor. However, when averaged over the sampling dates, minimum daily turgor potentials for *C. rubescens* and *C. geyeri* were 0.05 and 0.10 MPa, respectively, with the P/V technique, and −0.24 and −0.74 MPa, respectively, with the DP technique.

Discussion

Diurnal variation in ψ_l has been documented in a range of species (KLEPPER 1968; JACKSON 1974; PAVLIK 1980; WALLACE et al. 1983). As long as soil moisture was adequate, *Carex geyeri* and *Calamagrostis rubescens* also exhibited diurnal trends. Predawn ψ_l for the two species was similar except on July 27, the first sampling date after soil moisture began to decline. The higher predawn ψ_l in *C. geyeri* at that point, in spite of its typically more negative daytime values, was unexpected. How-

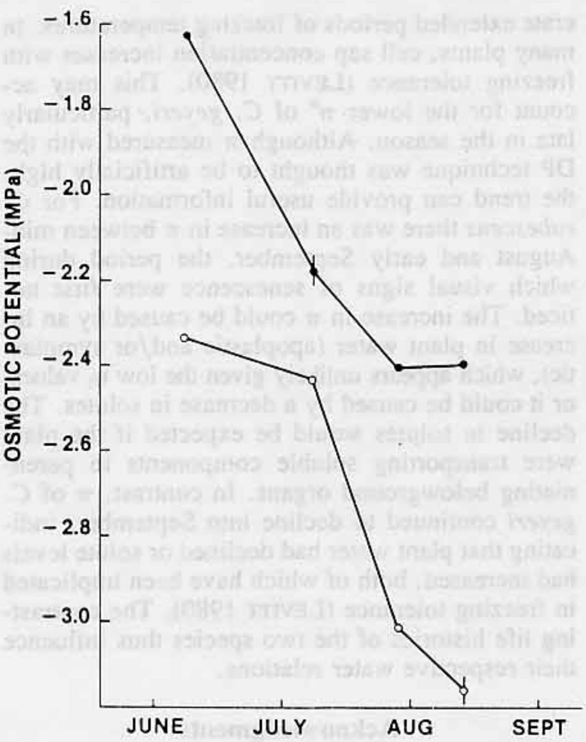

FIG. 3.—Seasonal changes in π° of *Carex geyeri* (open circles) and *Calamagrostis rubescens* (closed circles) as determined by the P/V technique. Vertical lines represent maximum variability (±1 SE) around each line.

ever. *C. geyeri* has a deeper rooting habit than *C. rubescens* (NIMLOS et al. 1968), which would have allowed *C. geyeri* to maintain higher predawn ψ_l until the deeper soil horizons had dried. The lower daytime ψ_l for *C. geyeri* must be considered in light of the fact that this species had a slightly higher stomatal conductance (SVEJCAR 1982) and a more negative π° than *C. rubescens*. However, by late August neither species exhibited the diurnal trends in ψ_l noted earlier. JACKSON (1974) found that *Lolium perenne* also lacked diurnal variation of ψ_l late in the season, when soil moisture was depleted. This trend may indicate the point at which plants are no longer able to absorb moisture from any horizon in the soil profile.

Information on growth patterns and physiology of rhizomes has lagged behind that of aboveground plant parts. Rhizomes of the studied species showed little diurnal fluctuation in ψ_r, particularly in comparison to leaves, and there was a steep water potential gradient (1.8–2.3 MPa) between leaves and rhizomes of both species. Roots of *Nicotiana tabacum* and *Picea sitchensis* also showed limited diurnal fluctuation and steep potential gradients with aboveground organs (DE ROO 1969; HELKVIST et al. 1974). In addition, DE ROO noted that the expected potential gradient between roots and soil did not develop at low soil moisture levels; i.e., roots had less negative water potentials than that of the soil. Rhizomes of *C. geyeri* and *C. rubescens* have a similar response: ψ_r of both species were more negative than soil moisture potential until mid- to late July, when soil moisture declined and the gradient inverted.

TABLE 3

MINIMUM DAILY TURGOR (MPa) FOR CAREX GEYERI AND CALAMAGROSTIS RUBESCENS ESTIMATED USING EITHER THE DP OR P/V TECHNIQUE

Date and technique	*C. rubescens*	*C. geyeri*
June 5:		
DP	.06	−.62
P/V	.00	−.01
July 13:		
DP	−.35	−.78
P/V	.18	−.08
July 27:		
DP	−.38	−.66
P/V	.28	.43
August 10:		
DP	−.30	−.89
P/V	−.28	.05

Soil moisture measurements included only the top 30 cm of soil, and both species root below that level (NIMLOS et al. 1968). Perhaps moisture was extracted from lower levels over part of the season. However, even in late August, when ψ_l was between −2.50 and −3.00 MPa and showed no predawn recovery for either species, ψ_r did not reach values more negative than −0.80 MPa. The adaptive significance of and the mechanisms responsible for the inverted potential gradient are difficult to assess, given the limited information on rhizome physiology and growth. It appears that there is a substantial resistance to water flow in the crown of these two species, as MEYER and RITCHIE (1980) found in *Sorghum bicolor*. The importance of high water content in rhizomes was indicated by MCINTYRE (1976), who found that decreasing water content caused an inhibition of bud activity in *Agropyron repens*. For *C. geyeri* and *C. rubescens*, this process would be particularly important early in the season, when the majority of new tillers are initiated.

Total water potential can be useful in determining plant water stress (KRAMER 1983). It is often necessary, however, to consider π and turgor potential as well (TURNER 1981). In my study, assessment of water potential components varied with the technique used to measure π. Results from the DP technique did not reveal major differences between the two species during the growing season, whereas π° from P/V curves was 0.25–0.77 MPa more negative for *C. geyeri* than for *C. rubescens*.

There is substantial evidence that the DP technique results in artificially high values of π, which in turn produces estimates of negative turgor (Brown 1972; Tyree 1976; Campbell et al. 1979; Markhart et al. 1981; Turner 1981). Oertli (1984) argued that plant cells are generally incapable of withstanding negative turgor pressures and will collapse and shrivel when exposed to such pressures.

Dilution of osmotic water in the symplast with relatively pure apoplastic water is generally considered to result in artificially high estimates of π with the DP technique. The proportion of water in the apoplast and symplast influences the degree of dilution. At full turgor, apoplastic water is thought to range from 3% to 50%, depending on plant type (Turner 1981). In my study, the DP technique yielded estimates of negative turgor for both species, but, when averaged over the season, values were three times more negative for *C. geyeri* (−0.74 MPa) than for *C. rubescens* (−0.24 MPa). Estimates of minimum daily turgor were more negative than −0.10 MPa in only one case when the P/V technique was used. This indicates that the degree of dilution and, thus, proportion of bound water were greater for *C. geyeri* and makes interspecific comparisons based on DP values unreliable. However, π° from the P/V technique shows that *C. geyeri* can have a lower afternoon ψ_l than *C. rubescens* without sustaining a loss of turgor.

The contrasting life histories of the two species may account for some of the differences in water relations. Leaves of *C. rubescens* die in the fall, and new tillers are initiated each spring, whereas leaves of *C. geyeri* overwinter. In fact, leaves of *C. geyeri* may live 4 yr or more (G. S. Strickler, personal communication). Plants that overwinter in the interior Pacific Northwest must be able to tolerate extended periods of freezing temperatures. In many plants, cell sap concentration increases with freezing tolerance (Levitt 1980). This may account for the lower π° of *C. geyeri*, particularly late in the season. Although π measured with the DP technique was thought to be artificially high, the trend can provide useful information. For *C. rubescens* there was an increase in π between mid-August and early September, the period during which visual signs of senescence were first noticed. The increase in π could be caused by an increase in plant water (apoplastic and/or symplastic), which appears unlikely given the low ψ_l values, or it could be caused by a decrease in solutes. The decline in solutes would be expected if the plant were transporting soluble components to perenniating belowground organs. In contrast, π of *C. geyeri* continued to decline into September, indicating that plant water had declined or solute levels had increased, both of which have been implicated in freezing tolerance (Levitt 1980). The contrasting life histories of the two species thus influence their respective water relations.

Acknowledgments

This work was made possible by the support provided by Dr. M. Vavra and the Oregon Agricultural Experiment Station. I also thank Drs. R. Miller and D. Chilcote for loan of equipment and helpful suggestions during the study. Helpful suggestions on the manuscript were provided by Drs. L. Wallace, W. K. Smith, and an anonymous reviewer. The manuscript was submitted as Technical Paper 7160, Oregon Agricultural Experiment Station.

LITERATURE CITED

Brown, R. W. 1972. Determination of leaf osmotic potential using thermocouple psychrometers. Pages 198–210 *in* R. W. Brown and B. P. VanHaveren, eds. Psychrometry in water relations research. Utah Agric. Exp. Station, Utah State University, Logan.

Campbell, G. S., R. I. Papendick, E. Rabie, and A. J. Shayo-Ngowi. 1979. A comparison of osmotic potential, elastic modulus, and apoplastic water in leaves of dryland winter wheat. Agron. J. **71**:31–36.

De Roo, H. C. 1969. Water stress gradients in plants and soil-root systems. Agron. J. **61**:511–515.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service Gen. Tech. Rep. PNW-8.

Hall, F. C. 1973. Plant communities of the Blue Mountains in eastern Oregon and southeastern Washington. USDA Forest Service PNW R6 Area Guide 3-1.

Helkvist, J., G. P. Richards, and P. G. Jarvis. 1974. Vertical gradients of water potential and tissue water relations in sitka spruce trees measured with the pressure chamber. J. Appl. Ecol. **11**:637–667.

Jackson, D. K. 1974. The course and magnitude of water stress in *Lolium perenne* and *Dactylis glomerata*. J. Agr. Res. **82**:19–27.

Klepper, B. 1968. Diurnal pattern of water potential in woody plants. Plant Physiol. **43**:1931–1934.

Knight, D. H., B. S. Rogers, and C. R. Kyte. 1977. Understory plant growth in relation to snow duration in Wyoming subalpine forest. Bull. Torrey Bot. Club **104**:314–319.

Kramer, P. J. 1983. Water relations of plants. Academic Press, New York.

Levitt, J. 1980. Responses of plants to environmental stresses. Vol. **1**. Chilling, freezing and high temperature stresses. Academic Press, New York.

McIntyre, G. I. 1976. Apical dominance in the rhizome of *Agropyron repens:* the influence of water stress on bud activity. Can. J. Bot. **54**:2747–2754.

Markhart, A. H., N. Sionit, and J. M. Siedow. 1981. Cell wall water dilution: an explanation of apparent negative turgor potentials. Can. J. Bot. **59**:1722–1725.

Meyer, W. S., and J. T. Ritchie. 1980. Resistance to water flow in the sorghum plant. Plant Physiol. **65**:33–39.

Monk, C. D. 1966. An ecological significance of evergreenness. Ecology **47**:504–505.

Nimlos, T. J., W. P. Van Meter, and L. A. Daniels. 1968. Rooting patterns of forest understory species as determined by radioiodine absorption. Ecology **49**:1146–1151.

Nowak, R. S., and M. M. Caldwell. 1984. Photosynthetic activity and survival of foliage during winter for two bunchgrass species in a cold-winter steppe environment. Photosynthetica **18:**192–200.

Oertli, J. J. 1984. Water relations in cell walls and cells in the intact plant. Z. Pflanz. Boden. **147:**187–197.

Pavlik, B. M. 1980. Patterns of water potential and photosynthesis of desert sand dune plants, Eureka Valley, California. Oecologia **46:**147–154.

Regehr, D. L., and F. A. Bazzaz. 1976. Low temperature photosynthesis in successional winter annuals. Ecology **57:**1297–1303.

Sampson, A. W. 1917. Important range plants: their life history and forage value. USDA Bull. 545.

Svejcar, T. 1982. Seasonal and diurnal changes in the water relations of elk sedge (*Carex geyeri*) and pinegrass (*Calamagrostis rubescens*). Ph.D. diss. Oregon State University, Corvallis.

Turner, N. C. 1981. Techniques and experimental approaches for the measurement of plant water status. Plant Soil **58:**339–366.

Tyree, M. T. 1976. Negative turgor pressure in plant cells: fact or fallacy. Can. J. Bot. **54:**2738–2746.

USDA-Forest Service. 1937. Range plant handbook. Government Printing Office, Washington, D.C.

Wallace, J. S., J. A. Clark, and M. McGowan. 1983. Water relations of winter wheat. 3. Components of leaf water potential and the plant-soil waer potential. J. Agr. Sci. **100:**581–589.

Wilson, J. R., J. M. Fisher, E. D. Schulze, G. R. Dolbey, and M. M. Ludlow. 1979. Comparison between pressure-volume and dewpoint-hygrometry techniques for determining the water relations characteristics of grass and legume leaves. Oecologia **41:**77–88.