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Simulation of Leaf Conductance and Transpiration in *Juniperus occidentalis*

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Abstract. Western juniper (*Juniperus occidentalis* Hook.) is a conifer species well adapted to semi-arid rangelands in portions of the western United States. Over a 2-yr period (1983–1984), water relations of mature western juniper trees were observed and soil temperature, soil water, air temperature, vapor density deficit (D_a), and solar radiation were recorded. Data from 1983 were used to develop and calibrate a leaf conductance model for western juniper. The model was then tested against 1984 data. A daily soil water budget was maintained by coupling the conductance model with the hydrology component of the model SPUR (Simulation of Production and Utilization of Rangelands). Results indicate that the model successfully simulated seasonal conductance trends. Conductance was strongly affected by soil temperature and D_a in spring, while soil water pressure and D_a were important during summer. Simulated western juniper conductance rose to maximum in spring and was usually within one standard deviation of observed values. In the 1984 simulation, western juniper transpired 141 mm of water, 47% of the total evapotranspiration for the site, and 44% of 1984 precipitation. Simulated western juniper conductance increased whenever environmental conditions moderated in late winter and spring. Juniper withdrew 37 mm of water between January and May 1984, suggesting it has potential to significantly alter watershed value and site productivity. For. Sci. 40(1): 5–17.

Additional key words. Computer model, SPUR, transpiration, water balance, evapotranspiration.

Western juniper (*Juniperus occidentalis* Hook.) is a conifer species well adapted to semi-arid rangelands in portions of the western United States. It occurs throughout eastern Oregon, eastern Washington, northeastern California and southern Idaho (Burkhardt and Tisdale 1976, Caraher 1978). During the last 100 yr this species has increased in density, actively invading adjacent sagebrush-grass communities. Increased density and distribution of western juniper has been attributed to reduced fire frequency, heavy grazing history, changes in climate, and increased seed rain, either singly or in concert (Philips 1910, Leopold 1924, Cottam and Stewart 1940, Parker 1945).

The conversion of shrub steppe communities to juniper woodlands has influenced ecological processes on the landscape. As western juniper increases on a site, understory production decreases, subsurface flow decreases, and sediment production increases (Gifford 1973, Buckhouse and Mattison 1980, Baker 1984, Vaitkus and Eddleman 1986). Also, effective precipitation is reduced because only a portion of the precipitation intercepted by the juniper canopy reaches the ground (Eddleman 1983, Young et al. 1984). The end result is that as western juniper density increases, the site becomes increasingly arid, herbaceous production is depressed, and watershed quality is diminished.

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Because of western juniper's increased presence on semi-arid uplands, information is needed to evaluate the effects of these woodlands on the hydrologic cycle. Models have been developed for other conifers (Kaufmann 1982, 1984, Running 1984); however, little work has been reported for western juniper. Recent water relations research has investigated relationships between western juniper conductance rates and environmental conditions (Miller and Shultz 1987). This information provides the necessary data to develop a physiologically based conductance model for a western juniper woodland. Such a model will permit scientists and managers to make appropriate decisions regarding management of western juniper. In the present study we developed a conductance model for western juniper. Objectives were to simulate diurnal leaf conductance and to estimate canopy transpiration and water balance in a moderate density, even-aged western juniper stand.

METHODS

STUDY SITE

The leaf conductance model was developed using data collected at the Squaw Butte Experimental Range located in the northern Great Basin, in southeastern Oregon. The study site was in an *Artemisia tridentata* ssp. *vaseyana*/*Festuca idahoensis* habitat type at 1360 m elevation (Winward 1970). Western juniper encroachment began on the study site just after the turn of the century. Soil is a Typic Haploxeroll, varying from loam texture at the surface to gravelly loam at lower depths (Swanson 1982). Soils are underlain by columnar bedrock at approximately 112 cm. Average annual precipitation (39-yr mean) is approximately 283 mm, most of which is received as snow between September and June. During the study, precipitation was above average (Table 1), with 372 and 317 mm received in 1983 and 1984, respectively. March 1983 was much wetter than average in both years, and the entire soil profile was at or near field capacity during early spring.

DATA COLLECTION

Data for model development and testing was obtained by measuring western juniper stomatal conductance (g_l) (cm $*$ s^{-1}) during 2 growing seasons, between

TABLE 1.

Monthly precipitation (mm) received at the Squaw Butte Experiment Range during the calibration year (1983) and the testing year (1984). Both years were above average for fall and winter accumulations. Precipitation in August 1984 was the highest on record for that month. Means are for a 39-yr period.

Year	Jan	Feb	Mar	Apr	May	June	Jul	Aug	Sep	Oct	Nov	Dec	Total
1983	12	37	53	19	32	10	19	17	15	27	45	86	372
1984	4	11	66	27	17	37	15	53	2	45	35	5	317
Mean	34	23	24	20	31	24	9	16	14	23	31	34	283
Median	28	18	23	17	27	19	6	9	11	20	26	31	235

January 1983 and September 1984. Detailed descriptions of methods are reported elsewhere (Miller and Shultz 1987). Environmental data included precipitation (mm), air and soil temperature (°C), vapor density deficit (D_a) ($g * m^{-3}$), gravimetric soil water content (%), and solar radiation ($cal * cm^{-2} * s^{-1}$). Leaf conductance was measured with a steady state porometer (LiCor, Li-1600) fitted with a cylindrical chamber. Juniper total leaf area (LA) (m^2) was estimated from basal circumference (Miller et al. 1987), and leaf area index (LAI) was derived based on LA per tree and trees $* ha^{-1}$. All plant measurements were collected on mature trees. Analysis of data collected in 1983 indicated that solar radiation, soil temperature, soil water pressure (ψ_s) (MPa) and D_a were important factors that could be used to predict diurnal patterns of g_l (Miller and Shultz 1987).

MODEL OVERVIEW

The conductance model (JUOC) was developed on a DEC Micro-VAX using the VAX FORTRAN programming language. Later, the program was transferred to an 80386-based computer using Microsoft FORTRAN Version 5.0. JUOC operates at an hourly time step. At the start of each day, precipitation (mm), diurnal temperature extremes (°C) and daily solar radiation ($cal * cm^{-2} * d^{-1}$) are input (Table 2, Figure 1). JUOC simulates g_l for a moderate density (up to 150 trees/ha) even-aged stand of western juniper growing in the northern Great Basin. Transpiration (J) ($\mu g * cm^{-2} * s^{-1}$) is calculated based on g_l and D_a. Descriptive parameters for the juniper stand are input at the beginning of the simulation, and do not change (Table 2). Stomatal conductance is based on current soil temperature at 10 cm, soil water pressure in the wettest layer, and overnight minimum temperature. Stomatal conductance is set to the maximum potential rate just after sunrise. As the day progresses, ambient temperature and D_a rise toward a diurnal maximum and conductance rate declines. Hourly J is summed to get total daily transpiration per unit LA. Stand transpiration is estimated at the end of the day and reported as mm of water. At the end of the day, soil water is uniformly removed from the soil profile, down to the maximum rooting depth. In this study we assumed a rooting depth of 86 cm, and a 102 cm depth of profile.

Daily soil water balance is maintained by coupling the conductance model,

TABLE 2.

Driving variables input to the model on a daily basis and constant parameters used to describe the western juniper stand.

Driving variable		Constant parameter	
Name	Units	Description	Value
Day	day of year	Tree density	75 trees $\cdot ha^{-1}$
Precipitation	$mm \cdot d^{-1}$	Basal circumference	110 cm
Maximum air temp.	°C	Crown diameter	275 cm
Minimum air temp.	°C	Total leaf area	216 $m^2 \cdot tree^{-1}$
Solar radiation	$cal \cdot cm^{-2} \cdot d^{-1}$	Leaf area index	1.6
		Soil depth	102 cm
		Rooting depth	86 cm

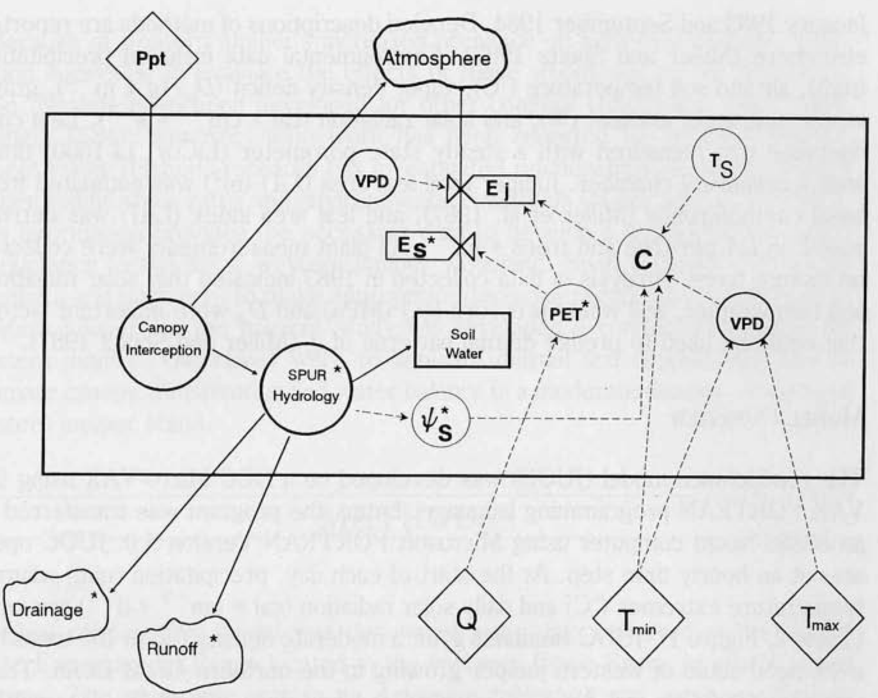

FIGURE 1. Flow diagram of the western juniper conductance model JUOC. Water flow is shown as solid lines; information flow as dashed lines. Driving variables are precipitation (*Ppt*), solar flux (*Q*) and diurnal temperature extremes ($T_{\min}$ and $T_{\max}$). Symbols with an asterisk (*) denote routines in the rangeland model, SPUR, which estimate soil water pressure ψ_s, daily potential evapotranspiration (*PET*), and soil water evaporation (E_s). The simulated conductance (*C*) is based on current soil and atmospheric conditions. Western juniper transpiration rate (E_j) is determined by *C* and D_a.

JUOC, with the upland hydrology component of SPUR (Simulation of Production and Utilization of Rangelands) (Renard et al. 1987) (Figure 1). The SPUR hydrology model operates at both field and basin scales. We used the field scale version in the present effort. SPUR hydrology controls water routing to snow storage, snowmelt, runoff, soil storage, or deep percolation. Wight and Skiles (1987) provide user documentation and a detailed discussion of SPUR.

SOLAR RADIATION

Based on observations of Miller and Shultz (1987), JUOC closes western juniper stomates at sunset and opens them shortly after sunrise to maximum potential aperture. At sunset, g_l is set to an absolute minimum of 0.005 $\text{cm} * \text{s}^{-1}$. This rate has been reported for other conifer species (Hinckley et al. 1978), and we adopted it for use in JUOC. After sunrise g_l increases to the maximum potential rate, based on current environmental conditions. Modeled daily maximum conductance varies from 0.005 $\text{cm} * \text{s}^{-1}$ in winter months to 0.19 $\text{cm} * \text{s}^{-1}$ in spring during optimal environmental conditions.

SOIL TEMPERATURE

Soil temperature below 10°C has been shown to be a factor related to increased root resistance in several conifer species (Kaufmann 1975, Running and Reid

1980). In western juniper, xylem sap pressure (ψ_l) decreased linearly as transpiration increased, but the rate of decrease was greater when soils were cold (Miller and Shultz 1987). Data collected in 1983 were fit to a hyperbolic function which was determined by fitting to maximum observed conductances over a range of soil temperatures from 2 to 20°C (Figure 2).

$$G_t = 1.0 - e^{kx} * G \tag{1}$$

where

G_t = maximum potential conductance ($\text{cm} * \text{s}^{-1}$), based on soil temperature
$k = -0.158$
x = 10-day average soil temperature (°C) at 10 cm depth
$G = 0.19\ \text{cm} * \text{s}^{-1}$

SOIL WATER

Maximum daily g_l is highly correlated with predawn xylem water pressure ($P\psi_l$) (MPa) (Running 1976). $P\psi_l$ is linearly related to ψ_s in the root zone (Hinckley et al. 1978, Sala et al. 1981), permitting the use of ψ_s to predict changes in maximum g_l. In JUOC, a simple logistic function is used in which g_l is reduced after ψ_s falls below a critical level (-0.25 MPa), thereby producing a threshold type response (Figure 3).

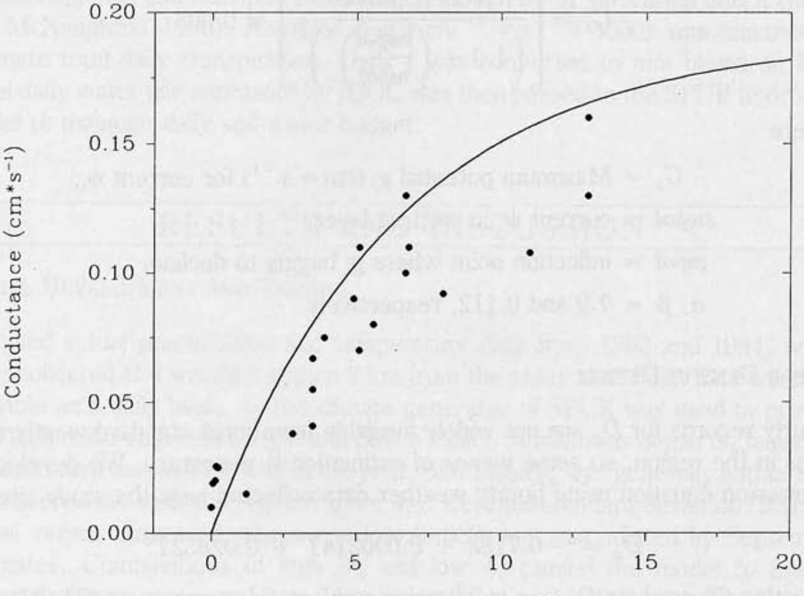

FIGURE 2. Theoretical relationship between western juniper leaf conductance ($\text{cm} * \text{s}^{-1}$) and soil temperature (°C). The function assumes that current soil water pressure is > -0.25 MPa and represents maximum potential conductance at a given soil temperature.

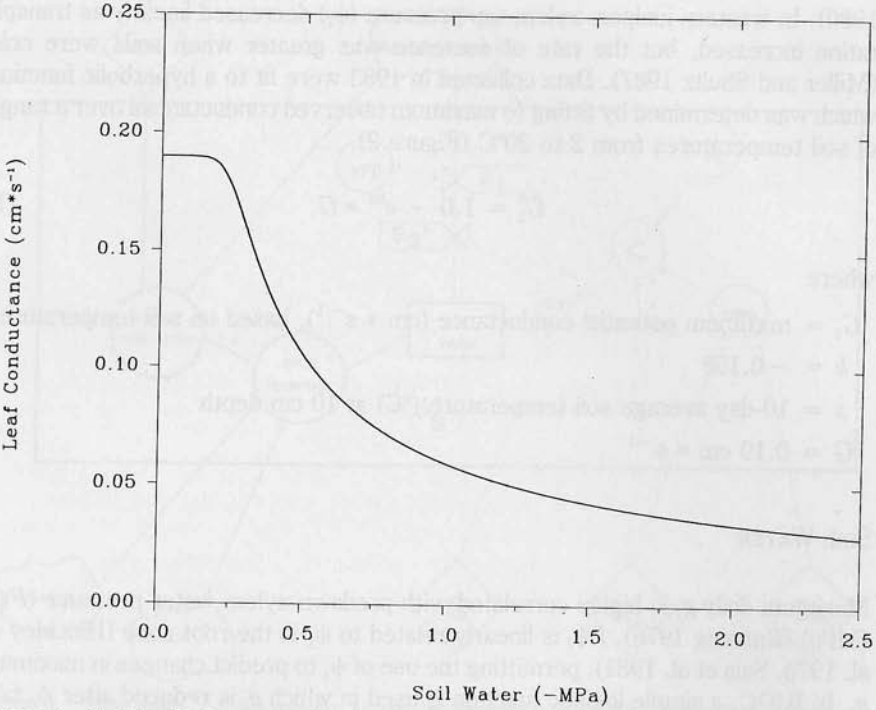

FIGURE 3. Relationship between soil water pressure (MPa), and western juniper leaf conductance. The model assumes that soil temperature is optimal.

$$G_s = \left[\frac{(0.19 - 0.005)}{\left(1.0 + \left(\frac{swpot}{mpot}\right)^{\alpha}\right)^{\beta}} \right] + 0.005 \tag{2}$$

where

G_s = Maximum potential g_l ($\text{cm} * \text{s}^{-1}$) for current ψ_s,
$swpot$ = current ψ_s in wettest layer,
$mpot$ = inflection point where g_l begins to decline,
α, β = 7.9 and 0.112, respectively.

VAPOR DENSITY DEFICIT

Hourly records for D_a are not widely available from most standard weather stations in the region, so some means of estimation is necessary. We developed a regression equation using hourly weather data collected near the study site.

$$D_a = -0.7188 + 0.000214T + 0.02852T^2 \tag{3}$$

Equation (3) predicts D_a ($\text{g} * \text{m}^{-3}$) using ambient air temperature (T) (°C), similar to the method presented by Reed and Waring (1974). The model fit the data well ($R^2 = 0.94$; $RSD = 2.04$; $n = 746$).

Stomatal response to D_a is described using a linear model similar to Miller and

Shultz (1987). In the present model, g_l decreases linearly with increased D_a, and the rate of decrease does not change with changing soil conditions. JUOC determines maximum potential conductance ($G_{\max}$) each day by determining whether soil water or temperature is more limiting to potential g_l. JUOC sets $G_{\max}$ to the lower of G_t [Equation (1)], or G_s [Equation (2)]. In addition, if overnight air temperature falls below 0°C, $G_{\max}$ is reduced by 0.005 cm $*$ s^{-1} $*$ $°C^{-1}$, similar to Kaufmann (1982). Finally, hourly conductance is determined by Equation (4):

$$g_h = G_{\max} - 0.00455 * D_a \tag{4}$$

where

g_h = resultant hourly conductance (cm $*$ s^{-1}), and
$G_{\max}$ = maximum potential conductance for current day.

During the 2-yr study, measured g_l generally did not increase as afternoon D_a decreased, even when soil water was at or near field capacity; therefore we did not allow the model to increase g_h in the afternoon as D_a declined.

TRANSPIRATION

Transpiration rate (J) (μg $*$ cm^{-2} $*$ s^{-1}) was estimated as the product of Equations (3) and (4):

$$J = g_h * D_a \tag{5}$$

Miller and Shultz (1987) reported that g_l did not differ between north and south aspects of western juniper canopies. This is likely attributable to the open structure of western juniper canopies. Coniferous stands are generally well coupled to the atmosphere, and transpiration is largely driven by air saturation deficit (Jarvis and McNaughton 1986). Hourly J (μg $*$ cm^{-2} $*$ s^{-1} $*$ 3600) was summed to estimate total daily transpiration. Daily J was converted to mm based on *LAI*. Total daily water use estimated by JUOC was then passed to the SPUR hydrology model to maintain daily soil water budget.

RESULTS AND DISCUSSION

MODEL DEVELOPMENT AND TESTING

We used actual precipitation and temperature data from 1983 and 1984, which were collected at a weather station 2 km from the study site. Solar data were not available on a daily basis, so the climate generator of SPUR was used to provide total daily solar radiation (Wight and Skiles 1987). Simulations began on January 1 and continued through the end of the year. Simulated g_h was generally within 1 SD of measured seasonal averages (Figure 4a). Residual standard deviation (RSD) of model versus measured values was low (0.029) but was inflated by September estimates. Combinations of high D_a and low ψ_s caused the model to predict stomatal closure on several days between late July and early September. Poorest agreement occurred on September 14, when model estimated g_h was 0.07 cm $*$ s^{-1} less than observed values. Part of this disagreement was attributed to differences in soil water content between the model and study site. Miller and

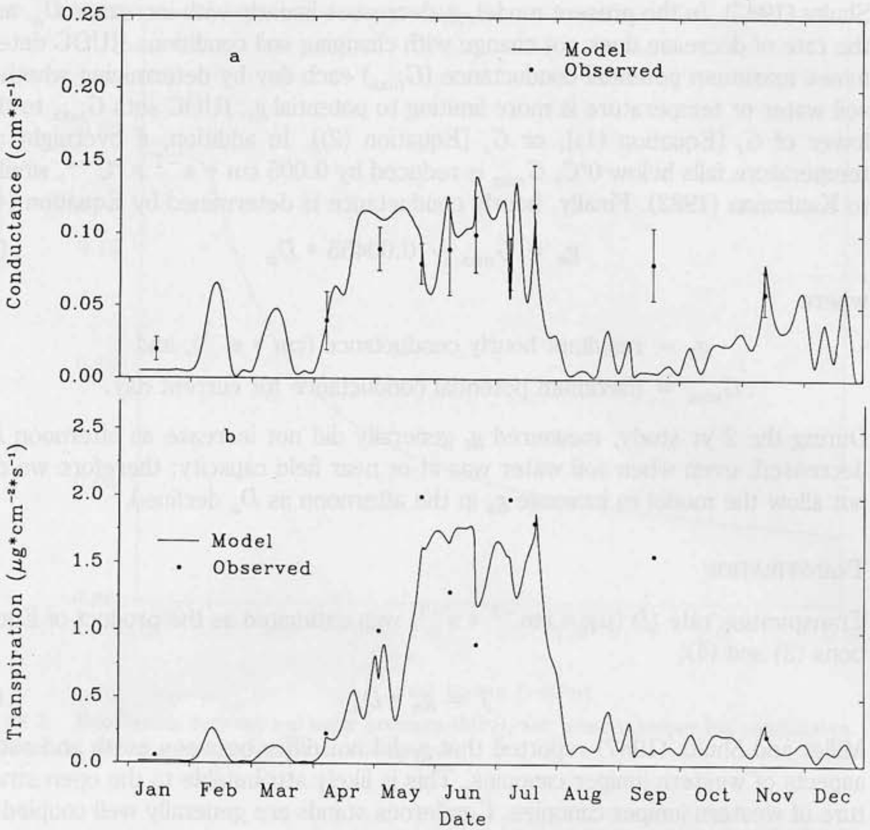

FIGURE 4. Midday (1400 h) values for (a) Seasonal patterns of modeled and measured (Miller and Shultz 1987) leaf conductance (cm $*$ s^{-1}) by western juniper during the calibration year 1983; error bars represent 1 standard deviation, (b) Modeled western juniper transpiration (µg $*$ cm^{-2} $*$ s^{-1}), compared to measured seasonal rates (Miller and Shultz 1987) during 1983.

Shultz (1987) noted that soil water at 100 cm remained above -0.03 MPa throughout the summer. Bulk flow of water was observed over exposed bedrock in a soil pit dug on the site. Juniper roots were observed at bedrock. We speculate subsurface water movement from upslope provided recharge to soil on the study site, decreasing juniper water stress. In October and November 1983, precipitation recharged the upper soil profile, and modeled midday g_h increased from August lows, closely approximating measured values.

During optimum environmental conditions, modeled maximum potential J is 1.9 µg $*$ cm^{-2} $*$ s^{-1}, at $D_a = 20.9$ g $*$ m^{-3}, in agreement with Miller and Shultz (1987), who reported a maximum rate of 2.0 µg $*$ cm^{-2} $*$ s^{-1} at $D_a = 25$ g $*$ m^{-3} in late May. Soils were at field capacity in spring, and J was primarily affected by soil temperature and evaporative demand. May 1983 midday transpiration increased to about 1.8 µg $*$ cm^{-2} $*$ s^{-1} (Figure 4b) and fluctuated with daily changes in D_a until early July, when ψ_s of the wettest layer decreased to about -0.3 MPa. By that time soil water pressure in the upper profile was at or below -1.5 MPa. As noted above, the model predicted stomatal closure in September, because of decreased ψ_s, resulting in a difference of about 1.4 µg $*$ cm^{-2} $*$ s^{-1} between measured and modeled values.

MODEL TESTING

After the model was calibrated with the 1983 dataset, the model was tested against measured conductance data from 1984 (Figure 5a). Midday g_h approximated measured values well throughout the spring and summer 1984, differing from seasonal means by more than 1 SD on only three dates, when modeled conductance was less than observed. Conductance increased in April, as soil and air temperatures began to increase. On April 18, observed and modeled conductances were 0.11 and 0.12 cm $*$ s^{-1}, respectively. Modeled soil temperature was 3°C greater than actual, causing slight overestimation of g_l. Later, on April 27, observed and modeled conductances decreased to 0.07 and 0.09 cm $*$ s^{-1}, respectively, even though soil conditions were near optimum. The model restricted g_h because the previous night minimum was -6°C. Available soil water declined in late July and restricted maximum potential g_h. Accordingly, midday g_h declined to about 0.05 cm $*$ s^{-1} in late July, and stomates were closed at midday in August. Measured plants kept stomates at least partially open in August, perhaps

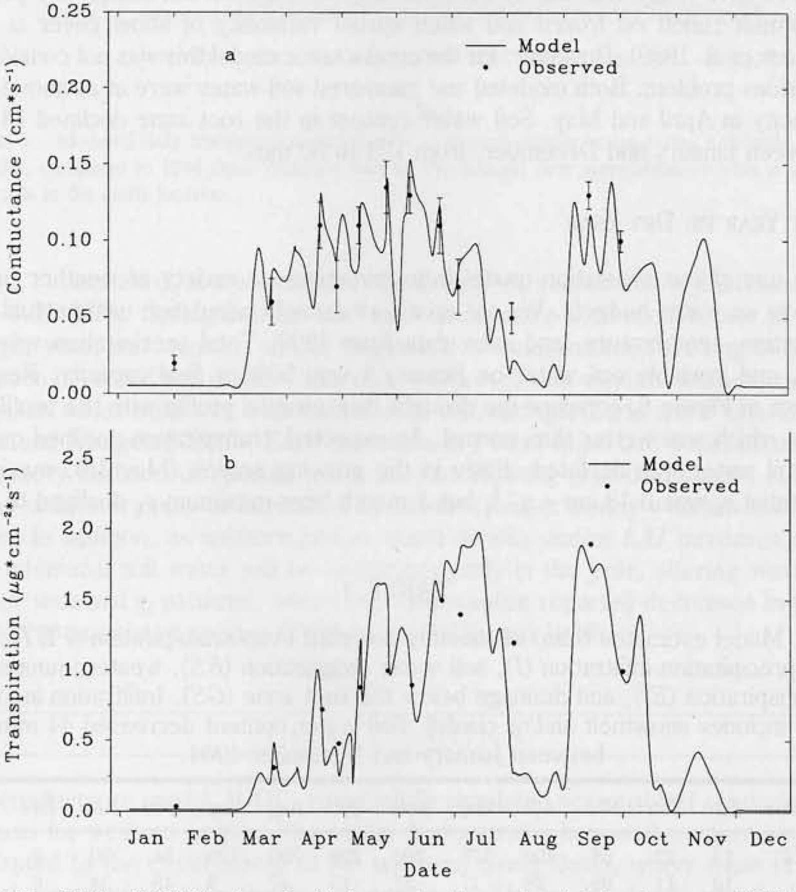

FIGURE 5. Midday (1400 h) values for (a) Seasonal patterns of modeled and measured (Miller and Shultz 1987) leaf conductance (cm $*$ s^{-1}) by western juniper during the validation year 1984; error bars represent 1 standard deviation, (b) Modeled western juniper transpiration (µg $*$ cm^{-2} $*$ s^{-1}), compared to measured seasonal rates (Miller and Shultz 1987) during 1984.

because of subsurface water movement at the study site, resulting from 33% greater than average precipitation between November 1983 and July 1984. Prior to mid-July, evaporative demand was the primary factor influencing g_h, while ψ_s became dominant in late July and August. Transpiration rates in 1984 closely followed seasonal trends (Figure 5b), except for August, when the model predicted stomatal closure. The model closely predicted the increased J in September, following significant rainfall in late August (Table 1) which increased ψ_s in the upper profile to -0.4 MPa during early September.

Table 3 gives water budget estimates for 1984. For the year, total evapotranspiration (ET) was 300 mm of which western juniper transpired 141 mm, about 47% of total ET. Under actual field conditions, it is likely that soil evaporation, and perhaps juniper transpiration, would be lower because other species would be present, accounting for more of the total ET. The model did not predict significant spring surface runoff, but instead routed excess water (94 mm) to deep storage, below the root zone. The predicted deep drainage resulted from heavy snow accumulation between November 1983, and March 1984.

Although not predicted, we did observe surface runoff as snow melted in 1984. Others have noted that the SPUR hydrology model does not adequately predict snowmelt runoff on frozen soil when spatial variability of snow cover is high (Wilcox et al. 1989). However, for the conductance model this was not considered a serious problem. Both modeled and measured soil water were at or above field capacity in April and May. Soil water content in the root zone declined 44 mm between January and December, from 124 to 80 mm.

WET YEAR VS. DRY YEAR

One use of our simulation model is to investigate a variety of weather profile effects on water budgets. We set up a 1-yr drought simulation using actual precipitation, temperature, and solar data from 1990. Total precipitation was 176 mm, and available soil water on January 1 was 50% of field capacity. Results, shown in Figure 6, compare the drought transpiration profile with the profile for 1984 which was wetter than normal. As expected, transpiration declined quickly as soil water was depleted. Early in the growing season (May 15), maximum potential g_h was $0.13 \text{ cm} * \text{s}^{-1}$, but 1 month later maximum g_h declined to 0.08

TABLE 3.

Model estimates (mm) of monthly potential evapotranspiration (*PET*), precipitation infiltration (*I*), soil water evaporation (*ES*), western juniper transpiration (*Ej*), and drainage below the root zone (*GS*). Infiltration amount includes snowmelt and/or rainfall. Soil water content decreased 44 mm between January and December 1984.

Variable	Jan	Feb	Mar	Apr	May	June	Jul	Aug	Sep	Oct	Nov	Dec	Total
PET	13	22	56	109	178	200	228	200	130	54	30	9	1229
I	18	11	89	28	17	37	15	47	3	45	34	6	350
ES	3	5	21	26	18	31	9	10	13	8	12	3	159
Ej	1	1	4	9	22	28	33	7	24	8	3	1	141
GS	11	13	21	39	10	0	0	0	0	0	0	0	94

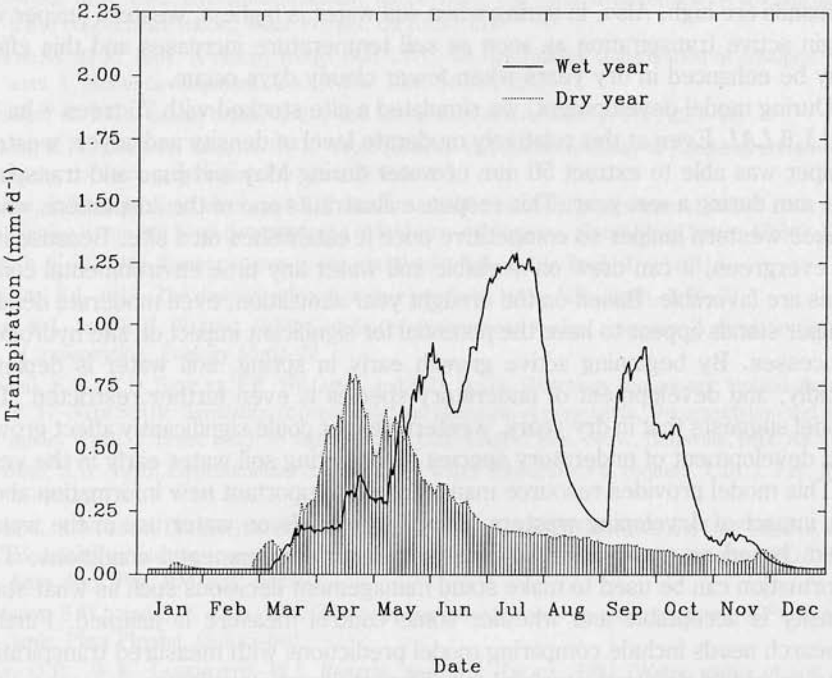

FIGURE 6. Modeled daily transpiration patterns for a western juniper stand during a drought year (1990), compared to 1984 data. Weather data for the drought year were obtained from weather records at the study location.

cm $* \mathrm{s}^{-1}$ because ψ_s in wettest layer had already decreased below the threshold of -0.25 MPa. Springtime air and soil temperature increased earlier in the drought year, and western juniper began active transpiration, resulting in early depletion of stored soil water. Others have reported that western juniper growth increases under mild wet winters and cool wet springs (Earle and Fritts 1986, Fritts and Xiangding 1986). Early increases in J have important implications for understory herbaceous species which are just initiating growth. Drought effects on the understory may be intensified by western juniper's early withdrawal of soil water. In addition, as western juniper stand density and/or *LAI* increases on a site, additional soil water will be withdrawn early in the year, altering western juniper seasonal g_l patterns, which may help explain reported decreases in production of associated species (Vaitkus and Eddleman 1986).

CONCLUSIONS

The conductance model, JUOC, successfully simulated seasonal leaf conductance patterns for western juniper. The model demonstrates how well western juniper is adapted to the environment of the northern Great Basin, where most of the annual precipitation is received as winter snow. The model closely matched observed springtime conductance, with g_h usually within 0.02 cm $* \mathrm{s}^{-1}$ of observed seasonal values. When soil conditions are optimal, the model demonstrates that juniper will maintain at least partially open stomates, even when evaporative demands are high. Also, in spring when soil water is highest, western juniper will begin active transpiration as soon as soil temperature increases and this effect may be enhanced in dry years when fewer cloudy days occur.

During model development, we simulated a site stocked with 75 trees $* \text{ha}^{-1}$, and 1.6 *LAI*. Even at this relatively moderate level of density and cover, western juniper was able to extract 50 mm of water during May and June and transpired 141 mm during a wet year. This response illustrates one of the adaptations which makes western juniper so competitive once it establishes on a site. Because it is an evergreen, it can draw on available soil water any time environmental conditions are favorable. Based on the drought year simulation, even moderate density juniper stands appear to have the potential for significant impact on site hydrologic processes. By beginning active growth early in spring, soil water is depleted rapidly, and development of understory species is even further restricted. The model suggests that in dry years, western juniper could significantly affect growth and development of understory species by depleting soil water early in the year.

This model provides resource managers with important new information about the impact of developing western juniper woodlands on water use in the watershed, based on stand density, basal area, and environmental conditions. This information can be used to make stand management decisions such as what stand density is acceptable and whether some control measure is justified. Further research needs include comparing model predictions with measured transpiration data on widely differing sites and for different climatic conditions.

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