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BIOMASS ACCUMULATION AND RADIATION USE EFFICIENCY OF HONEY MESQUITE AND EASTERN RED CEDAR

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Abstract—Rangeland models that simulate hydrology, soil erosion and nutrient balance can be used to select management systems which maximize profits for producers while they minimize adverse impacts on water quality. Values are needed for parameters that describe the growth of invading woody species in order to allow simulation of their competition with grasses. Three attributes useful for describing and quantifying plant growth are: the potential leaf area index (LAI) or ratio of leaf area divided by ground area; the light extinction coefficient (k) that is used to calculate the fraction of light intercepted by leaves, applying Beer's law; and the radiation-use efficiency (RUE) or amount of dry biomass produced per unit of intercepted light. Objectives in this study were to measure LAI, k, and RUE for eastern red cedar (*Juniperus virginiana* L.) and honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*), without competing plants, as a first step toward simulating their growth. Seedlings were planted in the field at Temple, Texas, USA in early 1992 and kept free of competition from herbaceous plants. During 1993, 1994 and 1995 data were collected on biomass, leaf area and intercepted photosynthetically active radiation (PAR) for individual trees. Both tree species showed exponential biomass increases. At the end of the 1995 growing season, mean LAI values were 1.16 for cedar and 1.25 for mesquite. Mean k values were 0.34 for mesquite and 0.37 for cedar. Radiation use efficiency for aboveground biomass was 1.60 ± 0.17 (mean ± standard deviation) g per MJ of intercepted PAR for cedar and 1.61 ± 0.26 for mesquite. The rapid growth in 1995 was accompanied by greater leaf area and thus greater summed intercepted PAR. These values are critical for quantifying growth of these two species. © 1998 Elsevier Science Ltd. All rights reserved

Keywords—Light interception; leaf area index; Beer's law.

1. INTRODUCTION

Robust simulation models are useful decision making tools in dealing with the economic risks of rangeland production and with water quality issues arising from rangeland management practices. Such models simulating hydrology, soil erosion and the nutrient balance can be used to make decisions on managing resources, maximizing returns to producers and minimizing impacts on water quality. Models can help in decisions for optimizing grazing strategies, forage selection and fertilizer application rates in a wide range of latitudes, soils and rainfall zones. Inclusion of competing woody species in rangeland models will increase such models' usefulness and versatility.

A description of plant growth commonly used for modeling[1–4] involves leaf area development, light interception using Beer's law[5] and conversion of intercepted light into biomass assuming a conservative radiation use efficiency (RUE)[6]. The equation using Beer's law to calculate the fraction of intercepted light (FI) is:

$$\mathrm{FI} = 1 - \exp(-k^*\mathrm{LAI})$$

where k is the light extinction coefficient. While values for k, LAI, and RUE have been reported for some woody species, they have yet to be reported for two species commonly competing with grasses: eastern red cedar and honey mesquite.

Reported one-sided LAIs vary widely for deciduous trees, with eucalyptus having some of the smallest values and hybrid poplar having some of the largest. In an excellent literature review, Anderson[7] found values of 2.6–8.9 for several deciduous tree species. Anderson measured eucalyptus LAI values between 0.8 and 2.0 in an arid area of

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Australia. Apple (*Malus domestica* Borkh.) LAI ranged from 1.5 to 2.6[8] and oak (*Quercus*) values were 4–7[9–11]. Intensively managed poplar (*Populus*) LAIs were 7–9[12–15].

Conifers show an even greater range of one-sided, projected LAIs, ranging from 0.8 to 10.6[7]. LAIs were 2–3 for slash pine (*Pinus elliotti*)[16] and three *Pinus* species in Scotland[10]. Reported LAIs were 3–4 for lodgepole pine (*Pinus contorta* Douglas ex Loudon)[17], 6–7 for red pine (*Pinus resinosa* Ait.) and white pine (*P. strobus* L.)[11], and 4–11 for Sitka spruce (*Picea sitchensis* (Bong.) Carr.)[18,19].

Light extinction coefficients (k) of trees are between 0.5 and 0.6 for a diverse group of species. Linder[20] used a k value of 0.5 for eucalyptus (*Eucalyptus globulus*). Values for k ranged from 0.50 to 0.58 for four fast growing tropical trees[21]. Mean values were 0.51 for three *Pinus* species in Scotland[10], 0.52 for willow (*Salix viminalis*) and poplar (*Populus trichocarpa*)[22], 0.53 for northern red oak (*Quercus rubra* L.)[11], and 0.55 for slash pine (*Pinus eliotti*)[16]. Johnson and Lakso[23] reported values of 0.55–0.60 for apple trees (*Malus domestica* Borkh.) while hybrid poplar (*Populus trichocarpa* X *Populus deltoides*) had a mean of 0.56[15].

Tree aboveground RUE values are generally between 1.3 and 1.9 g MJ^{-1} intercepted PAR, below common crop means of 2.2–3.5[24]. Mean RUE values were 1.5 for poplar in Pennsylvania and Wisconsin, USA[14] and balsam fir (*Abies balsamea* (L.) Mill)[25]. RUE was 1.65 for loblolly pine (*Pinus taeda* L.)[26], 1.3–1.7 for Monterey pine (*Pinus radiata*)[20,27], 1.8 for white birch (*Betula papyrifera* Marsh)[25], and 1.9 for Sitka spruce[19]. For eucalyptus, Linder[20] reported a low value of 0.9 while Landsberg and Hingston[28] found a value of 2.2 in the absence of drought stress. Four fast-growing tropical tress, including *Eucalyptus camaldulensis*, had maximum values of 1.7–2.7[21]. Intensively managed willow and poplar in Scotland had values of 2.4–3.4[22].

These studies provided reasonable values for these variables for woody species. To simulate growth of cedar and mesquite, similar measurements are needed. The objective in this study was to measure these variables for eastern red cedar and honey mesquite in the field in a deep soil, with adequate nutrients, to allow better quantification of their potential growth.

2. MATERIALS AND METHODS

This experiment was conducted in the field, rather than a glasshouse, to avoid altered light quality, restricted rooting volume in pots, and unrepresentative high relative humidity. Plots were on a Houston Black clay (fine montmorillonitic, thermic Udic Pellusterts) at the Grassland, Soil and Water Research Center near Temple, Texas, USA. Seedlings were planted 1 m apart in 0.69 m rows. Trees were removed during the 3 years when trees were measured, to avoid interplant competition. Each replication was seven rows (5 m) wide, with lengths of 75 m for eastern red cedar and 37 m for honey mesquite. There were four replications of each species.

Cedar seedlings about 0.15 m tall were planted on 19–21 February 1992. They were from the Oklahoma Department of Agriculture (Oklahoma City, Oklahoma, USA). Mesquite seedlings about 0.08 m tall were planted on 20–24 March 1992. These were germinated from seeds collected at the Grassland, Soil and Water Research Center.

Intensive hand hoeing each year, combined with chemical weed control, ensured that competition with herbaceous plants did not restrict tree growth. In 1992, plots were sprayed with 4.43 kg ha^{-1} active ingredient of Pendulum (pendimethalin, `(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzenamine) and 526 g a.i. ha^{-1} of Vantage (2-(1-(ethoxyimino)butyl)-5(2-(ethylthio)propyl)-3-hydroxy-2-cyclohexen-1-one) on 18 August. In 1993, weeds were hand sprayed with Roundup (isopropylamine salt of glyphosate) at 2% a.i. on 15 and 16 April and sprayed with 526 g a.i. ha^{-1} of Vantage on 21 April. In 1995, weeds were sprayed with 2% a.i. Roundup on 17 March.

Fertilizer was applied in early 1994 and 1995 to avoid nutrient stress limitations to growth. Fertilizer consisted of 112 kg N ha^{-1} and 27 kg P ha^{-1} as urea (46-0-0) and 18-46-0 applied on 6 March, 1994 and 100 kg N ha^{-1} and 45 kg P ha^{-1} as 33-0-0 and 0-46-0 applied on 24 February, 1995.

Due to the large variability among trees, biomass increase and summed intercepted PAR were calculated for individual trees. Initial biomass of a group of trees was calculated from their stem volumes on the first harvest date each year. As these trees were harvested during the year, their above-ground dry weight change was calculated. Radiation use efficiency was calculated for each tree as the change in above-ground biomass divided by its summed intercepted PAR during the same interval. Each spring in 1993, 1994 and 1995, 18 trees per replication were labeled for sampling. Each tree's height, stem diameters at the base and at half total height, and number of main stems were measured. A stem diameter was the mean of two orthogonal measurements. Stem volume was calculated as the lower part of a cone (a frustum of a right circular cone) for the bottom half of a stem and as a right circular cone for the top half. Three of these trees in each replication were immediately harvested. Above-ground dry biomass was regressed on stem volume for the 12 trees initially harvested each year. These equations were used to estimate initial biomass of the remaining 15 trees in each replication. Similar measurements have been applied to woody species to estimate biomass or leaf area[29–35].

In 1993, initial mesquite measurements of replications 1, 2, and 3 were taken on 20 May. Initial measurements for replication 4 of mesquite and for all replications of cedar were taken on 25 May. Destructive mesquite harvests were made on 26 May (replications 1 and 2), 1 June (replications 3 and 4), 2 July, 20 July, and 30 September. Destructive harvests of cedar were made on 3 June, 2 July, 20 July, and 30 September. Three cedar trees per replication were sampled to get root biomass on 3 June and on 18 August. For mesquite, root biomass was measured on the 12 trees of the 26 May–1 June harvest and on three trees harvested on 18 August. Fraction intercepted PAR (FIPAR) of mesquite was measured on 25–27 May, 30 June, 2 July, 20 July, and 30 September. FIPAR of cedar was measured on 2 June, 8–9 June, 20 July, and 30 September.

In 1994, newly labeled cedar trees were measured on 22 March for height and diameter. On 26 April, height and diameter of mesquite were measured for all replications. Mesquite was harvested on 20 May, 31 May, 22–24 June, and 20 July. Cedar was harvested on 22 March, 20 June, and 19 July. FIPAR of cedar was measured on 22 March, 17–20 June, and 18 July. FIPAR of mesquite was measured on 26 April, 18–24 May, and 20 July.

In 1995, initial measurements were made for both species on 20 April. Mesquite harvests were on 26 April, 23 May, 20 June, 18 July, and 13–15 September. Cedar harvests were 25 April, 23 May, 19 June, 20 July, and 12 September. Cedar FIPAR was measured on 25 April, 22 May, 19 June, 19–20 July, and 12 September. Mesquite FIPAR was measured on 25 and 27 April, 23–26 May, 20 June, 18 July, and 12 September.

Measurements of FIPAR were taken between 11:00 and 13:00. Multiple readings at ground level were taken with an 0.8 m long, linear sensor which measured PAR (Decagon Inc., Washington, USA). Readings were made over ground area sufficient to capture the tree shadow, with dimensions of this sampled area recorded. Measurements of PAR were also taken above the trees just before and after each series of measurements underneath, to estimate the mean fraction of PAR intercepted (FIPAR). Linear interpolations between dates of FIPAR measurements were used to calculate daily estimates for each tree. Thus, for each tree, the change in dry weight was divided by the PAR intercepted by leaves to get the radiation use efficiency (RUE). Mesquite PAR interception was corrected by measuring light interception before and after leaf removal for each harvested tree. The factor to correct the fraction intercepted on a date was the mean of $1 - \text{FIPAR}$ (without leaves)/FIPAR (with leaves). Three randomly selected trees per replication were harvested. Trees were dried to constant weight at 70°C in a forced air drier, and leaves and stems were weighed.

Leaf area per tree was calculated for mesquite trees harvested in 1995 and for cedar trees harvested in all three years. The area of a fresh leaf subsample of each mesquite tree harvested in 1995 was measured with an LI3100 leaf area meter (LiCor Inc., Nebraska, USA). Total leaf area of each of these trees was calculated using the fresh weight of this subsample and the fresh weight of all the leaves for each tree. The projected one-sided leaf area was calculated for 18 cedar trees harvested on 3 June 1993 and 15 trees harvested on 24 April 1996. Branches were separated from the main stem and weighed. The leaf area of a subsample of these branches, of known fresh weight, was measured. Leaf area was the product of the subsample leaf area and the ratio of total branch plus leaf fresh weight divided by subsample branch plus leaf fresh weight. Leaf area of the 33 measured cedar trees was regressed on total

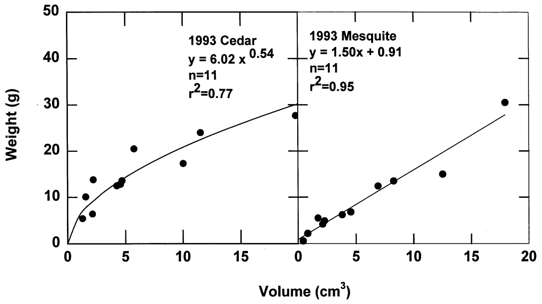

Fig. 1. Initial biomass each spring as a function of stem volume in 1993 for eastern red cedar and honey mesquite. Each data point represents one tree.

above-ground dry weight. Two equations, one for trees less than 400 g and one for those greater than 400 g, were then used to calculate leaf area of all cedar trees harvested in 1993, 1994, and 1995.

3. RESULTS

Equations for dry weight as a function of stem volume at the first harvest date each year were used to estimate the dry weight of the remaining trees at first harvest. Thus, dry weight changes during the season were calculated from the differences, using the dry weight of trees as they were harvested later in each year. These equations for dry weight as a function of stem volume were sometimes lines and sometimes power functions. The data for cedar were fitted with power functions in 1993 and 1994 and with a linear function in 1995 (Fig. 1 and Table 1). In 1993, one outlier was not included when the function was fitted.

The range of initial cedar biomass changed greatly over the years. Weights were less than 35 g in 1993. In 1994, weights were as large as 190 g and in 1995 were as large as 1350 g. For mesquite, the functions were power functions the last two years and a linear function in 1993. One outlier was deleted before fitting functions in 1993 and 1994. Again, initial dry weights increased greatly over the years. Values were less than 50 g in 1993, as large as 157 g in 1994, and greater than 1240 g in 1995.

Table 1. Regression equations for initial biomass each spring as a function of stem volume for eastern red cedar and honey mesquite

	Cedar			Mesquite		
Year	Equation	*n*	r^2	Equation	*n*	r^2
1993	$y = 6.0\,x^{0.54}$	11	0.77	$y = 1.5\,x + 0.91$	11	0.95
1994	$y = 4.75\,x^{0.84}$	12	0.94	$y = 3.4\,x^{0.44}$	11	0.92
1995	$y = 1.94\,x + 128$	12	0.85	$y = 1.98\,x^{0.80}$	12	0.86

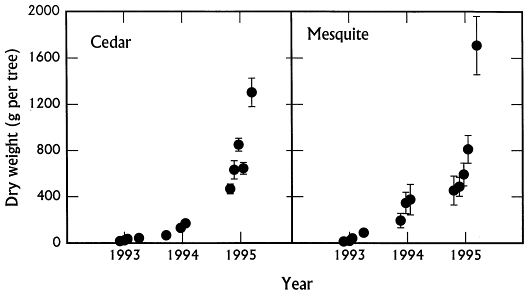

Fig. 2. Mean above-ground tree biomass at different harvest dates for eastern red cedar and honey mesquite. Error bars are the standard errors for the measurement date. Error bars not shown are smaller than the symbol for the mean.

Both tree species showed an exponential dry matter increase over time (Fig. 2). The growth rate accelerated each year after 1993. Growth was slow in 1993 and 1994 in spite of the absence of competing grasses. The final mass per tree was greater for mesquite than for cedar.

While RUE tended to decrease with later sampling, values were similar across harvest dates if two outliers were omitted for both species (Table 2). The first harvest in 1995 and the last in 1993 were noticeably different from the other values. Without these two harvests, RUE values were 1.60 ± 0.17 g per MJ intercepted PAR (mean ± standard deviation) for cedar and 1.61 ± 0.26 for mesquite. The rapid growth in 1995 was accompanied by greater leaf area and thus greater summed intercepted PAR.

Table 2. Radiation use efficiency with calculated from the initial harvest in the spring until different harvest dates for honey mesquite and eastern red cedar

	Mesquite	Cedar
	g per MJ intercepted PAR	
Day of Year		
1993		
183	1.41	1.86
201	1.36	1.50
273	0.93	0.54
1994		
173(168)*	1.82	1.38
201(200)*	1.27	1.37
1995		
144(143)*	2.37	3.49
171(170)*	1.94	2.00
199(200)*	1.93	1.79
257(254)*	1.56	1.28

*Day number in parenthesis is for cedar when different from mesquite.

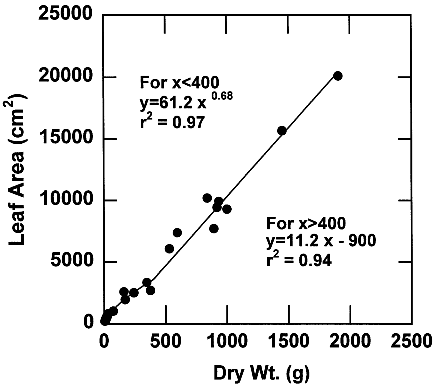

Fig. 3. Leaf area as a function of above-ground biomass for eastern red cedar.

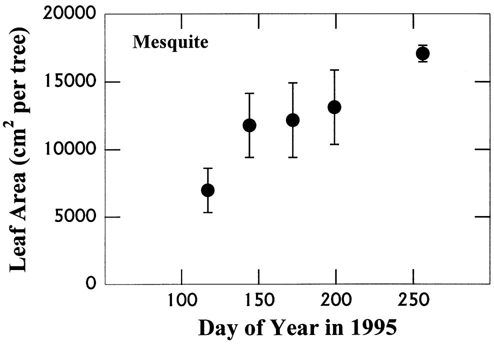

Fig. 5. Leaf area per tree on different harvest dates for honey mesquite. Error bars are the standard errors for the measurement date. Error bars not shown are smaller than the symbol for the mean.

Cedar leaf area as a function of above-ground dry weight was described with two functions (Fig. 3). Trees less than 400 g were described with a power function. To make the two functions continuous, the linear regression for trees greater than 400 g was forced through the *x*, *y* value predicted for the first equation at *X* equals 400 g.

Cedar leaf area increased slowly through 1993 and 1994, with a rapid increase in 1995, similar to the increase in biomass (Fig. 4). Assuming that every second tree was removed within the rows (1.37 m^2 ground area per tree), the final cedar LAI was 1.16. Mesquite leaf area per tree in 1995 was similar to the area for cedar on the first harvest date and was greater than the area for cedar at later dates (Fig. 5). Assuming the same plant spacing, mesquite LAI reached 1.25.

Extinction coefficients for Beer's law were calculated, assuming one tree per 10 m^2 ground area. The mean *k* value for mesquite (±SD) was 0.34 ± 0.04 over four dates during the period April–July, 1995. For cedar, *k* was 0.37 ± 0.08 over seven dates during the three years of the measurements. Using the measured light interception and assuming zero interception in the area not occupied by the tree, mesquite *k* at one tree per 10 m^2 was within 2% of *k* for spacing of 2–100 m^2 per tree. Likewise cedar *k* at this spacing was within 8% of *k* for spacing of 2–100 m^2 per tree each year. Thus, these *k* values should be reasonable over a wide range of spacing.

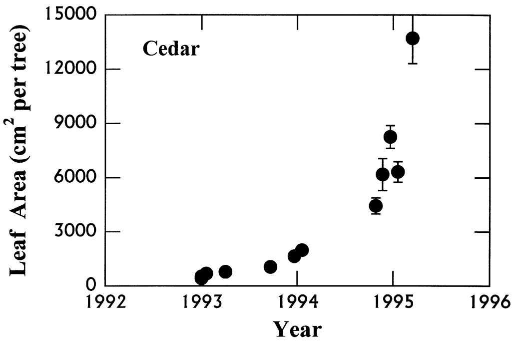

Fig. 4. Leaf area per tree on different harvest dates for eastern red cedar. Error bars are the standard errors for the measurement date. Error bars not shown are smaller than the symbol for the mean.

Mesquite had a greater fraction of its total biomass in roots than did cedar in 1993. Mesquite trees harvested 26 May or 1 June had shoot:total biomass of 0.51 with a CV of 15%. On 3 June, cedar shoot:total biomass was 0.65 with a CV of 7%. Mesquite shoot:total biomass on 18 August was 0.62 and CV was 11% across replication means. On this date, cedar shoot:total biomass mean was 0.85 with a CV of 4%.

4. DISCUSSION

This experiment covered an interval critical for the establishment of these trees in grasslands. By the end of 1995, mesquite trees were, on average, 1.8 m tall and cedars were 1.4 m. Such tree canopies would be above the leaves of competing grasses.

The results with LAI and RUE presented here are similar to those in the literature for other trees, as discussed above. My LAI values are similar to the 0.8–2.0 reported by Anderson[7] for eucalyptus in an arid area of Australia. Such low LAI values are characteristic of environments often limited by drought. Grier and Running[36] found a strong relationship between tree LAI and available water for sites in Oregon. Their results indicated that when soil water was limiting, the disadvantage of reduced light interception with lower leaf area was more than compensated for by reduced transpiration. My RUE values are similar to the mean of 1.68 for several of the tree species discussed above. Causes of large RUE with early harvests and low values with late should be investigated in future experiments. In early 1995, trees may have relied largely on previously-stored assimilate for growth. The small RUEs for the last harvest in 1993 may have been due to late season stress reducing growth. Perhaps production of the root systems during these years was restricting top growth. Leaf area index can be simulated with 1.16 for cedar and 1.25 for mesquite at high plant densities by the end of the fourth growing season. The pattern of simulated cedar LAI over time should follow a power curve for the first four years. For mesquite, the LAI should rapidly increase in the early part of the growing season, but show some growth throughout the season.

The data suggest that a value of 0.35 for light extinction coefficient, with a RUE of 1.6 may be used to simulate the above-ground biomass of both species during most of the periods of active growth. Applying the shoot:-total biomass ratios for 1993, factors were estimated to correct the RUE for the shoot in order to calculate the RUE for the total plant, including roots. These factors were 1.55 for mesquite and 0.94 for cedar. The value less than one for cedar implies that there was some translocation out of the roots during the growing season. Total plant RUE was thus 2.50 for mesquite and 1.50 for cedar. To achieve realistic simulations of above-ground biomass, differential partitioning to roots between the two species will be needed.

The light interception for cedar and mesquite was less efficient than that for trees described in the literature. This can be explained more easily for cedar than for mesquite. Clumping of leaf area and mutual shading within a cedar tree would be expected to cause a lower k value. Substantially less PAR is intercepted when k equals 0.35 than when k equals 0.55. At LAI equal to 1.0, FIPAR for our trees is only 70% of what it is for k equal to 0.55. This percentage is 80% for LAI equal to 3.0 and 88% for LAI equal to 5.0.

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