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Leaf area index and normalized difference vegetation index as predictors of canopy characteristics and light interception by riparian species on the Lower Colorado River

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Abstract

Leaf area index (LAI) and normalized difference vegetation index (NDVI) were compared for riparian species along a 350 km stretch of the Lower Colorado River in the United States and Mexico. The species included two native trees, cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*), and two salt-tolerant shrubs, saltcedar (*Tamarix ramosissima*) and arrowweed (*Pluchia sericea*), exhibiting large differences in leaf type and canopy architecture. LAI was measured with a Licor 2000 plant canopy analyzer calibrated against biomass measurements of LAI, whereas NDVI was measured by low-level aerial photography using a DyCam digital camera with Red (R)–Blue (B)–near infrared (NIR) bands. In addition, reflectance spectra were measured for leaf samples collected from plants in the field. Leaf samples of all species had similar reflectance spectra in the visible (VIS) and NIR, hence similar NDVI values, ranging from 0.62 to 0.72 ($P > 0.05$). LAI values of field plants varied over a relatively narrow range, with mean values of 3.50, 3.28, 2.81 and 3.69 for cottonwood, willow, saltcedar and arrowweed, respectively. However, field plants showed distinct species differences in NDVI, with the following mean values: cottonwood (0.686), willow (0.600), saltcedar (0.473) and arrowweed (0.254) (all significantly different at $P < 0.05$). Differences in NDVI among field plants could be explained by differences in the light extinction coefficient, *k*, for plant canopies, according to the formula: $\text{fIRs} = (1 - e^{-k\text{LAI}})$, where fIRs is the fraction of incident light intercepted by the canopy. At one extreme, cottonwood had broad leaves that faced the sun, and a calculated *k* of 1.25, whereas at the other extreme, arrowweed had linear leaves that were near to vertical, and had a *k* of 0.15. Ecophysiological implications of the differences among the species are discussed.

Keywords: *Tamarix ramosissima*; *Populus fremontii*; *Salix gooddingii*; *Pluchia sericea*; LAI; NDVI; Riparian plant cover; Remote sensing; Colorado River; Mexico

1. Introduction

Western US riparian zones have undergone remarkable changes over the past century, due to disruption of the natural flow regime and the spread of invasive species (Stromberg, 2001). On the Lower Colorado River, the native trees, cottonwood (*Populus*

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fremontii) and willow (*Salix gooddingii*), have largely been replaced by an introduced salt-tolerant shrub, saltcedar (*Tamarix ramosissima*), growing in association with a native salt-tolerant shrub, arrowweed (*Pluchea sericea*) (Busch and Smith, 1995; Nagler et al., 2001; Zamora-Arroyo et al., 2001). Loss of native trees has degraded the habitat value of the riparian zone for wildlife, and programs to restore native trees are underway (Stromberg, 2001). At the same time, riparian vegetation is the second largest user of western river water, after irrigated agriculture (DiTomaso, 1998). As much as 50% of surface flows can be consumed by riparian plants along the major western rivers (Dahm et al., 2002). Careful monitoring of the vigor and evapotranspiration (ET) of native and introduced species is required to implement species recovery programs and manage riparian water supplies (Congalton et al., 1998; Goodrich et al., 2000).

Recently, Bowen ratio and eddy covariance flux towers have been established on some western rivers, to monitor ET and carbon exchange for representative riparian plant associations (Cleverly et al., 2002; Dahm et al., 2002; Devitt et al., 1998; Goodrich et al., 2000). These provide accurate, real time data on riparian physiological processes for the first time. Our objective was to develop models of canopy structure and radiative properties for the main plant types on the Lower Colorado River, which can ultimately be used to scale flux tower data over large river stretches. Due to the patchy nature of the riparian zone, a scaling method that works over mixed scenes containing multiple species and areas of bare soil will be needed. We used ground measurements and low-level aerial photography to measure leaf area index (LAI) and normalized difference vegetation index (NDVI), respectively, for natural stands of cottonwood, willow, saltcedar and arrowweed growing along a 350 km stretch of the Lower Colorado River in the US and Mexico. From these, and ancillary, measurements we were able to describe canopy architecture and the canopy radiation balance for each species and mixed scenes along the river.

The form in which LAI appears in models of ET and photosynthesis is as a predictor of the incident light intercepted by a canopy (IRs) (Inoue and Moran, 1997; Leopold, 1975; Pearcy et al., 1991; Nouvellon et al., 2000; Nagler et al., 2003; Monteith and Unsworth, 1990):

$$\mathrm{IRs} = R_\mathrm{s}(1 - \mathrm{e}^{-k\mathrm{LAI}}) \quad (1)$$

where R_s is the incident solar radiation and k the light extinction coefficient.

Canopy radiative transfer processes are diagrammed in Fig. 1. The fraction of intercepted radiation (fIRs) is IRs/R_s. LAI is defined as the one-sided leaf area projected horizontally on the ground (Asner et al., 2003). The coefficient k is related to leaf spectral properties and leaf angles in the canopy (Campbell, 1986; Norman and Campbell, 1991; Nouvellon et al., 2000). Canopies with linear, vertical leaves have k values of 0.3 or less, whereas canopies with flat, horizontal leaves have k values of 1.0 or more (Campbell, 1986; Leopold, 1975). The range of k among plants may span two orders of magnitude (0.1–10) (Campbell, 1986). Plants with higher k values intercept more light per unit leaf area than plants with lower k values.

LAI can be estimated by biomass sampling or optical methods (Asner et al., 2003; White et al., 2000). Biomass sampling is labor intensive, especially for shrubs and trees, but optical methods need to be validated by biomass sampling for each plant type, as typical canopies violate many of the assumptions built into the optical methods (White et al., 2000). Optical methods include the Licor LAI-2000, used in this study, and the Ceptometer quantum line sensor, a set of photosensors that measures incident and reflected light above and below the canopy. The term k is difficult to measure directly due to the wide range of leaf angles in a canopy (Norman and Campbell, 1986; Nouvellon et al., 2000). The LAI-2000 provides estimates of leaf angle that can be used to estimate k, but these are calculated by a non-linear equation that has very low resolution for leaf angles between 0° and 35° and 70–90° (0° leaf angle is horizontal and 90° is vertical; Licor, 1992). Two of the four species in this study had leaf angles in the low-resolution ranges (see Section 3). If LAI is known, k can also be determined by measuring light transmission through the canopy from Eq. (1), but this requires many measurements due to irregularities in most canopies (White et al., 2000). Hence, determining canopy radiation characteristics from ground measurements alone is challenging.

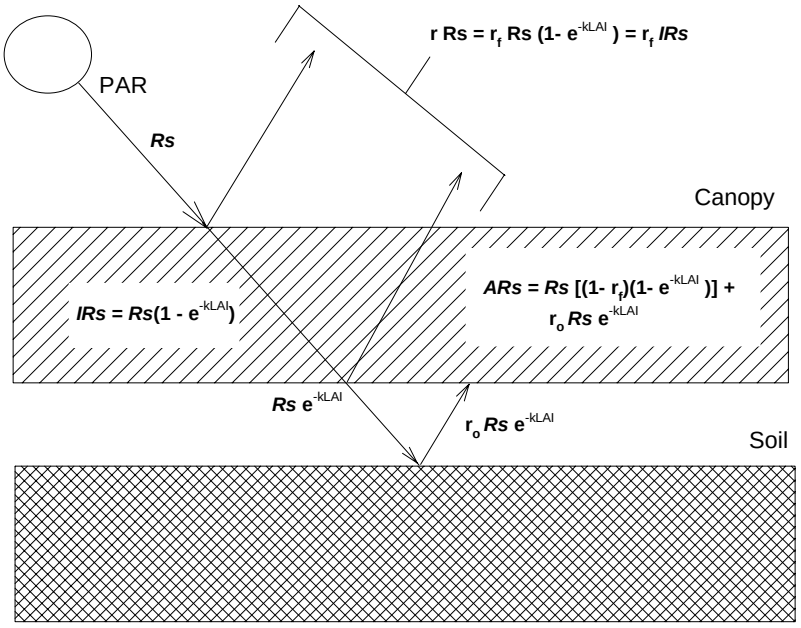

Fig. 1. Diagram of the radiation transfer processes for an idealized plant canopy. R_s is the incident photosynthetically active radiation (PAR); $R_s\,e^{-k\mathrm{LAI}}$ the light transmitted through the canopy; IRs the light intercepted by the canopy; $r_o R_s\,e^{-k\mathrm{LAI}}$ the fraction of transmitted light reflected from the ground; ARs the light absorbed by the canopy; r_f the fraction of light reflected from the canopy; rRs the amount of light reflected from the canopy.

The radiation balance of a canopy can be determined more directly by remotely sensed spectral data, because the spectral measurements incorporate such factors as leaf spectral properties, canopy architecture and viewing geometry that influence light interception (Colwell, 1974; Inoue and Moran, 1997). For many applications, it can be assumed that the fractional absorptance of R_s (fARs) can be expressed as a linear function of a spectral vegetation index such as NDVI, and that fIRs α fARs α NDVI (Inoue and Moran, 1997; Monteith and Unsworth, 1990; Goward and Huemmrich, 1992). This has been shown both experimentally (e.g. Gao et al., 2000; Inoue, 2003) and more formally by showing that the spectral ratio of reflected near infrared (NIR) and red light from canopies (ρNIR/ρRed) is a unique (approximately linear) function of the amount of radiation *intercepted* and therefore *absorbed* by a canopy (Monteith and Unsworth, 1990). While NDVI can provide an integrated estimate of the canopy radiation balance, it cannot provide separate estimates of LAI or *k* (Monteith and Unsworth, 1990). LAI is needed in models of ET and photosynthesis that incorporate leaf area or leaf biomass into their calculations. The coefficient *k* is needed to model how light interception varies with changes in LAI for different species according to Eq. (1), an important part of the light harvesting strategy of a plant species (Monteith and Unsworth, 1990).

In our study, we used ground measurements of NDVI values for pure leaf samples and remotely sensed NDVI values for natural stands of each plant type to estimate fIRs and fARs for each plant type. We also used remotely sensed NDVI values to estimate fractional vegetation cover for mixed scenes along the river. The light extinction coefficient, *k*, for each species was then calculated from Eq. (1) using LAI values determined on the ground by LAI-2000 measurements validated by biomass sampling. These species vary markedly in their light-interception strategies. fIRs and fARs were higher for the native trees than for the saltcedar bushes or arrowweed groundcover and in general, fractional vegetation cover and fARs were low for mixed scenes along the river.

2. Materials and methods

2.1. Study sites

Six sites along the lower Colorado River in the US and Mexico were selected for ground measurement of LAI and eight sites were flown over with a light aircraft for determination of NDVI by aerial photography with a three-band (Red–Blue–NIR wavelength region) digital camera (Nagler et al., 2001). Reflectance spectra of pure leaf samples were made at three sites. The sites extended from the delta of the Colorado River in Mexico to Topock Marsh at the Havasu National Wildlife Refuge near Needles, California, covering approximately 350 km of river (Table 1). Except for Topock Marsh, where LAI was not measured, the LAI and NDVI sites covered the same river stretches. However, plants were not paired for measurement of both LAI and NDVI at any site. Measurements were made over a 4-year period during late spring or summer. Not all plant types were measured at each site.

2.2. Measurement of LAI with the Licor, LAI-2000

The Licor LAI-2000 plant canopy analyzer (Lincoln, NE) was used to collect LAI data according to methods in their manual (Licor, 1992). The instrument measures how much light is attenuated at several angles as it passes through the canopy, then, with internal software, it calculates LAI according to Beers law (Monteith and Unsworth, 1990). Light is gathered by a hemispherical lens that projects intercepted radiation onto five detectors arranged in concentric rings, corresponding to angles ranging 90–73, 74–62, 58–47, 43–32 and 29–16° from the horizontal. Among the assumptions built into the calculations of LAI by the LAI-2000 software is that the canopy forms a uniform cover in all directions over the sensor with randomly distributed foliage elements. Based on this geometry, the LAI-2000 calculates LAI and foliage orientation by the amount of light reaching the sensors and the relative path length of light through the canopy at all five lens angles (see Licor (1992) for a discussion of the theoretical details).

The LAI-2000 has features that allow data to be collected under non-ideal canopies. The lens can be covered with a view cap so that only a portion of the hemisphere is measured. In calculating LAI, the shallower view angles can be dropped if they collected light from open sky rather than canopy. For individual trees, which seriously violate the assumption of a continuous overhead canopy if they are taller than they are wide, LAI can be calculated by entering the tree dimensions into the calculation. The LAI-2000 software

Table 1
Location of sampling sites for LAI and DyCam-NDVI measurements on the Lower Colorado River

Site no.	Location	Description	Sample date
LAI sites			
1	32°720′N, 114°718′W	Morelos Dam, Arizona	September 19, 2002
2	32°514′N, 114°875′W to 32°358′N, 115°155′W	Riparian zone in Mexico	June 15, 1999
3	32°681′N, 114°328′W	Gila River east of the junction with the Colorado River, near Wellton, AZ	June 7, 2000
4	32°706′N, 114°726′W	Mittry Lake, Arizona	September 19, 2002
5	32°228′N, 115°083′W	Along the riparian zone in Mexico	June 6–7, 2001
6	32°702′N, 114°567′W	Junction of the Gila and Colorado River, Arizona	June 5–8, 2000
NDVI sites			
1	32°730′N, 114°613′W	North of Gila and Colorado junction	April 26, 2001
2	32°683′N, 114°758′W	Gila and Colorado confluence	April 26, 2001
3	32°830′N, 114°417′W	Near Laguna Dam	April 26, 2001
4	32°728′N, 114°608′W	Mittry Lake, Arizona	April 26, 2001
5	32°372′N, 114°963′W	Riparian corridor, Mexico	April 25, 2001
6	32°245′N, 115°001′W	Riparian corridor, Mexico	April 25, 2001
7	32°712′N, 114°138′W	Gila River east of junction with Colorado River, near Wellton, AZ	April 26, 2001
8	34°765′N, 114°513′W	Topock Marsh	May 18, 2002

then calculates actual path lengths through the canopy based on canopy dimensions rather than by assuming a continuous overhead canopy.

For measurements of LAI in this study, a 90° view cap was placed over the lens, restricting the view to a fourth of a hemisphere. The sensor was placed near the bottom of the canopy and was moved to five different spots within 1 m^2 at the base of the canopy to sample the variability within the canopy. At each location, approximately 10–20 individual plants, or plant stands, of each riparian species encountered were measured. Plants were representative of the range of sizes and canopy characteristics present at each site. Hence, both individual plants and closed canopies of plants were measured. For saltcedar and arrowweed, the uniform canopy assumption was generally met, and uncorrected LAI values were reported. Cottonwood and willow trees were much taller than they were wide, so LAI estimates were calculated based on tree dimensions estimated in the field. Furthermore, we excluded the two shallowest lens angles from the calculation of LAI, as these path lengths did not always pass through the tree canopy.

2.3. Comparison of LAI by LAI-2000 and by biomass sampling

Saltcedar, willow and cottonwood were measured at LAI site 4 (Mittry Lake) while arrowweed comparisons were made on a stand of plants growing in Tucson, AZ. Destructive sampling of whole trees or shrubs was not practical, so methods for estimating LAI from smaller-scale biomass samples were developed, using allometric relationships to scale to whole plants (Norman and Campbell, 1991). Different methods were used for each species, as dictated by their different growth habits.

Saltcedar stands have numerous, branched stems terminating in bunches of needle-like foliage elements. The stands can be treated as continuous canopies of more or less constant leaf density. LAI was determined by LAI-2000 at different spots within a canopy, then the foliage elements above the LAI-2000 sensor were harvested to determine LAI by biomass sampling. Eight measurements were taken in a dense, continuous stand, 5–6 m in height. The LAI sensor was placed within the canopy, LAI recorded, and then all the green foliage in a column, within a framed, cross-sectional area of 0.25 m^2 over the sensor, was harvested. Although the sensor view angle covers an area of canopy larger than that of the biomass sample, it was assumed that the sample over the sensor was representative of the canopy within the sensor field of view.

Arrowweed grows in dense thickets of individual, vertical stems arising from underground rhizomes. LAI was determined in a single stand of arrowweed with a well defined set of originating stems. LAI was measured at 20 locations within the canopy with the LAI-2000. Then all stems supporting the canopy were counted (104) and the basal diameter of each stem was measured with a micrometer to an accuracy of 0.5 mm. The projected area of the canopy on the ground (3.28 m^2) was calculated based on measurements of widest and narrowest canopy widths. Then five main stems were selected at random for determination of leaf area. The leaf area of five stems was projected to the whole stand by the ratio of cross-sectional area of sampled stems to total stems, and LAI was calculated by dividing total leaf area by canopy area.

Cottonwood and willow biomass LAI was estimated by relating the basal area of the tree trunk to the cross-sectional area of the branches, then determining the leaf area supported by a subsample of the branches. Cottonwood and willow trees were sampled in a mixed-stand plantation, which had been established at this site six years previously. Trees were about 7 m tall, 2–3 m in canopy width, and covered about 70% of the ground area. LAI-2000 measurements were made on 8–10 trees for each species. Biomass samples were taken from the plantation by collecting two, leaf-bearing side branches from each of the sampled trees, after recording LAI-2000 values. A range of branch sizes (0.1–2 cm in diameter) was collected, representing the range of variability of leaf-bearing branches on the trees. To extrapolate to whole trees, three other measurements were made on each tree: (i) diameter of the main trunk or trunks near ground level (some trees split into two or more main branches at ground level), (ii) the height of the tree, and (iii) the width of the canopy in the north–south and east–west directions. The trunk, branch and canopy width measurements were made directly, but tree height was estimated by an observer standing at least three tree heights from the tree and visually projecting a 1.5 m

measuring stick, held at the bottom of the tree, to the top of the tree.

To project the leaf area of the branch samples to leaf area of whole cottonwood and willow trees, the relationship between branch cross-sectional area and leaf area was determined from the sampled branches. Then, the relationship between main stem or trunk cross-sectional area and branch area was determined by measuring the diameter of trunks and all secondary branches arising from the trunks for selected trees. From these two regression equations tree leaf area was extrapolated from the leaf area of sampled branches.

For all species, leaves were sampled and dried, and the dry weight:leaf area relationship was used to calculate leaf area. This relationship was determined by placing leaves randomly, in a single layer on a 21 cm × 28 cm sheet of graph paper with 2700 square grids. The number of grid-intersections covered by leaves was used as a measure of the fraction of paper covered; the leaf sample was then dried and the leaf:weight relationship ($g\,m^{-2}$) determined. The accuracy of this method (from the binomial distribution) is within 2% when half the intersections are covered by leaf material.

2.4. Collection of NDVI data by aerial photography

NDVI was calculated from the reflectance (ρ) values as follows:

$$\mathrm{NDVI} = \frac{\rho\mathrm{NIR} - \rho\mathrm{Red}}{\rho\mathrm{NIR} + \rho\mathrm{Red}} \quad (2)$$

Data were collected as described in Nagler et al. (2001). A Cessna 185, equipped with a belly mounted sensor array was flown over the target areas at 150–1000 m above ground level (AGL). For sites 1–7, the DyCam Modular 4 Agricultural Digital Camera (DyCam-ADC) (Woodland Hills, CA) was used, whereas for site 8 a newer model ADC was employed. Both had sensors in the Blue (455–465 nm), Red (635–667 nm) and NIR (835–870 nm). BRIV 32 software (Heinold, 2000) was used to calculate NDVI for each pixel and produce mean values for each image. Resolution of the images was 0.15 m at 150 m AGL (0.67 ha), 0.5 m at 500 m AGL, and 1.0 m at 1000 m AGL. The ADC images were taken in sets of 24 images, and approximately 6 sets were collected over a site. Images were generally collected between 8 a.m. and 12 p.m.

The DyCam image data are in digital numbers (DN) which do not correspond to reflectance values. We calibrated the DyCam against reflectance-based values at Topock Marsh, using DyCam images collected on May 22 and an enhanced thematic mapper (ETM+) image acquired on 18 May 2002. We identified sites with pure vegetation and soil signals (Nagler et al., 2001), and regressed DyCam and ETM+ values for soil, arrowweed, saltcedar and willow. The relationship was $\mathrm{ETM+_{NDVI}} = 1.01^{*}\ \mathrm{DyCam_{NDVI}} + 0.12$ ($r = 0.96^{***}$). We extracted NDVI values for soil and each plant type from DyCam images by sampling pixels within 10–15 individual plant canopies or soil locations per image. Individual plant types could be easily distinguished (Nagler et al., 2001), except that cottonwood and willow canopies looked the same. These two species were only distinguished from each other at Topock Marsh (site 8), where cottonwoods were grown in a restoration plot. Since willows are three times more abundant than cottonwoods on the river (Zamora-Arroyo et al., 2001), we assumed that most of the trees sampled at other sites were willow.

We also used whole-scene NDVI values of images ($n = 25$) to correlate NDVI with fractional vegetation cover. We excluded scenes with water as it produced a very low (negative) background NDVI. We quantified fractional cover on the photos using an unsupervised classification program in ERDAS Imagine (Atlanta, GA). Using the visible bands only, we divided pixels into four classes, which clearly separated soil (non-green pixels) from vegetation (three classes). These classes did not correspond to pure vegetation types so they were not useful in distinguishing between species.

2.5. Determination of leaf spectra and NDVI for ground-based data

Ground-based NDVI of leaf samples using a hand-held radiometer were collected at three of the LAI sites (LAI site 3, LAI site 6, and NDVI site 7) (Table 1). Samples of freshly harvested leaves, representing the range of sizes available on the plants, were placed in non-reflective, black-painted, wooden plates (39 cm × 39 cm × 2.54 cm), stacked thickly (>8 leaf layers) and arranged so only leaf material

of each plant type was visible (Nagler et al., 2001). Spectral reflectance was acquired in the 400–900 nm range using an SE-590 spectroradiometer. Reflectance factors were calculated as the response of the instrument to the sample scene divided by the response of the instrument to a painted-$BaSO_4$ reference standard (30 cm × 45 cm) (Biehl and Robinson, 1983). NDVI was calculated using reflectance values of the leaf material in the Red (630–690 nm) and NIR (790–960 nm), wavelength bands that matched the thematic mapper bands. These optically thick samples are referred to as "stacked leaves" measurements.

2.6. Statistical analyses and other methods

LAI and NDVI data for each species was subjected to a two-way ANOVA in which site and species were the categorical variables. When ANOVA's were significant, means were separated using Tukey's test. LAI and NDVI data are displayed as box plots, in which the top and bottom halves of the box are each 25% quartiles, the mid-line is the median, the error bars encompass the 95% confidence interval, and individual points are outliers.

3. Results

3.1. Plant and leaf characteristics

Pictures of each plant type showing leaf shape and angles are in Fig. 2. Leaf inclination angles (20 per species) were measured with a protractor on detached branch samples of each plant type. Arrowweed grows in dense thickets, 2–3 m high, made up of strongly vertical stems growing from underground rhizomes, that produce side branches at angles of 60–70° (90° = vertical). The small, linear leaves tend to be appressed to the stems, and mean leaf angle of 20 typical leaves was 74°. During the day, leaf tips tend to orient towards the sun, so that the flat part of the leaf is parallel to the sun angle, minimizing light interception. By contrast, cottonwood has rounded, flat leaves that are displayed nearly horizontally, with a mean angle of 16°; these leaves tend to track the sun during the day so the flat part of the blade is perpendicular to the sun. Saltcedar grows in dense thickets that are not nearly as vertical as arrowweed. It has minute, scale-like leaves arranged in cylindrical clusters on terminal stems, so that the foliage elements resemble conifer needles. The foliage elements hang downward from stems at a mean angle of 132°, or 48° from horizontal. Willow has flat, linear leaves that tend to hang downward, with a mean angle of 138°, or 42° from horizontal. It must be emphasized that the reported angles are from a few static measurements made on detached branches, whereas in a natural canopy, leaf angles will be in flux.

We measured the relationship between leaf weight and leaf area ($g\,m^{-2}$) for each species to use in estimating LAI by biomass sampling. Values were 193, 112, 81 and 71 $g\,m^{-2}$ for arrowweed, saltcedar, cottonwood and willow, respectively.

Leaves also exhibited color differences. Arrowweed is pubescent and tends to reflect light, appearing silvery gray to blue; cottonwood and willow are bright green; and saltcedar, which accumulates salts in its foliage elements, also tends to reflect light and appears as bluish green. These visual differences were apparent in the reflectance spectra of stacked leaves (Fig. 3). Arrowweed was more reflective than the other species across the range of wavelengths. With respect to PAR (450–700 nm), cottonwood and saltcedar reflected 6% of incident light, while willow and arrowweed reflected 9 and 12%, respectively. Stacked leaves had similar NDVI values ranging from 0.62 to 0.72 (mean = 0.69, $P > 0.05$, Fig. 3). Differences among sites were larger than differences among species.

3.2. Comparison of LAI by Licor-2000 and biomass sampling

LAI measured by LAI-2000 and biomass sampling were compared for each species on natural stands of plants. Allometric measurements on cottonwood and willow were used to scale leaf area of leaves on individual branches to leaf area of whole trees; both species exhibited a 1:1 relationship between cross-sectional area of trunks and secondary and tertiary branches, and linear relationships between leaf area and cross-sectional stem area (Fig. 4). These relationships allowed us to calculate LAI for these plants independent of the LAI-2000 measurements, but the measurements are only valid for the stand of plants sampled. In particular, leaf area per branch varied widely among different plant stands and at

Fig. 2. Typical branches and leaves of four riparian species from the Lower Colorado River. Branches were from the sunlit part of the canopy and have the same orientation in the photographs as they had on the intact plant. Arrowweed, saltcedar and willow are side views, whereas cottonwood is a top view.

different times of year (not shown). Cottonwood produced similar values for LAI by Licor and biomass methods when the Licor software was used to calculate LAI based on canopy dimensions (Fig. 5). For willow, the LAI-2000 measurements were slightly higher than the biomass LAI but the difference was not significant ($P > 0.05$). Saltcedar and arrowweed gave similar values of LAI when measured by Licor and biomass sampling (Fig. 5).

3.3. LAI of natural stands of plants

LAI was measured by LAI-2000 at six sites. ANOVA showed that LAI differed significantly among sites (Fig. 6) and among species (Table 2, $P < 0.05$). Saltcedar LAI values were generally 2–3, but at Mittry Lake South, they were 5–7. These plants were growing in moist soil and by the time they were measured in September 2002, they had

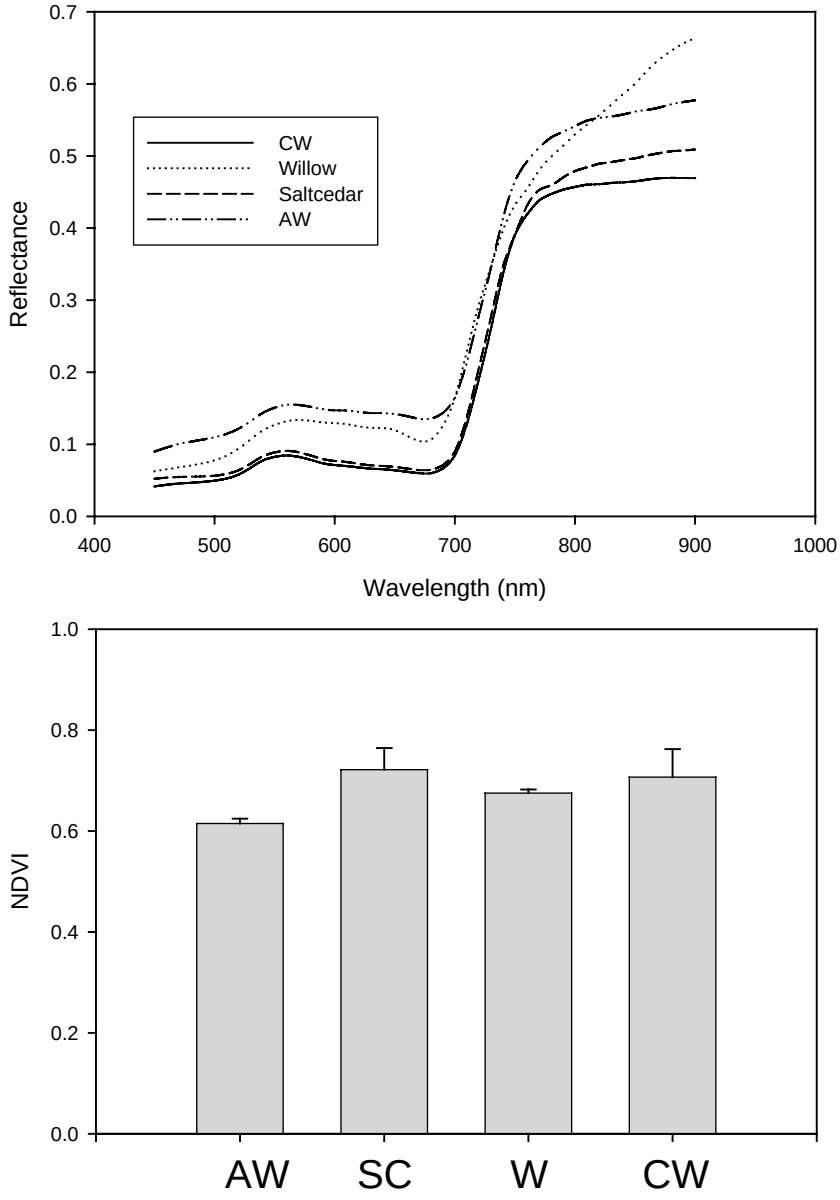

Fig. 3. Reflectance spectra (top) and calculated NDVI values of cottonwood, willow, saltcedar and arrowweed stacked leaves measured by the SE-590 spectro-radiometer. The spectra are results from a single set of measurements, whereas the NDVI values are means for leaves measured over three different sites along the Lower Colorado River. Error bars are standard errors.

produced very dense foliage throughout the stand. However, LAI was measured near the interface between road and plant stand, where LAI is expected to be the highest, because we were unable to penetrate into the middle of the stand. Arrowweeds, cottonwood and willows had LAI values generally in the range of 3–4. The box plots in Fig. 6 show that there was considerable variability in LAI, and CVs ranged from 40 to 50% within each species (Table 2). Across sites, saltcedar had significantly

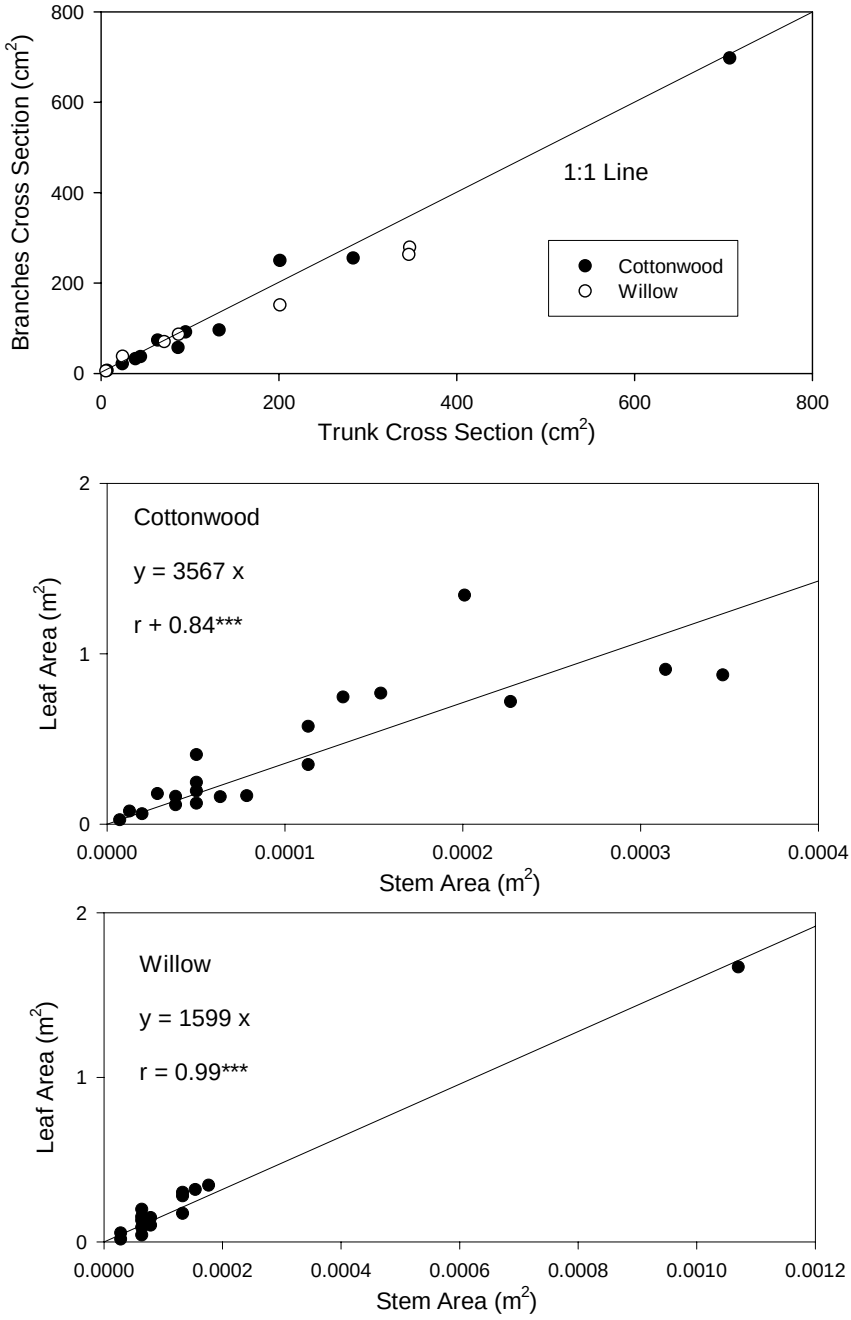

Fig. 4. Top—relationship between primary trunk cross-sectional area and cross-sectional area of secondary and tertiary branches for cottonwood and willow trees used to calculate biomass LAI values. Number of branches measured per trunk ranged from 5 to 32. Middle and bottom—relationship between cross-sectional area of branches and leaf area of cottonwood and willow trees measured for LAI.

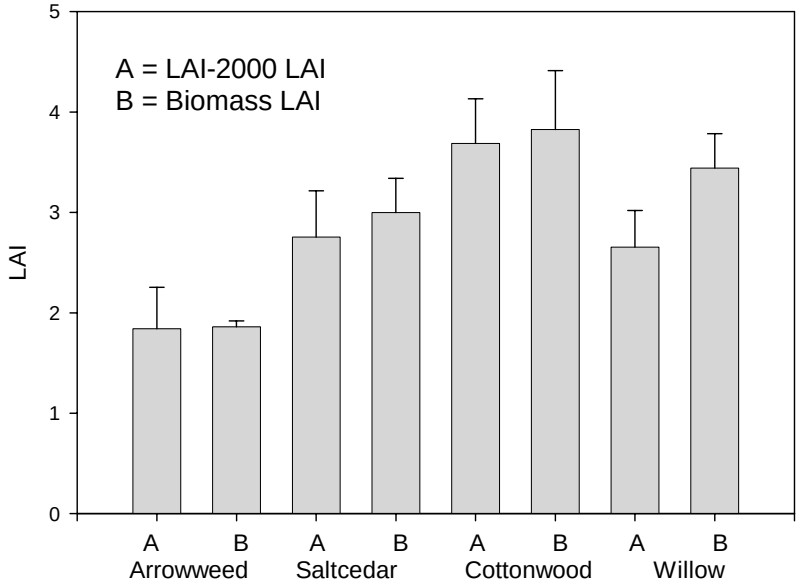

Fig. 5. Comparison of Biomass LAI and Licor LAI-2000 LAI for arrowweed, saltcedar, cottonwood and willow. Error bars are standard errors.

lower LAI than cottonwood or arrowweed ($P < 0.05$).

3.4. NDVI of natural plant stands

DyCam images were obtained on aerial campaigns in 2001 and 2002 and analyzed for eight sites on the river. On most of the DyCam images, cottonwoods and willows could not be distinguished from each other and were combined, but at Topock Marsh (site 8) we identified a field of cultivated cottonwoods with willows nearby, to extract separate NDVI signals.

Table 2
Mean, standard error of mean, and sample size of LAI and NDVI measured at eight sites on the Lower Colorado River by Licor-2000

	Plant			
	Cottonwood	Willow	Saltcedar	Arrowweed
LAI	3.50 a	3.28 a	2.81 b	3.69 a
S.E.M.	0.16	0.16	0.134	0.196
CV (%)	39.5	40.0	48.6	37.2
N	74	71	104	49
NDVI	0.686 a	0.600 b	0.473 c	0.254 d
S.E.M.	0.011	0.010	0.010	0.008
CV (%)	8.4	10.6	63.6	59.7
N	30	106	106	74

Means followed by different letters are different at $P < 0.01$.

NDVI values varied significantly across sites (Fig. 7) and by species (Table 2). Unlike the results with stacked leaves (Fig. 3) there were clear species differences, with cottonwoods > willows > saltcedar > arrowweed across sites (Table 2).

3.5. NDVI and fractional vegetation cover of mixed scenes

NDVI values in Fig. 7 were point measurements within individual canopies. We also measured whole-scene NDVI values (each image covered approximately 700 m × 1000 m) and regressed them against fractional vegetation cover for each scene, determined by separating green from non-green pixels in the visible bands using a pixel classification program (Fig. 8). We found a significant linear relationship between NDVI and fractional cover ($r = 0.81^{***}$). For these 25 scenes, mean NDVI was 0.23 and mean fractional cover was 0.40.

3.6. Calculating k from NDVI and LAI measurements

The linear relationship between fractional cover and NDVI supports other studies showing that canopy IRs

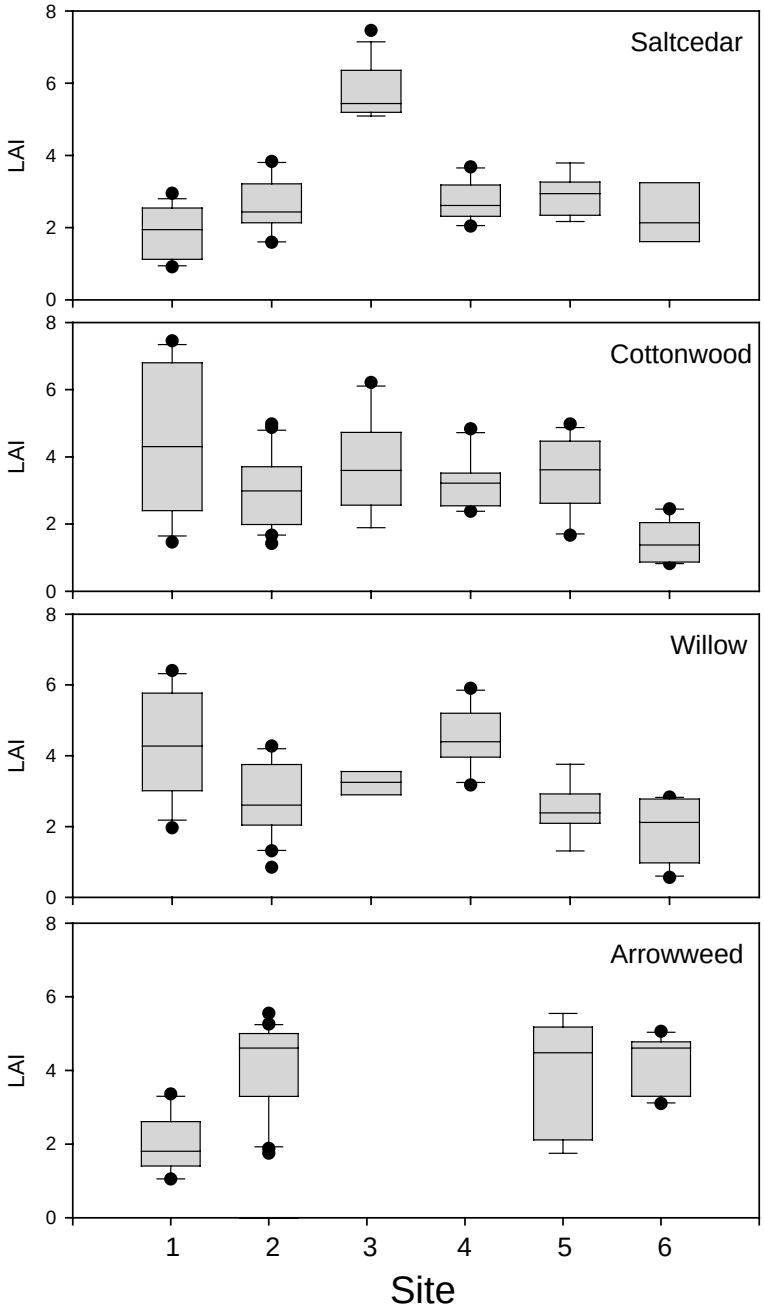

Fig. 6. Box plots showing LAI values of four riparian species at six sites on the Lower Colorado River.

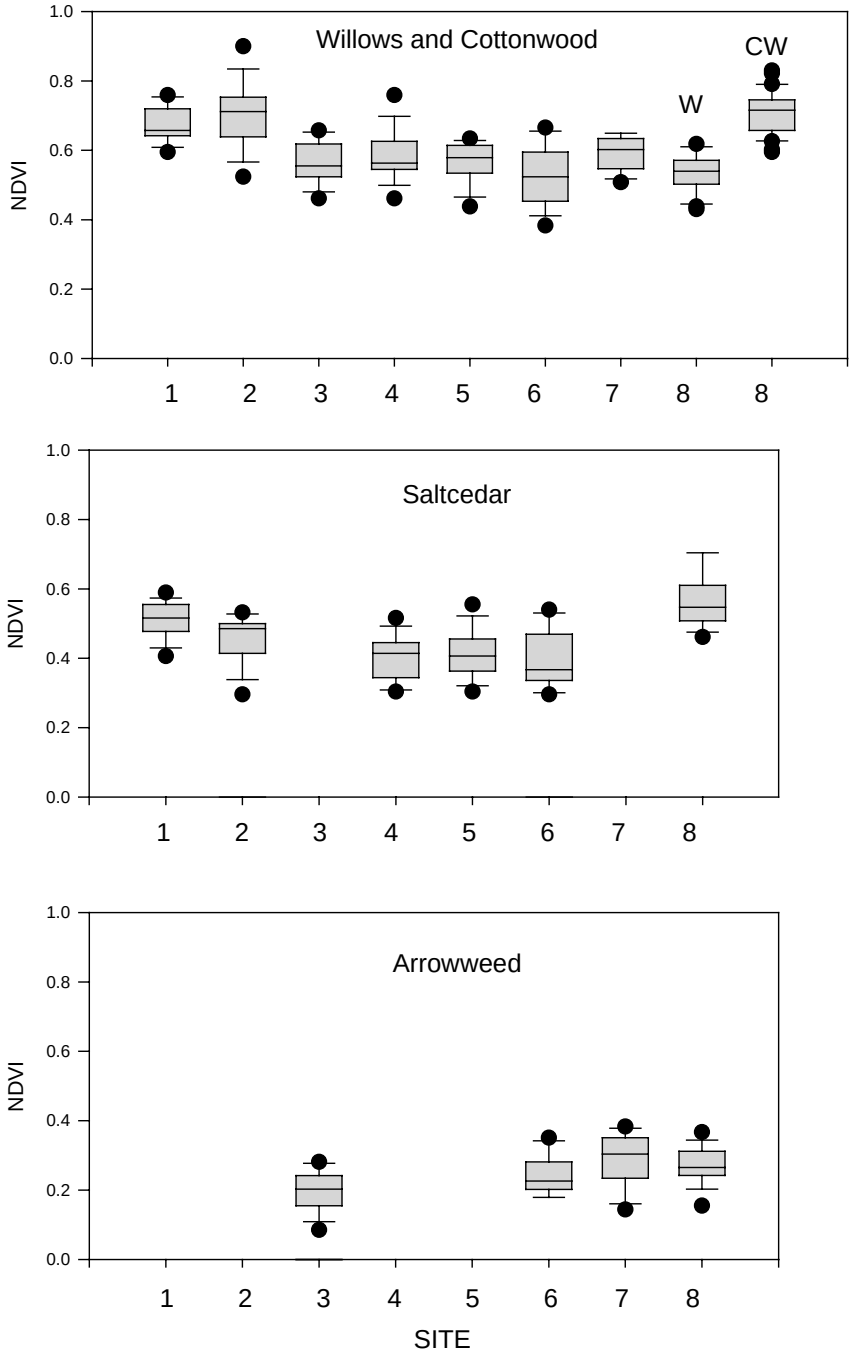

Fig. 7. Box plots showing NDVI values for mixed willows and cottonwoods, saltcedar and arrowweed at eight sites on the Lower Colorado River. At site 8, cottonwood and willow were measured separately. Data are from a DyCam ADC flown on a light aircraft. NDVI values were based on reflectance values for Red and NIR.

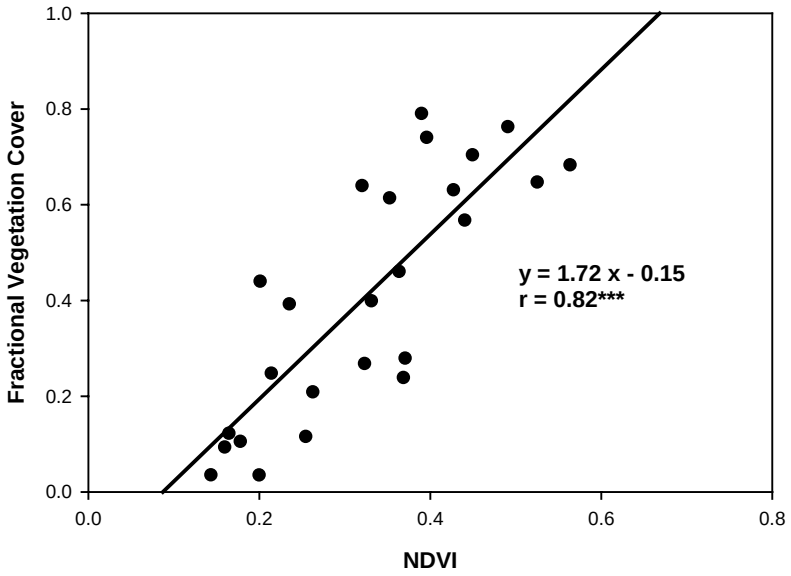

Fig. 8. Relationship between NDVI (based on reflectance values) and fractional vegetation cover for 25 whole-scene images acquired with a DyCam ADC flown over the Lower Colorado River at 150–350 m AGL.

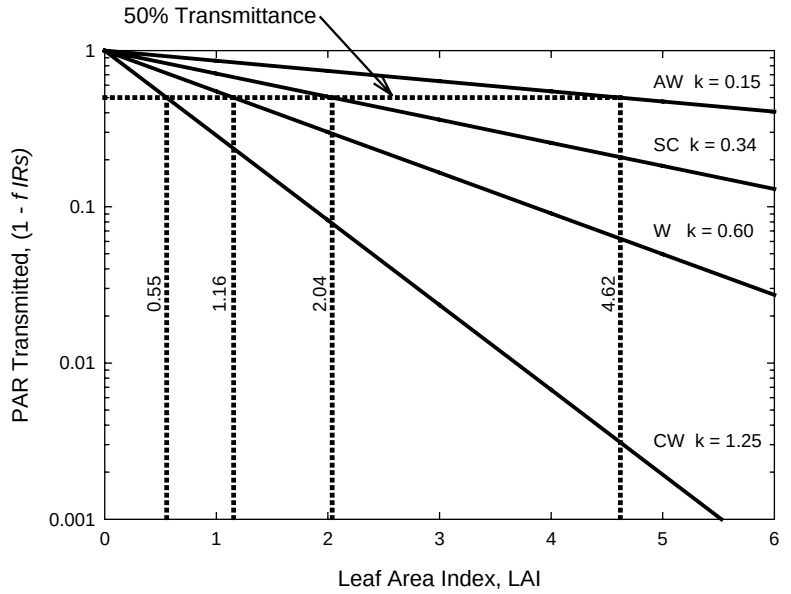

Fig. 9. Relationship between PAR transmitted through the canopy and LAI based on k values for cottonwood, willow, saltcedar and arrowweed determined in the present study, where $I_T/I_O = e^{-k\mathrm{LAI}}$. Drop lines show the LAI which produces 50% light transmittance through the canopy.

and ARs are also proportional to NDVI (Inoue and Moran, 1997; Monteith and Unsworth, 1990). We rearranged Eq. (1) to solve for k:

$$k = -\frac{\ln(1 - \text{fIRs})}{\text{LAI}}$$

Note that $(1 - \text{fIRs})$ is the fraction of light transmitted through the canopy. Assuming a linear relation between NDVI and canopy fIRs (Inoue and Moran, 1997), we used the NDVI for bare soil as fIRs = 0, and the mean value of "stacked leaf" NDVI as fIRs = 1, and calculated fIRs of a canopy of any species as

$$\text{fIRs} = 1.61\text{NDVI} - 0.12 \quad (3)$$

We then used mean values of NDVI and LAI for each species over all the sites (Table 2) to calculate $(1 - \text{fIRs})$ and k for natural stands of each species, and displayed PAR transmitted $(1 - \text{fIRs})$ as a function of LAI and k to illustrate differences among species (Fig. 9). Fig. 9 shows that the projected LAI needed to achieve 50% light interception varies markedly among species due to differences in k values, from 0.6 for cottonwood to 4.6 for arrowweed.

4. Discussion

4.1. LAI values

The LAI-2000 assumes a uniform canopy with randomly distributed leaves within the canopy, conditions which are often violated by plants in the field (White et al., 2000). Hence, it is necessary to compare LAI-2000 readings with biomass sampling or other independent estimates of LAI to check the validity of the measurements (Asner et al., 2003). In our study, LAI values measured by biomass sampling and LAI-2000 were within 10% of each other for saltcedar and arrowweed. Cottonwood and willow also produced similar values by the two methods when LAI-2000 measurements were corrected by adding tree dimensions into the calculation of LAI.

Several studies have suggested that saltcedar might have higher LAI than native trees along western US rivers, leading to higher rates of ET (Sala et al., 1996; Schaeffer et al., 2000; DiTomaso, 1998). To our knowledge, however, this is the first study that compared LAI values for numerous plants over a large stretch of river. Saltcedar did have LAI values of 5–7 at one site, but at most sites the values were lower, and saltcedar overall had the lowest LAI values among species.

4.2. Reflectance spectra and NDVI values

All four species in this study have similar, but not identical, spectral properties in the visible and NIR wavelength region, and similar NDVI values for stacked pure leaf samples. However, the NDVI values for field canopies were distinctly different, ranging from 0.25 for arrowweed to 0.69 for cottonwood, with cottonwood > willow > saltcedar > arrowweed. Assuming that NDVI was proportional to fIRs for these species (e.g. Inoue and Moran, 1997), natural stands of plants appear to differ greatly in the amount of light intercepted by their canopies despite similar LAI values. This appeared to be mainly due to differences in leaf angles within the canopies rather than differences in reflectance properties of individual leaves.

4.3. Light extinction coefficient and fARs

Calculated values of k were the lowest for arrowweed (0.15), with its near vertical leaves and stems, and the highest for cottonwood, with horizontal leaves (1.25). Saltcedar and willow, with linear, drooping leaves were intermediate. The k values are what are expected for plants with these different canopy structures (Campbell, 1986; Leopold, 1975) and can explain differences in NDVI among species for natural stands of plants. At a given LAI, plants with lower k values intercept less light than plants with higher k values. The k value for cottonwood is subject to error, as the NDVI of stacked leaves was similar to the mean value of natural canopies, and the difference between the two was needed to calculate $(1 - \text{fIRs})$. The value of 1.25 compares to values of 0.9–1.1 for other broad-leaved plants such as clover and sunflower (Monteith and Unsworth, 1990).

fARs is more directly related to physiological functions such as ET and photosynthesis than fIRs (Monteith and Unsworth, 1990). fARs can be calculated for pure leaf samples using data in Fig. 3. fARs for natural stands of plants can be calculated from their NDVI values in the field compared to NDVI and

fARs values for pure leaf samples. Mean values of fARs for natural stands across sites were 0.93, 0.71, 0.65 and 0.32 for cottonwood, willow, saltcedar and arrowweed, respectively. For the 25 mixed scenes along the river, fractional cover was only 0.40 and mean canopy fARs based on whole-scene NDVI values was only 0.25.

4.4. Ecophysiological implications of the findings

Plants with low *k* values are often full-sun plants that can achieve high LAI (up to 10 for some grasses), leading to high potential primary productivity (Leopold, 1975; Monteith and Unsworth, 1990). On the other hand, xeric-adapted plants may also have low *k* values as part of a strategy to minimize radiation absorption to conserve water (Jones, 1983). In the present case, arrowweed had much lower light interception than the other species, and it had other xeric adaptations such as higher leaf reflectance, and reduced leaves. Saltcedar also had lower light interception than the native trees, and both arrowweed and saltcedar are more salt tolerant than the native trees (Glenn et al., 1998). The floodplains of western rivers have become increasingly xeric and saline, because seasonal overbank flooding has been reduced by dams and water diversions, and the riparian environment now favors saltcedar and arrowweed over the native trees. On the other hand, when a pulse flood regime is returned to a river stretch, as in the delta of the Colorado River in Mexico, native trees have regenerated on the floodplain despite the presence of saltcedar and arrowweed (Zamora-Arroyo et al., 2001). Pulse floods reduce soil salinity and increase soil moisture, and under these conditions, cottonwoods and willows can successfully compete with saltcedar and arrowweed because they grow taller and intercept more of the incident PAR.

Very high ET rates have been attributed to saltcedar on western rivers. For example, DiTomaso (1998) cited figures as high as 3–4 m per year determined by indirect methods. On the other hand, recent estimates by Bowen ratio (Devitt et al., 1998) or eddy covariance (Cleverly et al., 2002) flux towers produced much lower values, 0.74–1.4 m per year for typical stands. The present study and previous studies (Nagler et al., 2001; Zamora-Arroyo et al., 2001) showed that fractional vegetation cover on the Lower Colorado River is modest (0.4–0.6) and fARs for mixed scenes is low. Hence, it is reasonable to conclude that rates of physiological processes such as ET and photosynthesis that depend on fARs will be low to moderate on this river system.

4.5. Conclusions

As with other studies of canopy characteristics of natural plant stands, our estimates of LAI, *k* and canopy radiation properties are approximations, and are subject to both measurement error and violation of the assumptions about canopy properties built into the LAI-2000 (White et al., 2000). Nevertheless, NDVI proved to be a useful tool for determining fractional vegetation cover and estimating radiative properties of canopies in this biome. Combined with ground measurements of LAI and leaf reflectance properties, it could be used to predict light extinction coefficients of the different plant types. CV's of NDVI measurements were generally under 10%, whereas ground measurements of LAI had CV's on the order of 40%. NDVI values provide information on fARs independent of species or fractional cover, hence it could be an appropriate scaling tool for projecting physiological processes that depend on fARs over large riparian areas with mixed vegetation types and variable amounts of plant cover. Combined with models of ET for these species (Nagler et al., 2003), the relationships between *k* and LAI shown in Fig. 9 could be used to predict ET for each species as a function of LAI, ARs, and environmental conditions.

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