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POSTFIRE STAND STRUCTURE IN A SEMIARID SAVANNA: CROSS-SCALE CHALLENGES ESTIMATING BIOMASS

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Abstract. Algorithms relating remotely sensed woody cover to biomass are often the basis for large-scale inventories of aboveground carbon stocks. However, these algorithms are commonly applied in a generic fashion without consideration of disturbances that might alter vegetation structure. We compared field and remote sensing estimates of woody biomass on savannas with contrasting disturbance (fire) histories and assessed potential errors in estimating woody biomass from cover without considering fire history. Field surveys quantified multilayer cover (MLC) of woody and succulent plants on sites experiencing wildfire in 1989 or 1994 and on nearby unburned (control) sites. Remote sensing estimates of the woody cover fraction (WCF) on burned and control sites were derived from contemporary (2005) dry-season Landsat Thematic Mapper imagery (during a period when herbaceous cover was senescent) using a probabilistic spectral mixture analysis model. Satellite WCF estimates were compared to field MLC assessments and related to aboveground biomass using allometry.

Field-based MLC and remotely sensed WCFs both indicated that woody cover was comparable on control areas and areas burned 11–16 years ago. However, biomass was approximately twofold higher on control sites. Canopy cover was a strong predictor of woody biomass on burned and control areas, but fire history significantly altered the linear cover–biomass relationship on control plots to a curvilinear relationship on burned plots. Results suggest predictions of woody biomass from "generic" two-dimensional (2-D) cover algorithms may underestimate biomass in undisturbed stands and overestimate biomass in stands recovering from disturbance. Improving the accuracy of woody-biomass estimates from field and/or remotely sensed cover may therefore require disturbance-specific models or detection of vegetation height and transforming 2-D vegetation cover to 3-D vegetation volume.

Key words: allometry; Arizona, USA; carbon pools; carbon sequestration; Landsat; mesquite; Prosopis velutina; *remote sensing; Santa Rita Experimental Range, Arizona, USA; woody biomass.*

INTRODUCTION

Aboveground biomass is a fundamental component of terrestrial carbon budgets and biosphere metabolism. In arid and semiarid regions characterized by savannas, shrublands, and woodlands, tracking changes in aboveground biomass in response to stress and disturbance requires tracking changes in the abundance of shrubs and arborescents. Over the past century, woody-plant abundance has been increasing in dryland ecosystems, including grasslands, worldwide (Archer 1994, van Auken 2000, Archer et al. 2001). Collectively, increases in woody-plant abundance in drylands are thought to comprise a significant but highly uncertain portion of the carbon sink in the United States (e.g., Pacala et al. 2001, Schimel et al. 2001, Houghton 2003) and Australia (e.g., Gifford and Howden 2001, Burrows et al. 2002, Henry et al. 2002). Much of this uncertainty reflects a poor accounting of the rate and spatial extent of changes in shrub and tree mass. Our ability to monitor and project future states of dryland ecosystems in response to predicted changes in climate, atmospheric chemistry, and disturbance regimes will depend on our ability to accurately assess the contribution of woody plants to vegetation structure and biomass.

Direct quantification of aboveground woody biomass is time and labor intensive and causes significant disturbance. As a result, direct assessments are seldom feasible or practical. A widely used alternative involves the development of regression equations that predict aboveground biomass from nondestructive measurements of plant height, basal area, canopy area, etc. These allometric approaches have been widely used in drylands to estimate shrub and tree biomass (e.g., Ludwig et al. 1975, Chojnacky 1991, Northup et al. 2005, and references therein). While these allometric relationships are useful in estimating woody biomass at the plot scale (e.g., Miller et al. 2003, Barbosa and Fearnside 2005) it is logistically difficult to apply them across large areas and over time. However, when used in

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conjunction with remote sensing products that generate vegetation indices and fractional vegetation cover, they offer the potential to inventory and monitor aboveground carbon stocks in woody plants and the change through time over large and remote areas (e.g., Gower et al. 1999, Asner et al. 2003, Dong et al. 2003, Zheng et al. 2004).

The consistency of woody cover–mass relationships in areas with different land tenures and disturbance regimes has seldom been evaluated. Perturbations influencing the structure of woody plants in arid and semiarid ecosystems include herbivory (Augustine and McNaughton 2004, Baxter and Getz 2005), brush management (Scifres 1980, Chidumayo 2002, Asner et al. 2003), and fire (Ben-Shahar 1998). The latter, either wild or prescribed, is geographically widespread in wildlands and can rapidly alter ecosystem structure. How might a disturbance such as fire alter cover–mass relationships? One of the primary regeneration strategies of woody species after perturbation is sprouting from stems or roots surviving the fire (Biswell 1974, Midgley 1996, Menges and Hawkes 1998, Bond and Midgley 2001). Morphological characteristics of plants vegetatively regenerating after fire include shorter stature and higher root : shoot ratios than unburned counterparts (Midgley 1996). Thus, it is reasonable to expect that the structure of woody-plant communities, and hence algorithms relating remotely sensed woody-plant canopy cover to biomass, may vary as a function of fire history. How robust are remote sensing estimates of woody-plant biomass based on woody cover–mass relationships? Do "generic" cover–biomass algorithms (e.g., algorithms ignoring disturbance history) accurately quantify biomass on sites with contrasting disturbance histories? We addressed these questions by (1) quantifying the relationship between aboveground live woody biomass (hereafter "woody biomass") and woody cover on burned and control sites in a semiarid savanna at plot and landscape scales using field-based and remote sensing techniques, respectively, and (2) determining whether knowledge of fire history could improve the accuracy of woody-biomass estimates derived from cover. Based on the premise that woody plants vegetatively regenerating from fire are likely to reestablish canopy area more quickly than biomass, we hypothesize that fire would alter cover–biomass relationships such that generic cover–biomass algorithms would overestimate woody biomass on areas recovering from fire.

Methods

Study area

The study was conducted on the 200-km^2 Santa Rita Experimental Range (SRER) (31.83° N, 110.85° W), approximately 50 km south of Tucson, Arizona, USA. Established in 1902, the SRER is the oldest experimental range in the United States (Sayre 2003). Elevations at SRER extend from 884 to 1585 m. Annual precipitation at 1200 m elevation is variable, averaging 250 mm in dry years and 500 mm in wet years. Precipitation increases gradually with elevation and is bimodally distributed, with more than half falling in summer (McClaran et al. 2002). Mean annual temperature at 1310 m is 17.9°C (National Climate Data Center, *available online*).[4] Lower elevations are characterized by long, gently sloping alluvial fans cut by canyons and arroyos at higher elevations. Plant communities are dominated by native grasses, introduced grasses (primarily *Eragrostis lehmanniana* Nees), and mesquite (*Prosopis velutina* Wooten) shrubs, the latter having increased in cover since the early 1900s. See McClaran (2003) for additional details on vegetation, soils, and climate. Fire is common in semiarid savannas such as those at the SRER (McPherson 1995). Our study focused on two areas with known recent fire histories. One fire burned ~500 ha on 9 June 1989; another fire on 2 June 1994 burned ~4047 ha (Womack 2000, McClaran 2003). Studies assessing the impacts on *P. velutina* 18 months (DeBano et al. 1996) and eight years (Gottfried et al. 2003) after the 1994 fire indicated that ~90% of the *P. velutina* plants were impacted.

Satellite data pre-processing

Landsat Thematic Mapper (TM) was used to assess the effects of the 1989 and 1994 fires on woody-plant cover and biomass. Landsat TM is a multispectral space-borne sensor containing six visible, near-infrared (NIR) and shortwave infrared (SWIR) bands with a nominal spatial resolution of 30 × 30 m and one thermal band. Cloud-free Landsat TM images were acquired for five dates: 9 June 1989, 25 June 1989, 4 April 1994, 23 June 1994, and 5 June 2005. The paired 1989 and 1994 images represented dates immediately before and after the two fires and were used to locate burned areas. The image from the 2005 dry season was used to estimate current woody cover.

Image pre-processing entailed radiometric calibration, including geometric rectification and removal of atmospheric effects. All images were ortho-rectified based upon preregistered Landsat images and a digital elevation model. The root mean square error of ortho-rectification was controlled to less than half of a pixel (<15 m) for each image. A second-degree polynomial geometric model and nearest neighbor resampling was utilized so that the inherent spectral information was not altered by image registration and resampling. Atmospheric corrections utilized the cosine of the solar zenith angle correction (COST) model (Chavez 1996). This model is an improved dark-object subtraction model that corrects for additive path radiance and multiplicative transmittance effects. It is solely based on the digital image and does not require in situ field measurements or acquisition of atmospheric profiles at the time of satellite

[4] ⟨http://www.ncdc.noaa.gov/oa/ncdc.html⟩

TABLE 1. Allometric models relating shrub and cactus canopy area (CA; cm^2 or m^2) or radius (r; cm) to dry biomass (M; g or kg/plant).

Species (n)	Model†	R^2	Reference
Prosopis velutina (31)	$\ln(M_{kg}) = -0.67 + 1.54 \ln(CA_1, m^2)$	0.97	*personal observations*
Isocoma tenuisecta (27)	$\ln(M_g) = -4.81 + 1.25 \ln(CA_1, cm^2)$	0.95	*personal observations*
Celtis pallida (36)	$\ln(M_g) = 1.02[6.78 + 1.41 \ln(CA_2, m^2)]$	0.88	Northup et al. (2005)
Opuntia engelmannii (26)	$M_{kg} = [(4.189 \times r^3)^{0.965}]/10^5$	0.95	Vogl et al. (2004)

† Equations for canopy areas and radius: $CA_1 = \pi \mathcal{R}^2$, where $\mathcal{R}$ = ([longest axis/2] + [perpendicular axis/2])/2; $CA_2 = \pi$(longest axis/2)(perpendicular axis/2); and r = ([center height/2] + [longest diameter/2])/2, where center height and longest diameter are measured in cm.

overflight. This model is suitable for long-term, multitemporal studies in which there is lack of historical ground atmospheric correction information and is as accurate as models requiring in situ atmospheric field measurements and sophisticated radiative transfer codes (Chavez 1996). The COST model has been validated in dryland environments and performs well when sun zenith angles are <45°.

Burn severity maps

The normalized burn ratio (NBR) and differenced NBR (dNBR) (van Wagtendonk et al. 2004) were used to delineate the spatial extent of the 1989 and 1994 wildfires using paired sets of pre- and postfire images. The NBR was calculated using Landsat NIR (band 4, spectral range 0.76–0.90 μm) and SWIR (band 7, spectral range 2.08–2.35 μm) bands, and dNBR was calculated as the difference between prefire and postfire NBR:

$$\mathrm{NBR} = \frac{(\mathrm{TM4} - \mathrm{TM7})}{(\mathrm{TM4} + \mathrm{TM7})} \times 1000 \tag{1}$$

$$\mathrm{dNBR} = \mathrm{NBR}_{\mathrm{prefire}} - \mathrm{NBR}_{\mathrm{postfire}}. \tag{2}$$

The NBR (Eq. 1) reflects burn severity, and the dNBR (Eq. 2) is an index to enhance the identification and demarcation of burned areas where there is a loss of biomass during fire (U.S. Geological Survey, *available online*).[5] The dNBR is highly correlated with the composite burn index (van Wagtendonk et al. 2004), a field measure of burn severity, and is frequently used by the U.S. Forest Service to evaluate forest fires. The dNBR has also proven to be reliable for delineating fire scars in semiarid savannas (Holden et al. 2005, Lentile et al. 2006). Based on Forest Service criteria, pixels with a dNBR > 100 were classified as burned.

Field data

Twenty 40 × 40 m plots spanning the full spectrum of woody cover on the SRER were randomly selected with the aid of a pan-sharpened high-spatial-resolution (0.61 m) QuickBird image (DigitalGlobe, Longmont, Colorado, USA) acquired on 8 May 2005 and overlain with dNBR burn severity maps. Plots identified on images were located in the field using a global positioning system (Garmin GPS V, Garmin International, Olathe, Kansas, USA). Eight plots were situated in areas known to be fire-free for at least 20 years (hereafter referred to as control plots). Four plots were established in the 500-ha area burned in 1989, and eight plots were situated in the 4047-ha area burned in 1994 (these 12 plots hereafter referred to as burned plots). The canopy area of individual shrub and cactus plants occurring within a 20 × 40 m belt in each plot was estimated as described in Table 1. Canopy areas for shrubs were then summed, without regard to their understory vs. overstory status, to generate a single, multilayer plot-level estimate of woody cover (MLC). Aboveground biomass (leaf and wood) for each plant was estimated using previously established equations predicting plant mass from canopy area (Table 1). Woody biomass (in kilograms per square meter) was computed by summing across all plants and dividing total biomass by the belt area. Regression models (JMP IN version 4 [Sall et al. 2001]) using MLC as the independent variable to predict woody biomass were then developed for burned plots, for control plots, and for data pooled across burned and control plots. By contrasting the outcomes predicted from the model using pooled data (generic model) to that of models taking fire history into account (disturbance-specific models), we could assess potential errors in predicting woody biomass when fire history is unknown.

Estimation of woody biomass from satellite imagery

In southern Arizona, savannas generally exhibit the least amount of herbaceous green biomass during the driest and hottest months (May/June), just prior to the onset of summer monsoon rainfall in July/August. During the pre-monsoon period, the only green plants are trees, shrubs, and cacti. Hence, the green signal derived from satellite data acquired during this period represents woody and succulent plants. A pre-monsoon Landsat TM image collected on 5 June 2005 was analyzed using a probabilistic mixture model (Automated Monte Carlo Unmixing [AutoMCU; Asner and Lobell 2000]) to extract the woody cover fraction (WCF) and derive uncertainty estimates of sub-pixel cover fraction values. AutoMCU was originally designed for the SWIR region (2000–2400 nm) of hyperspectral data because of the stability and high separablility of green vegetation, litter, and bare-soil

[5] ⟨http://burnseverity.cr.usgs.gov/fire_main.asp⟩

spectral signatures within this part of the electromagnetic spectrum. However, the model also has been applied to multispectral Landsat TM and advanced spaceborne thermal emission and reflection radiometer (ASTER) data (Asner and Heidebrecht 2002). One important component of AutoMCU that makes it different from other mixture models is the use of a set (or a bundle) of spectral libraries with pure green vegetation, standing/surface litter, and bare-soils spectra (end members) (Bateson et al. 2000). Variability of spectral signatures for green vegetation (Asner 1998, Asner et al. 1998, Martin et al. 1998, Dennison and Roberts 2003), litter (Elvidge 1990, van Leeuwen and Huete 1996, Nagler et al. 2003), and bare soil (Stoner and Baumgardner 1981, Lobell and Asner 2002) end members has been documented. We assigned end member spectral signatures using a combination of field spectroradiometer data acquired in this study (Analytical Spectral Devices, Boulder, Colorado, USA) and data from existing dryland spectral libraries (Asner 1998, Asner et al. 1998, Batchily et al. 2003, Landmann 2003, Smith et al. 2005) (numbers of samples for green vegetation = 95, litter = 42, bare soil = 197). Due to low separablility of spectral signals of litter and bare soils in TM spectral space and our specific focus on woody cover, we combined litter and bare soils into a single end member termed "others."

The TM pixels containing field sampling plots were utilized to develop regression models that used WCF as the independent variable to predict field woody biomass and MLC with and without consideration of fire history. AutoMCU typically stabilizes after 30+ unmixing runs for hyperspectral data (Asner and Lobell 2000), and Asner et al. (2003) used 250 runs with Landsat Enhanced Thematic Mapper plus data on mesquite savannas in Texas. After a preliminary evaluation of accuracy, consistency, and computation efficiency, we used 750 iterations to unmix our TM data. In addition, we controlled the quality of unmixing by constraining the standard deviation of the WCF after unmixing.

Postfire recovery of woody biomass and cover

Recovery of woody biomass and cover following the 1989 and 1994 fires was assessed at a large spatial extent using remote sensing-based regressions to predict woody biomass and MLC from the WCF in burned and control settings. Stratified random sampling was used to select a large number of four 60×60 m pixels within burned ($n = 122$) and nearby control ($n = 141$) areas on a 5 June 2005 Landsat TM image. The WCF derived from these randomly selected pixels using AutoMCU was converted to woody biomass and MLC using the aforementioned regression models. The number of pixels in a given biomass or canopy cover class was divided by the total number of pixels sampled for each fire treatment to normalize woody-biomass and cover estimates on burned and control sites and to facilitate comparisons.

Error assessment of estimating woody biomass without considering fire history

A sensitivity analysis was conducted to examine the impacts of ignoring fire effects when estimating woody biomass from cover at different spatial scales. We quantified the difference (errors) between woody biomass estimated with generic models vs. disturbance-specific models. These differences are expressed as actual error, relative error ([actual error/true measurement] $\times$ 100; shown as a percentage), and overall actual and relative error (the summations of absolute underestimation and overestimation for actual and relative errors, respectively) across the range of MLC (0.10–0.82) and WCF (0.05–0.32) values encountered in the field plots.

RESULTS

Fire and cover–biomass relationships: plot scale

Mesquite was the dominant shrub, comprising >43% (mean = 90%) of the canopy area and >68% (mean = 93%) of the total woody biomass on all sites. Wildfire effects on woody-plant cover were spatially variable, with the large 1994 fire creating a more complex burned surface than the smaller 1989 fire (Fig. 1). An example of the effects of spatial and temporal heterogeneity in fire severity on shrub stand structure and biomass is illustrated in Fig. 2. Although shrub cover was comparable on these two burned plots (Fig. 2A, burned in 1989, MLC = 0.83; Fig. 2B, burned in 1994, MLC = 0.86), they differed almost twofold with respect to shrub biomass. These biomass differences corresponded to marked differences in shrub size-class distributions (numerous small plants on the one plot vs. fewer, larger plants on the other plot [see Fig. 2 inset table]). The relationship between woody biomass and MLC was linear with an $R^2 = 0.72$ when data from all sites was pooled (Fig. 3A). However, when data were segregated by fire history, the best-fit functional form of the MLC–biomass function differed on burned (nonlinear) vs. control sites (linear), and R^2 values increased 16% and 21%, respectively (Fig. 3B). Regressions using fire as a dummy variable indicated fire was significant at $P = 0.06$. Biomass on burned plots was consistently lower than that in control plots when MLC was <0.55, reflecting the low number of large *P. velutina* plants on burned plots (Fig. 4B) compared to control plots (Fig. 4A). When MLC and *P. velutina* cover were high, differences between control and burned plots were generally minimal, owing to similar *P. velutina* size-class distributions (Fig. 4C, D).

Fire and cover–biomass relationships: landscape scale

Predictions of woody-plant biomass from satellite-derived WCFs were significant ($P < 0.01$), but rather weak ($R^2 = 0.34$) for data pooled across all sites. Partitioning sites based on fire history improved R^2 values to 0.60 and 0.63 on burned (curvilinear relationship, $P = 0.02$) and control (linear relationship, $P <$

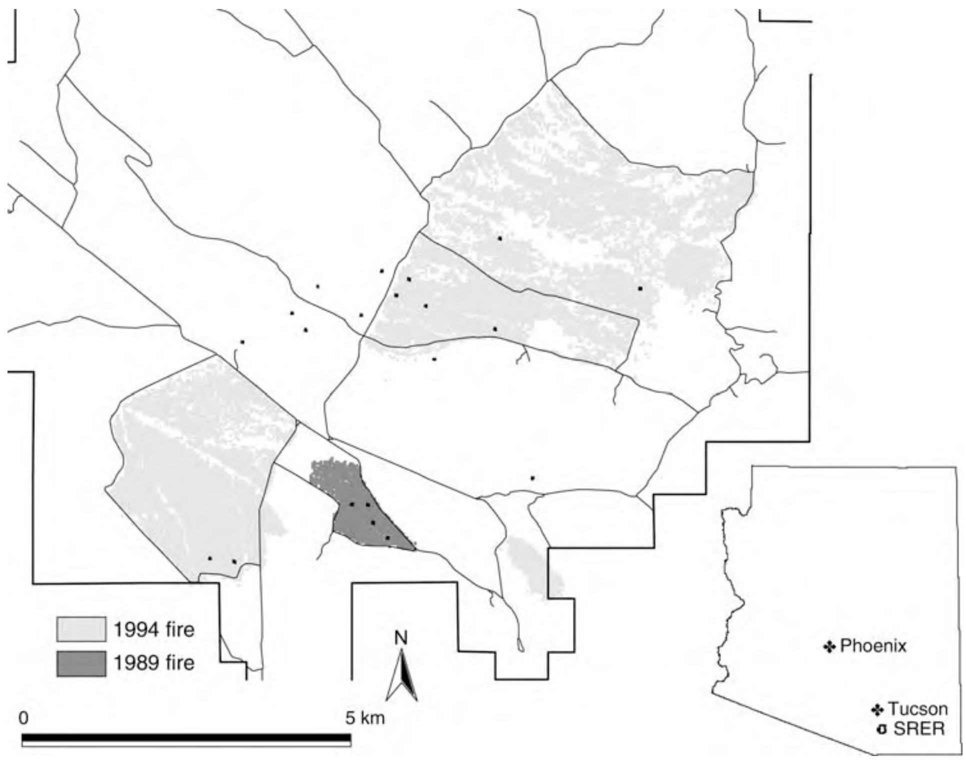


FIG. 1. Fire maps for the 1989 (dark-gray pixels) and 1994 (light-gray pixels) wildfires at the Santa Rita Experimental Range (SRER), Arizona, USA, showing areas where the differenced normalized burn ratio was >100. White areas are unburned since 1984, and black squares are field sampling plots. Linear features are roads and perimeter property boundary. Locations of SRER and major cities within Arizona are shown in the lower right corner.

0.01) sites, respectively (Fig. 5A). The relationship between field-based MLC and satellite-derived WCF was linear ($R^2 = 0.56$, $P < 0.01$; Fig. 5B). Segregating data by fire history failed to improve this R^2 significantly or yield statistically different best-fit functions ($P = 0.87$).

The assessment of postfire recovery at SRER showed that satellite-derived woody-plant cover was statistically comparable on burned and control sites ($P = 0.98$, $F_{1,261} < 0.01$; Fig. 6A). However, the mean biomass of shrubs was greater and less variable (lower CV) on control sites compared to sites burned in 1989 or 1994 ($P < 0.01$, $F_{1,261} = 123.82$) owing to a greater abundance of pixels with relatively high woody-plant biomass ($\geq$1.25 kg/m^2; Fig. 6B and inset table).

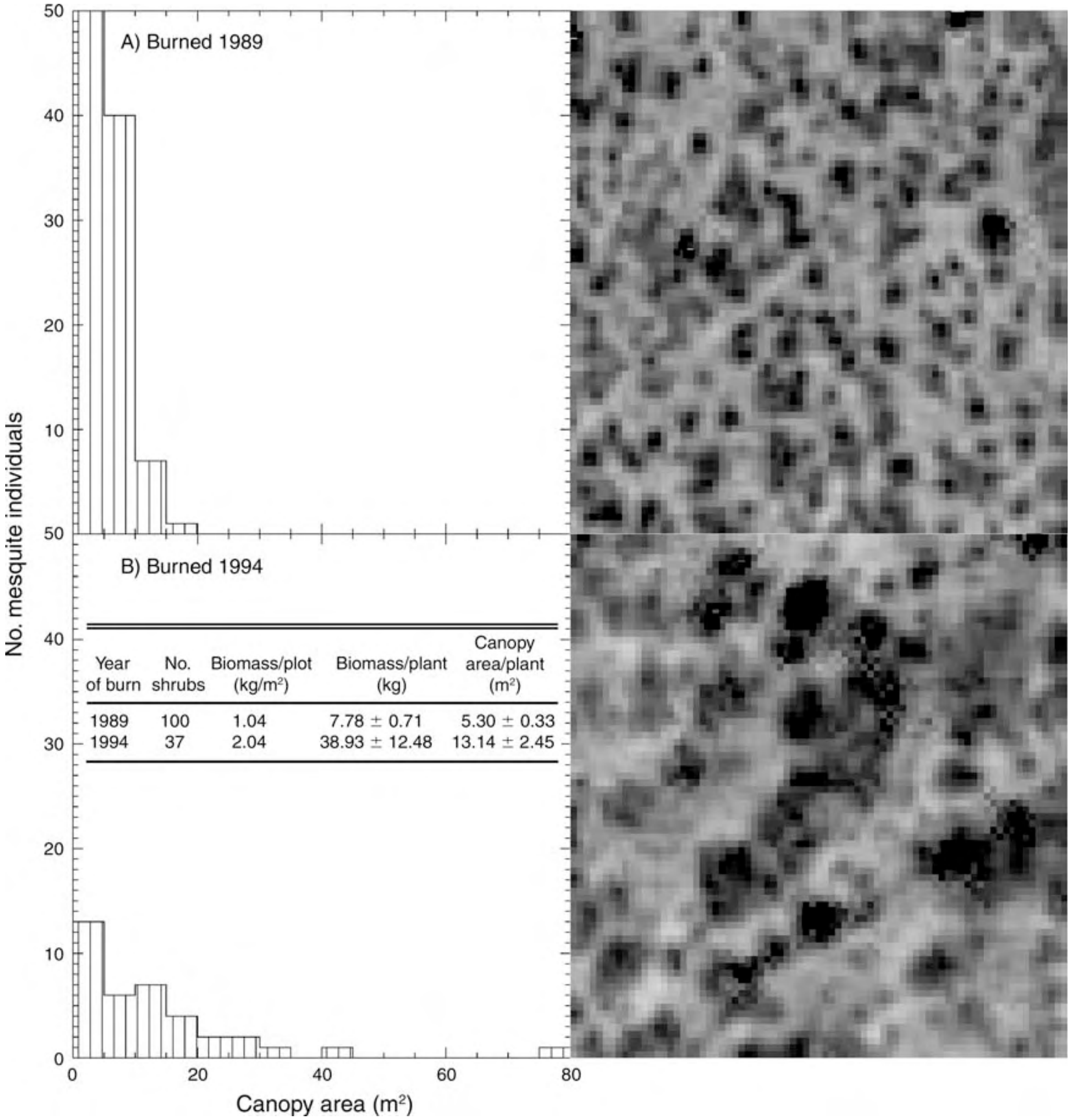
Sensitivity analysis

Predictions of woody biomass from MLC using generic algorithms that ignored fire disturbance always underestimated plot-scale biomass in control areas (Fig. 7A). The actual errors decreased linearly from 0.21 at the lowest MLC to 0.15 kg/m^2 at the highest MLC. In contrast, relative errors dropped exponentially from 78% at the lowest MLC to 7% at the highest MLC, with the greatest reductions occurring between MLC of 0.1 to 0.3. In recently burned areas, predictions based on generic algorithms overestimated biomass when MLC < 0.76. The maximum error of overestimation (0.28 kg/m^2) occurred at a MLC of 0.42, whereas the greatest relative error (94%) occurred at MLC of 0.17. Generally speaking, the largest actual errors (e.g., >0.4 kg/m^2) occurred at a medium range of MLC values (0.25–0.56); and large overall relative errors (e.g., >100%) took place at low MLC (0.11–0.28). At a landscape scale (Fig. 7B), predictions of woody biomass from WCF using generic equations always underestimated biomass in control areas. When WCF was <0.31, the generic model overestimated biomass in recently burned areas. Large overall actual errors (e.g., >0.6 kg/m^2) occurred at medium (0.17–0.26) and high (>0.3) WCF areas; significant overall relative errors (e.g., >100%) occurred in areas with low (0.09–0.17) WCFs.

DISCUSSION

Transformations of woody-plant stand structures after wildfire

Spatial variation in perturbations such as fire (e.g., Fig. 1) may accentuate preexisting heterogeneity in vegetation structure. Within a burned landscape, there may be some areas that escape fire, some areas that experience low-intensity fire, and some that experience high-intensity fire (e.g., Slocum et al. 2003). In portions



Year of burn	No. shrubs	Biomass/plot (kg/m²)	Biomass/plant (kg)	Canopy area/plant (m²)
1989	100	1.04	7.78 ± 0.71	5.30 ± 0.33
1994	37	2.04	38.93 ± 12.48	13.14 ± 2.45

FIG. 2. Size-class distribution of shrubs (primarily *Prosopis velutina*) and associated QuickBird images (pixel size ~0.61 m) of two 40 × 40 m plots with comparable multilayer cover (MLC). (A) Plot on an area burned in 1989 (MLC = 0.83 and 85% from *P. velutina*). (B) Plot on an area burned in 1994 (MLC = 0.86 and 80% from *P. velutina*). The embedded table shows total shrub counts and biomass for each plot and biomass and canopy area per plant on each plot (all values are reported as mean ± SE).

of the landscape experiencing fire, vegetation structure may be "reset" and homogenized to create relatively "even-aged" stands of shrubs (Figs. 2A and 4B). Woody-plant response to fire is also variable and is a function of fire behavior (rate of spread, intensity, and season), size of the woody plant at the time of the fire (smaller plants are generally more susceptible than larger plants), and time elapsed since the last fire (McPherson 1995). In some cases plants are top-killed and regenerate vegetatively; in other cases, plants may be killed and regeneration must be from seed. Field surveys at the SRER indicated that within the area burned in 1994, 10% of the *P. velutina* plants escaped the fire, 30% were killed, and 60% were shoot-killed or crown-scorched and recovered by sprouting (DeBano et al. 1996, Gottfried et al. 2003). Patterns observed in the plot depicted in Figs. 2B and 4D are consistent with these survey results. By contrast, the 1989 fire, which was overall more spatially uniform (Fig. 1), appears to have had a much different effect on vegetation structure (Figs. 2A and 4B).

At the plot and landscape scales, our data indicate that the 1989 and 1994 fires sufficiently altered vegetation structure to change the cover–mass relation-

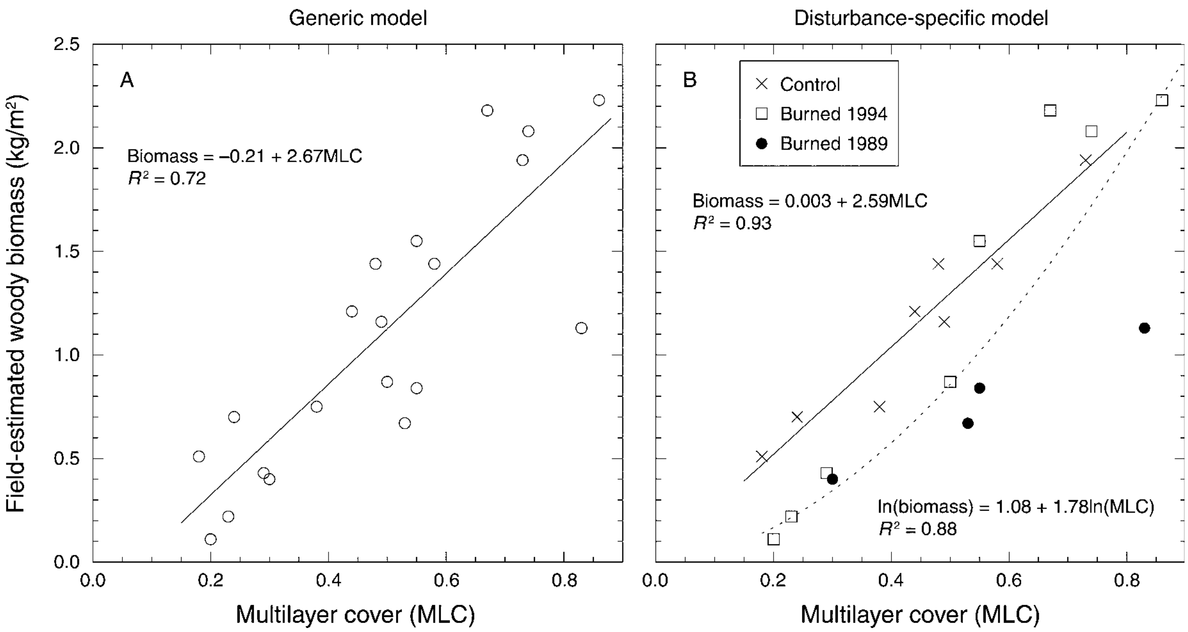


FIG. 3. The relationship between woody biomass and multilayer woody cover (MLC) from field observations (A) for data pooled across all sites (generic model) and (B) for data segregated based on the fire histories (disturbance-specific models).

ship from linear in control settings to nonlinear on burned areas. The relationship between canopy cover and biomass for individual *P. velutina* plants is nonlinear (Table 1), such that for larger plants, a small increase in canopy area translates into a large increase in biomass. Thus, the degree of departure from linearity in plot- and landscape-scale cover–biomass relationships will be a function of the number of relatively large plants on the site and the number of these that escape severe fire damage. The greater the number of large trees escaping fire on a site, the less the divergence in cover–mass relationships. This suggests large-scale estimates of biomass from cover may not be improved by knowledge of fire history (i.e., when an area burned) unless fire history maps are accompanied by information on fire impacts on stand structure within the area burned (e.g., burned severity or woody-plant size-class distributions). In many of the world's drylands, even simple information on fire history (date of burn, spatial extent) generally is unavailable, let alone information on post-fire stand structure. Remote sensing tools have the potential to resolve these limitations, but must be applied with caution and a full understanding of their limitations.

Quantifying woody-plant cover and biomass in semiarid savannas using remote sensing

It is a challenge to quantify green vegetation in dryland environments using remotely sensed data. Most pixels in a dryland landscape are a heterogeneous mixture of vegetation signals influenced by background reflectance from bright or dark soils and litter (Huete 1988, van Leeuwen and Huete 1996, Gao et al. 2000). Results showed that WCF (derived from AutoMCU) can be a salient variable to estimate MLC (Fig. 5B) and woody biomass (Fig. 5A) with known disturbance histories. However, by investigating randomly selected burned and control sites from Fig. 6, we found that the WCF was less sensitive in areas with high woody cover and that it saturated at 0.4 (MLC = 0.87). This saturation might result from the limitation of Auto-MCU treating savannas as two-dimensional (2-D) surfaces rather than 3-D volumes. This constraint would inhibit the utility of using satellite-derived WCF to predict woody biomass in areas with dense woody cover, although such areas are not commonly found in semiarid savannas where annual rainfall is <400 mm (Sankaran et al. 2005).

Recovery of semiarid savannas after recent fire disturbance

A large-scale comparison of WCF-based MLC between areas with contrasting fire histories indicated no differences in woody-plant cover (Fig. 6A). Thus, areal cover of woody plants on burned landscapes had recovered to that of control areas within 11–16 years. However, the variation in MLC in burned sites (CV = 34%) was slightly higher than that of control sites (27%), suggesting a slight amplification of spatial heterogeneity within burned areas. In contrast to MLC, the mean woody biomass in control sites was nearly twofold greater with lower spatial variation than in burned areas (Fig. 6B). Areas with <0.75 kg/m^2 woody biomass occurred in 67% of the pixels on burned sites, compared

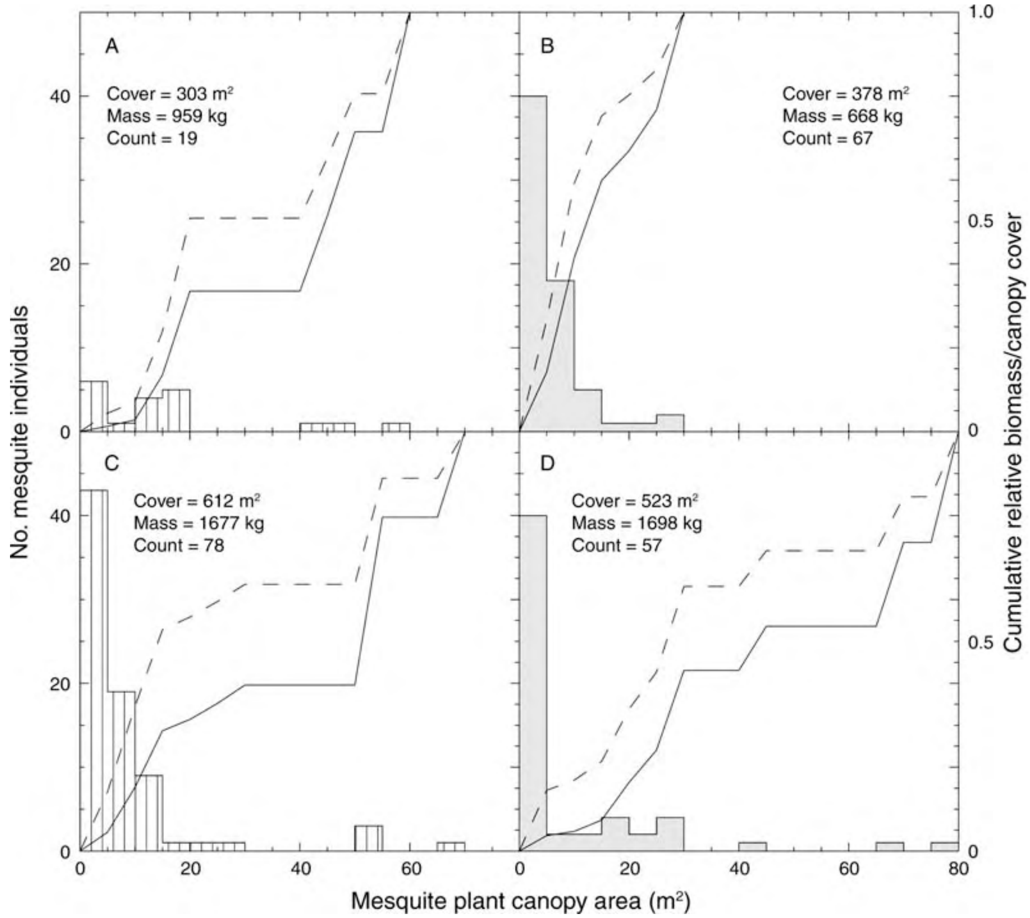


FIG. 4. Size-class distribution (left-hand *y*-axis), and cumulative relative biomass and canopy cover (solid and dashed lines, respectively) (right-hand *y*-axis) of the dominant woody species, *Prosopis velutina* (~93%), within 20×40 m belts in (A, C) control plots and (B, D) plots on sites burned in 1994 with medium (panels A, B; total canopy area = 303 and 378 m^2, respectively) and high (panels C, D; total canopy area = 612 and 523 m^2, respectively) canopy cover.

to only 14% in control sites. Furthermore, areas with >1.75 kg/m^2 of biomass were rare on burned sites (7% of pixels) but were abundant on control sites (38% of pixels). Collectively, these patterns suggest the recovery of woody biomass is still in progress after 11–16 years of regeneration, even though overall cover has returned to control plot levels.

Error in estimating woody biomass without considering fire history

The outcomes of sensitivity analyses at plot and landscape scales validated our hypothesis: fire would alter cover–biomass relationships such that generic cover–biomass algorithms would overestimate woody biomass on areas recovering from fire. The sensitivity analyses for field observations and remote sensing estimates were quite similar (Fig. 7A, B, respectively); the slight discrepancy may reflect differences in data resolution. Predictions of woody biomass based on generic models that did not consider fire disturbance underestimated biomass in control areas regardless of cover levels and overestimated biomass on burned sites. Remote sensing estimates showed that largest overall errors (e.g., >0.6 kg/m^2) occurred at medium (0.17–0.26) and high (>0.3) WCFs. Among randomly sampled pixels ($n = 1052$) from Fig. 6, 63% of WCFs fell within this range. Large relative errors (>100%) would occur at low WCFs locations ranging from 0.09 to 0.17, which was the case in ~30% of all sampled pixels.

Implications for estimating woody biomass in semiarid savannas

Accurate estimates of woody biomass are the foundation for small- and large-scale carbon exchange studies in terrestrial environments, and for scientists, decision makers, and governments charged with developing, implementing, and monitoring carbon sequestration programs. Indirect assessments of biomass from cover are typically the only practical means of quantifying woody biomass in ecosystems, and this approach is

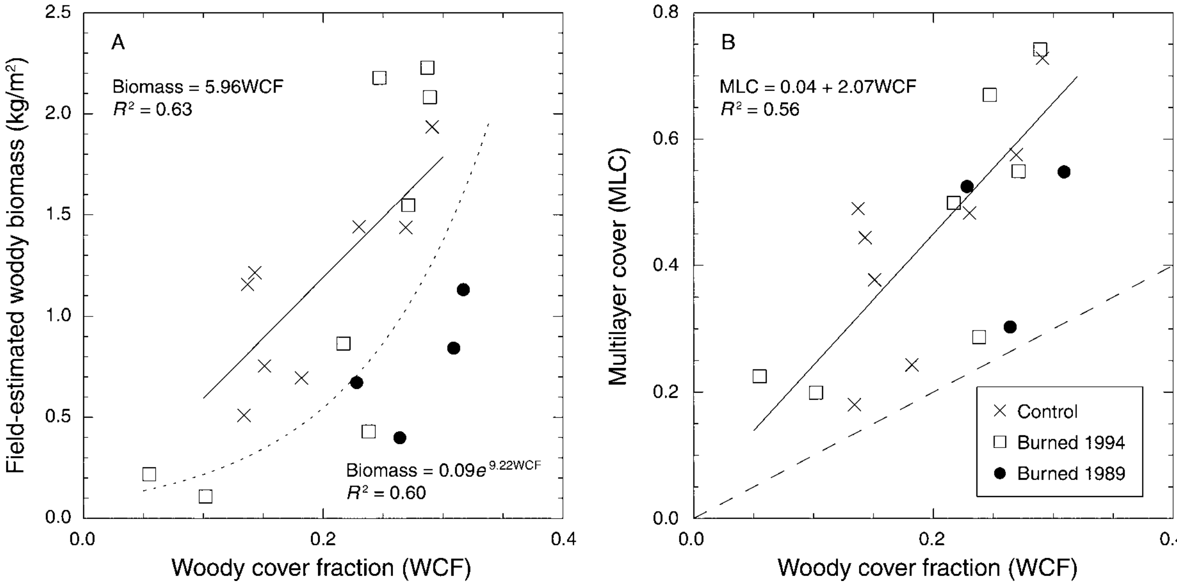
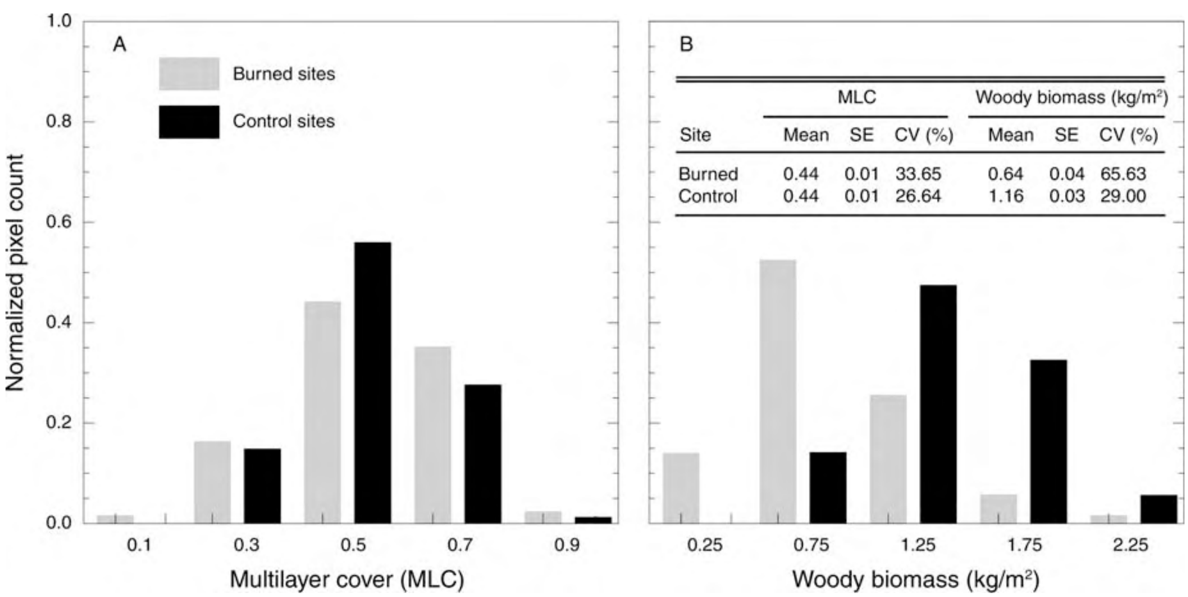


FIG. 5. (A) The relationships between field-estimated woody biomass and woody-cover fraction (WCF) derived from Landsat Thematic Mapper data using the AutoMCU model on burned (dotted line) and control (solid line) sites. (B) The relationship between multilayer woody cover (MLC) from field observations and WCF. The broken line represents a 1:1 relationship.

particularly attractive if it can be used in conjunction with satellite instrument arrays to quantify and monitor biomass over large, remote, and heterogeneous areas. Typically, cover–biomass algorithms are developed for individual plants of a given species at a given locale. These are then generalized and applied to other species and areas where specific algorithms are not available. As shown in this study, care must be taken when using these plant-scale algorithms to estimate biomass at plot and landscape scales at which plant size-class distributions may strongly influence results. In our study, fire history, via its influence on plant size-class distributions, strongly impacted the linearity of algorithms relating cover to biomass at plot and landscape scales. Although our study focused on fire, other disturbances and environmental stresses are also likely to influence cover–mass



Site	MLC Mean	MLC SE	MLC CV (%)	Woody biomass (kg/m²) Mean	Woody biomass (kg/m²) SE	Woody biomass (kg/m²) CV (%)
Burned	0.44	0.01	33.65	0.64	0.04	65.63
Control	0.44	0.01	26.64	1.16	0.03	29.00

FIG. 6. (A) Frequency distribution of multilayer cover (MLC) classes and (B) woody-biomass classes on burned and control areas. Values are derived from contemporary Landsat Thematic Mapper imagery (5 June 2005). Biomass and MLC were estimated using the regression models in Fig. 5. The inset table depicts mean, standard error (SE), and coefficient of variation (CV; %) of AutoMCU-estimated MLC and woody biomass for burned (n = 122) and control (n = 141) areas.

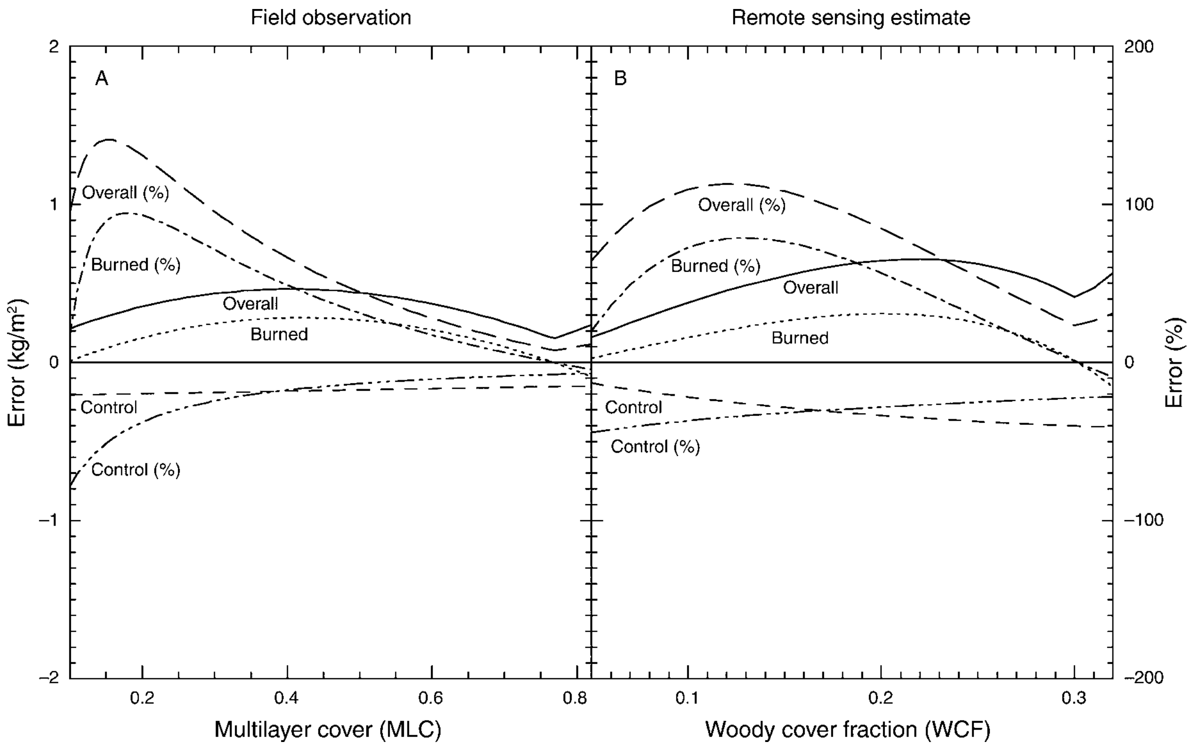


FIG. 7. Potential errors in estimating woody biomass without taking into account fire histories for (A) field observations and (B) remote-sensing-based analysis. The left-hand *y*-axis is the actual error; the right-hand *y*-axis is the relative error. Overall actual and relative errors are the summations of absolute actual and relative errors estimates, respectively, for pooled burned and control settings data.

relationships, though not necessarily in a similar fashion. Knowledge of the disturbance history and land tenure may therefore be pivotal for accurately estimating woody biomass at different scales. However, in most cases, historical, spatially explicit records of disturbance and management practices are not available, and even if they were, site- and disturbance-specific cover–biomass algorithms likely do not exist.

How then to proceed given these substantial constraints? One possibility would be to utilize air- or spaceborne light detecting and ranging (LiDAR) to quantify vegetation height (e.g., Hese et al. 2005, Farid et al. 2006) and then develop libraries of algorithms that relate plant cover and plant height to biomass. Adding the vegetation height dimension would generate a 3-D volumetric metric that may accurately represent aboveground biomass across a broad range of stress and disturbance histories without the need for site-specific knowledge of those stresses and disturbances.

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