

Aboveground biomass and leaf area index (LAI) mapping for Niassa Reserve, northern Mozambique

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Received 18 July 2007; revised 10 March 2008; accepted 13 May 2008; published 12 July 2008.

[1] Estimations of biomass are critical in miombo woodlands because they represent the primary source of goods and services for over 80% of the population in southern Africa. This study was carried out in Niassa Reserve, northern Mozambique. The main objectives were first to estimate woody biomass and Leaf Area Index (LAI) using remotely sensed data [RADARSAT (C-band, $\lambda = 5.7$ -cm)] and Landsat ETM+ derived Normalized Difference Vegetation Index (NDVI) and Simple Ratio (SR) calibrated by field measurements and, second to determine, at both landscape and plot scales, the environmental controls (precipitation, woody cover density, fire and elephants) of biomass and LAI. A land-cover map (72% overall accuracy) was derived from the June 2004 ETM+ mosaic. Field biomass and LAI were correlated with RADARSAT backscatter ($r_{\text{biomass}} = 0.65$, $r_{\text{LAI}} = 0.57$, $p < 0.0001$) from July 2004, NDVI ($r_{\text{biomass}} = 0.30$, $r_{\text{LAI}} = 0.35$; $p < 0.0001$) and SR ($r_{\text{biomass}} = 0.36$, $r_{\text{LAI}} = 0.40$, $p < 0.0001$). A jackknife stepwise regression technique was used to develop the best predictive models for biomass (biomass = $-5.19 + 0.074 * \text{radarsat} + 1.56 * \text{SR}$, $r^2 = 0.55$) and LAI (LAI = $-0.66 + 0.01 * \text{radarsat} + 0.22 * \text{SR}$, $r^2 = 0.45$). Biomass and LAI maps were produced with an estimated peak of 18 kg m^{-2} and $2.80 \text{ m}^2 \text{ m}^{-2}$, respectively. On the landscape-scale, both biomass and LAI were strongly determined by mean annual precipitation ($F = 13.91$, $p = 0.0002$). On the plot spatial scale, woody biomass was significantly determined by fire frequency, and LAI by vegetation type.

Citation: Ribeiro, N. S., S. S. Saatchi, H. H. Shugart, and R. A. Washington-Allen (2008), Aboveground biomass and leaf area index (LAI) mapping for Niassa Reserve, northern Mozambique, *J. Geophys. Res.*, *113*, G02S02, doi:10.1029/2007JG000550.

1. Introduction

[2] Savannas and woodlands are a major component of the world's vegetation covering one-sixth of the global land surface [Grace *et al.*, 2006] and one-half of the African continent [Menaut, 1983]. They account for about 30% of the primary production of all terrestrial vegetation [Grace *et al.*, 2006]. The southern African savannas cover 54% of the sub-continent and are part of the Sudan-Zambezian phytoregion. This region is important for its extension (covers most of the Central African plateau and its escarpments) and plant diversity of over 8,500 species [White, 1983]. Miombo woodlands (hereafter called miombo) are by far the most extensive vegetation type in the Zambezian phytoregion (covering about 70% of the phytoregion). Within this

region, miombo extends from Tanzania and southern Zaire in the north to Zimbabwe in the south, and across the continent from Angola, through Zambia, Malawi and Mozambique [Campbell *et al.*, 1996]. In Mozambique, the region of this study, miombo covers about two thirds of the territory [Saket, 1994].

[3] Resources from miombo are central to the livelihood of millions of rural and urban people across the region. In 1990, about 39 million people lived in areas covered by miombo, and an additional 15 million relied on miombo wood or charcoal as a source of energy [Campbell *et al.*, 1996]. Environmentally, miombo is characterized by high levels of biodiversity and have a regional and global contribution through emissions of trace gases from fires, soils, vegetation and animals, and by the sequestration of carbon in their soils and biomass [Scholes, 1997].

[4] The trio of fire, climate and the great herds of mammalian herbivores (such as elephants -*Loxodonta africana* Blumenbach) has long been considered the primeval sculptors of the southern African landscapes [Owen-Smith and Danckwerts, 1997]. Climate may set the limits to plant growth, but more often fire and herbivores determine structural and compositional vegetation patterns in the region [Bond, 1997]. The limited work conducted in the miombo region indicates that fire and elephants together act as a

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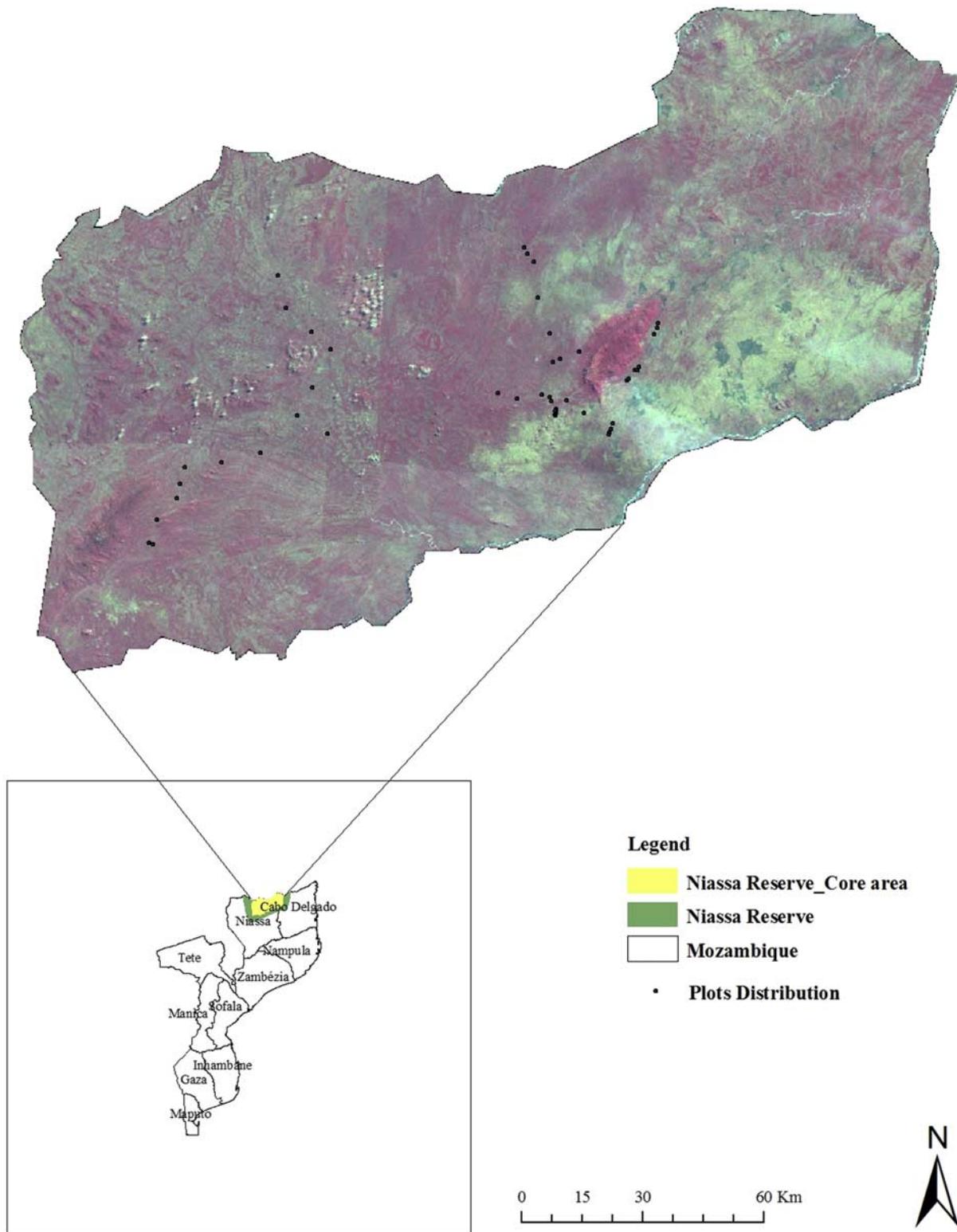


Figure 1. A Landsat ETM+ mosaic from June 2004 (band combination 4-3-2), of the 23,000-km² conservation area of Niassa Reserve in northern Mozambique showing the gradient of IR reflectance from east to west.

Table 1. List of Remote Sensing Data and Metrics from Landsat, SRTM, and RADARSAT

Data	Instrument	Acquisition Date	Source	Application in This Study	Original Spatial Resolution
Spectral reflectance	Landsat ETM+ (Path/Row: 167/68, 167/69, 166/68, and 166/69)	8 and 15 Nov 2001 (wet season)	CENACARTA – Mozambique	Plot allocation	30 m
NDVI, SR	Landsat ETM+ (Path/Row: 167/68, 167/69, 166/68, and 166/69)	11 and 17 Jun 2004 (dry season)	CENACARTA – Mozambique	Land cover map NDVI and SR extraction	30 m
Radar backscatter	RADARSAT 1 (C-band, HH polarization mode)	Jul 2004 (dry season)	Jet Propulsion Laboratory (JPL)	Biomass and LAI estimations	30 m
Elevation	SRTM	1999	http://www2.jpl.nasa.gov/srtm/	Land cover map	90 m

powerful restriction on the recruitment of trees. This ultimately decreases woody vegetation productivity [Guy, 1981, 1989; Ben-Shahar, 1998; Mapaure and Campbell, 2002; Walpole et al., 2004; Baxter and Getz, 2005; Ribeiro, 2007; Ribeiro et al., 2008], with consequences for carbon and energy balances [Houghton, 2005].

[5] Time and costs greatly limit field studies of large-scale spatial variations in vegetation. Moreover, the remoteness and low accessibility of some areas may constrain representative sampling. In this context, satellite remote sensing systems are potentially useful for obtaining information about vegetation structure and productivity [Lucas et al., 2004].

[6] This study is the first attempt to estimate large-scale variations in aboveground woody biomass (hereafter called biomass) and Leaf Area Index (LAI) in Niassa Reserve. Our overall objective is to quantify spatial variations of biomass (and carbon) and LAI within the Niassa Reserve in relation to environmental and disturbance factors. To achieve this objective three research questions were defined:

[7] 1. Can aboveground biomass, carbon stock density and LAI be estimated on a landscape-scale using remotely sensed data (RADARSAT and Landsat ETM+ derived vegetation indices) calibrated by field measurements?

[8] 2. Are there detectable spatial patterns, particularly gradients of biomass, carbon stock density and LAI, across Niassa Reserve?

[9] 3. At landscape and plot levels, are biomass and LAI differently influenced by environmental (precipitation, soil nutrients and vegetation cover) and disturbance (fire frequency and elephant density) factors?

2. Materials and Methods

2.1. Study Site

[10] The Niassa Reserve is located in northern Mozambique between the parallels 12°38'48.67"S and 11°27'05.83"S and the meridians 36°25'21.16"E and 38°30'23.74"E [WWF SARPO, 2002a, 2002b]. The core area of the reserve has an extension of 23,040 km². A buffer zone of five hunting blocks surrounding the core area brings the total area to over 42,300 km² (Figure 1) [Hatton et al., 2001].

[11] The climate of the area is tropical sub-humid, with mean annual precipitation (MAP) of 900 mm that increases from east (800 mm) to west (1,200 mm) and mean annual temperature (MAT) of 25°C that ranges from 20 to 26°C during the dry season (May–October). The wet

season runs from November to April with MAP of 900 mm and MAT of 30°C. The Reserve has a gently undulating landscape on a plateau with elevation ranging from 300 to 600 m above-sea level. The reserve has two main peaks, the Jao Mountain in the west with an elevation of 1,200 m above sea level (asl) and the Mecula Mountain in the east, which is 2,000 m high asl.

[12] Miombo covers about 72% of the total area of the reserve and is dominated by *Julbernardia* and *Brachystegia* tree species. Niassa Reserve has been described as containing the richest diversities of fauna and flora within Mozambique [Leo-Smith et al., 1997] and is a key conservation area of miombo in southern Africa.

[13] Apart from its extent, it is highly remote, has about 21,000 people living within the core area, and the highest concentration of elephants in miombo in the country. People are concentrated around the two main villages, Mavago in the west and Mecula in the east, and along the main road. Human intervention in Niassa Reserve during 20 years of Civil War (1981–1992) and Post-War (1993–1997) in Mozambique was limited. Consequently, Niassa Reserve has been considered one of the most pristine areas in the region.

[14] Fire and elephant herbivory are two important ecological factors within the Niassa Reserve. The fire season runs from May to October, with a peak in the late dry season (August to October). Fire frequency is greater in the eastern portion of the reserve (four to five times in five years) than the west (two to three times in five years) (N. S. Ribeiro et al., submitted manuscript). Fires are mainly anthropogenic ground fires and caused by subsistence hunting, pedestrian trade travel to Tanzania, honey collection and to a lesser extent slash and burn agriculture (around the two main villages of Mecula and Mavago) (P. Tilley and A. J. A. Abacar, unpublished data; Chande, personal communication). Niassa has the highest concentration of elephants in miombo in the country. In 2004, the elephant population was estimated at 13,000 animals, with the highest concentrations in the eastern Niassa Reserve. The elephant population in Niassa Reserve does not migrate much in and out of the reserve. Although they move around within the reserve, they tend to be concentrated on the eastern side, where food and water resources are readily available throughout the year. These restricted movements make the elephant population more or less stable, without wide variation in their distribution. This study was carried out in the 23,040 km² core area of Niassa Reserve to avoid

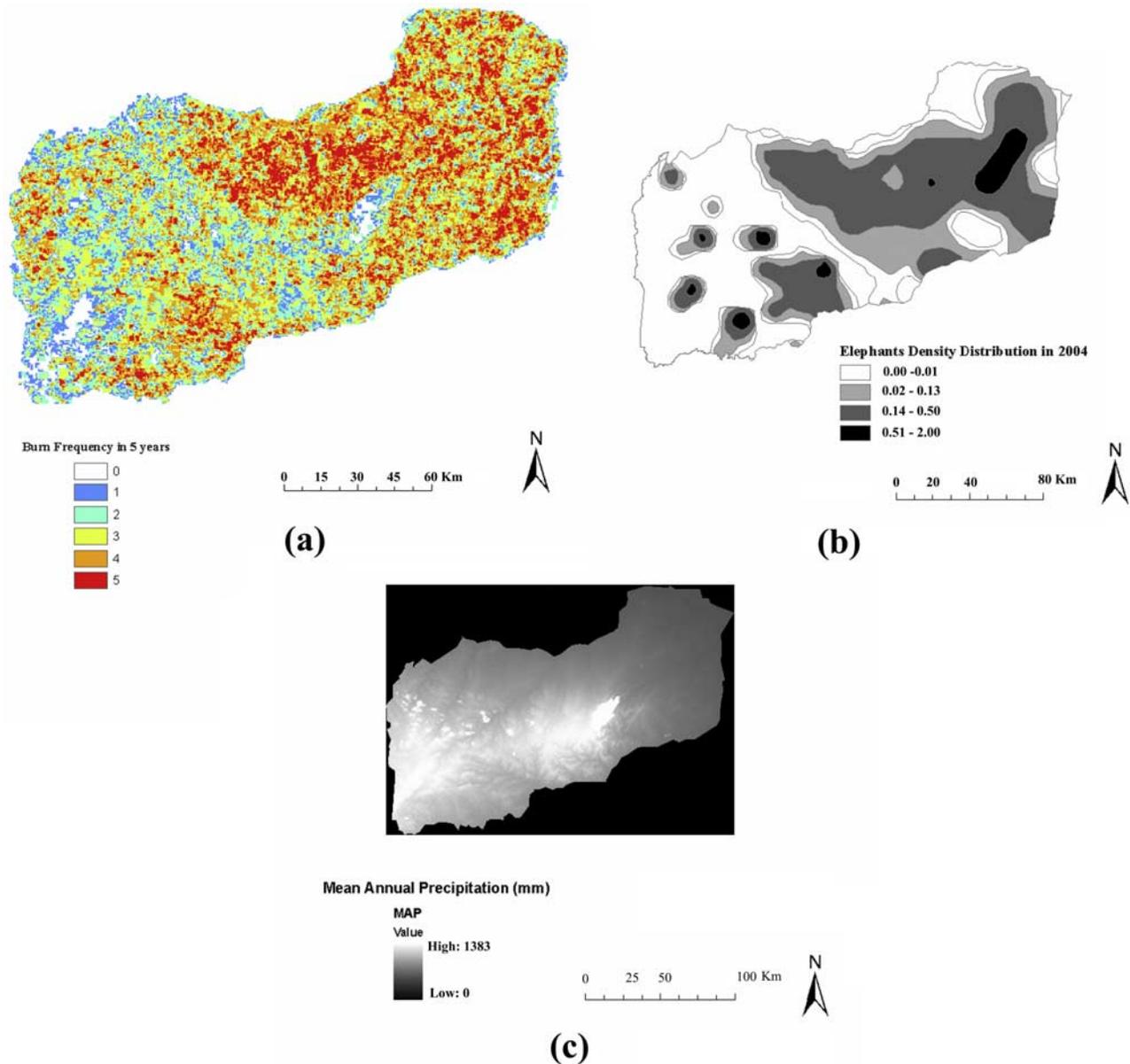


Figure 2. Data layers used as determinants of biomass and LAI: (a) Fire frequency during 5-year period (2001–2005); (b) elephant density for the year 2004; (c) mean annual precipitation (1950–2000).

confusion from the wildlife, fire and vegetation management interventions conducted in the buffer zone.

2.2. Data Acquisition

2.2.1. Field Data

[15] A gradient of increasing miombo density from east to west was observed in the decreasing reflectance of the infrared (IR) component of the wet season November 2001 4-scene mosaicked Landsat Enhanced Thematic Mapper plus (ETM+; Table 1; Figure 1). Previous research suggested that the spatial heterogeneity of this gradient is a function of higher fire frequency and elephant density in the eastern portion of the reserve and a 400 mm increase in precipitation from east to west [Ribeiro, 2007; Ribeiro *et al.*, 2008]. This observed spatial heterogeneity of vegetation density and

structure was used to determine the field sampling effort and plot allocation over the reserve (Figure 1).

[16] A total of fifty circular plots sized 30 m in diameter were established in homogeneous areas of vegetation, in July of 2004. Each plot was located and geo-referenced using a Geographic Positioning System unit (GPS Garmin III plus, ± 3 m accuracy). The limited accessibility of the area largely constrained field plot allocation.

[17] The following measurements were taken within each field plot: land cover type, diameter at breast height (dbh) of all trees with dbh above 5 cm, and woody LAI. Above-ground woody biomass was estimated for individual trees (dbh range from 5 to 50 cm) using an allometric equation developed by Mugasha and Chamshama [2002] for the Kitulungalo forest in Morogoro, Tanzania under similar

vegetation (dbh range from 1 to 50 cm) and edaphic-climatic conditions as Niassa Reserve:

$$WB = b_0 * (dbh^{b_1}) \quad (1)$$

where WB = woody biomass (kg tree⁻¹), dbh = diameter at breast height (cm), b_0 and b_1 = regression coefficients ($b_0 = 2.553$; $b_1 = 0.0625$).

[18] LAI was indirectly estimated in each plot with the LAI-2000 plant canopy analyzer (LiCOR, Inc., Lincoln, Nebraska) at the beginning of the wet season according to methods recommended by *Welles and Norman* [1991], *LI-COR* [1992], and *Hicks and Lascano* (1995) cited by *Malone et al.* [2002].

[19] Carbon stock density was estimated using a conversion coefficient of woody biomass of 50% [*Fang et al.*, 1996].

[20] Ten soil samples within the uppermost 10 cm of the topsoil (A horizon) were collected in each plot and analyzed for nitrogen (N), phosphorous (P) and organic matter (SOM) in the laboratory of the Faculty of Agronomy and Forestry, Eduardo Mondlane University in Maputo, Mozambique.

2.2.2. Remote Sensing Data

[21] Four atmospherically corrected ETM+ images from June 2004 were obtained from the Mozambican National Cartography Center (CENACARTA) and mosaicked into a single scene (Table 1).

[22] Microwave data from the 30 m RADARSAT backscatter (in decibels) from July of 2004, in Standard beam mode two was obtained from the NASA Jet Propulsion Laboratory (JPL). RADARSAT is a Synthetic Aperture Radar (SAR) C-band (5.7 cm wavelength and frequency of 5.2 GHz) instrument, which is sensitive to upper forest canopy structure and biomass (leaves and branches) of open forest and woodlands savannas (Table 1).

[23] Freely available Shuttle Radar Topography Mission (SRTM) digital terrain data obtained from the Website <http://www2.jpl.nasa.gov/srtm/> was resampled from 90 m to 30 m and used to separate the vegetation classes in the land cover mapping process.

2.2.3. Rainfall, Fire Frequency, and Elephant Density Data

[24] Burned areas over the 5-year period (2001 – 2005) were derived for the Niassa Reserve from the MODIS active fire and surface reflectance daily products (Figure 2) [*Justice et al.*, 2002; *Ribeiro et al.*, submitted manuscript].

[25] Mean annual precipitation (MAP) from 1950 to 2000 from the *Worldclim* data set was used in this study (Figure 2) [*Hijmans et al.*, 2005] (www.worldclim.org). This data set was interpolated by adjusting for elevation using the SRTM digital elevation data. As a consequence, MAP and SRTM are not strictly independent and show high correlation (Pearson $r = 0.97$). To avoid data redundancy SRTM elevation data are not used as an input to the biomass and LAI predictive models in this study.

[26] Elephant density has been aerially surveyed for the entire Niassa Reserve every two years since 1998 (*Craig and Gibson*, unpublished data, 1998, 2000, 2002, 2004). These data are archived as GIS layers and are available for use through the Niassa Reserve management institution.

The GIS layer used in this study contains the spatial distribution of elephant density in 2004 (Figure 2).

2.3. Data Preprocessing

[27] The four ETM+ scenes from June of 2004 were georeferenced using Ground Control Points (GCPs) collected in the field and then mosaicked. All other images were georeferenced to the ETM+ mosaic image in UTM projection (zone 37S, datum WGS84) by image-to-image registration at ≤ 0.5 Root Mean Square Error (RSME) using twenty control points that corresponded to river/stream bifurcations and other identifiable features at both the 30 m resolution and high panchromatic band at 15 m. Although the Landsat 7 ETM+ data after July 2003 has been collected in Scan Line Corrector (SLC)-off mode, all the plots and extracted data were outside areas of missing data.

[28] The “Simple Ratio” (SR [*Birth and McVey*, 1968]) and “Normalized Difference Vegetation Index” (NDVI [*Rouse et al.*, 1974]) were derived from the ETM+ mosaic image. These indices have been widely used as surrogates of biomass, LAI, and other important plant characteristics [*Huete et al.*, 2002]. The SR is the ratio between near-infrared (NIR) and red reflectance:

$$SR = NIR/Red \quad (2)$$

[29] The NDVI is a simple metric that is computed as follows:

$$NDVI = (NIR - Red)/(Red + NIR) \quad (3)$$

[30] Owing to the coherent nature of SAR, the orthorectified RADARSAT images needed to be despeckled. The refined Lee sigma speckle filter [*Lee*, 1981] was applied with an 11×11 window.

2.4. Data Analysis

2.4.1. Land Cover Map

[31] The possibility of distinguishing between different miombo densities is crucial to study biomass variations at the landscape level. Consequently, we produced a land cover map from the ETM+ mosaic according to an existing classification scheme for Mozambique [*Saket*, 1994].

[32] The classification proposed by *Saket* [1994] was based on Landsat images and integrates different categories of land use such as closed lowland forest (crown cover $>75\%$), medium closed lowland forests (crown cover between 50% and 75%), open lowland forests (crown cover between 25% and 50%), thicket, shrubland, wooded grasslands, grasslands, agriculture, long fallows, short fallows, mangroves and water. Miombo woodlands fall into the category of lowland forests of different densities.

[33] The land cover map was produced with a decision rule procedure in ERDAS imagine 8.7. This procedure performs a multistage classification, by using a series of binary decisions to place pixels into classes. Each decision divides the pixels into two classes based on an expression. Each new class can be divided into two more classes based on another expression [*Saatchi et al.*, 2007]. The procedure was based on maximum likelihood supervised classification of the ETM+ mosaic, a shape and spectral image segmen-

Table 2. Brief Description of the Land Cover Classes

Land Cover Class	Description
(1) High density woodlands	The crown cover of the upper stratum is greater than 75% and the herbaceous layer is poorly developed or totally absent.
(2) Medium density woodlands	The crown cover of the dominant layer ranges from 50 to 75%. A moderate dense shrub layer is normally present with a ground stratum normally sparse.
(3) Low density woodlands	The upper layer crown cover is between 25 and 50% and a well – established herbaceous stratum is normally present.
(4) Wooded grasslands	Mosaic of grass and other herbs with scattered or grouped woody plants and trees (crown coverage from 10 to 20%).
(5) Wooded gallery grasslands	Mosaic of grass and other herbs with scattered or grouped woody plants and trees (crown coverage from 10 to 20%). Occur along the streams and rivers.
(6) Mountain forests	Evergreen forests with more than 80% tree cover, which occur on the top and slopes of the Mecula and Jao Mountains.
(7) <i>Inselbergs</i>	Granitic formation rocks with no or little vegetation.
(8) Recently burned areas	Visually detected burned areas (black color in the 432 band combination of the ETM+).
(9) Clouds	Visually detected clouds (white color in the 432 band combination of the ETM+).
(10) Shadow	The shades of few clouds found in the ETM+ scene.

tation produced classification of bands 5 (MIR) and band 4 (NIR). In combination with the supervised classification, segmentation was used to improve class separability. In the final step, elevation data from SRTM were used to separate mountain forests from lowland woodlands.

[34] To clearly represent the varied vegetation density and having Saket's classification as a base, we defined 10 land cover classes appropriated for Niassa Reserve (Table 2).

[35] An accuracy assessment of the land cover map classification indicated an overall accuracy of 72%. It was performed by comparing the classification results to known

land cover reference data that consisted of the fifty field plots and 117 additional ground control points (GCPs) [Jensen, 2001].

2.4.2. Biomass Estimation

[36] The estimation algorithm was developed first by testing field estimations of biomass and LAI for normality using the *Proc Univariate* procedure in SAS 9.1 (SAS Institute Inc., 2000–2003). The test revealed that both variables are normally distributed. Average remote sensing measurements were extracted within a 3 * 3 window around each field plot. The 3 * 3 window was used to reduce the

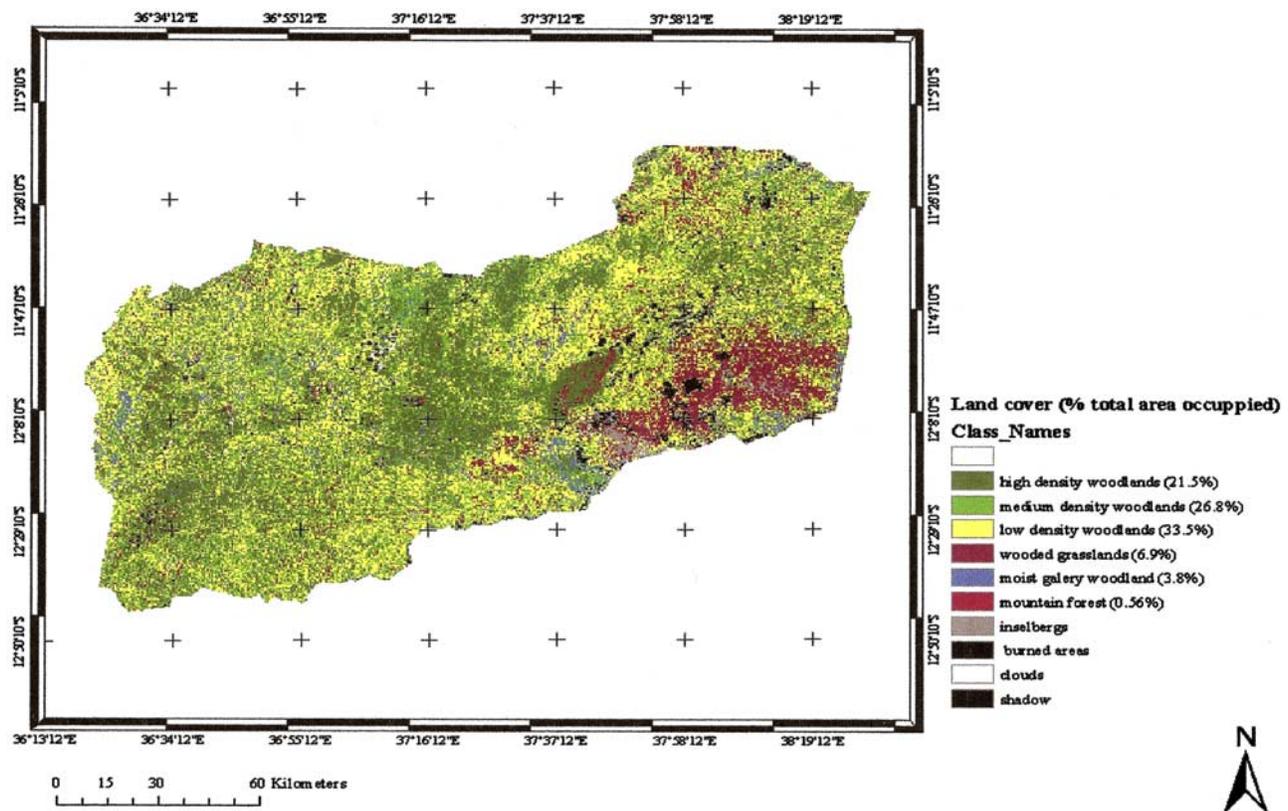


Figure 3. Vegetation map (and percentage of total area covered by each vegetation class) of the Niassa Reserve produced with 72% overall accuracy from the June 2004 ETM+ mosaic image using the decision rule method.

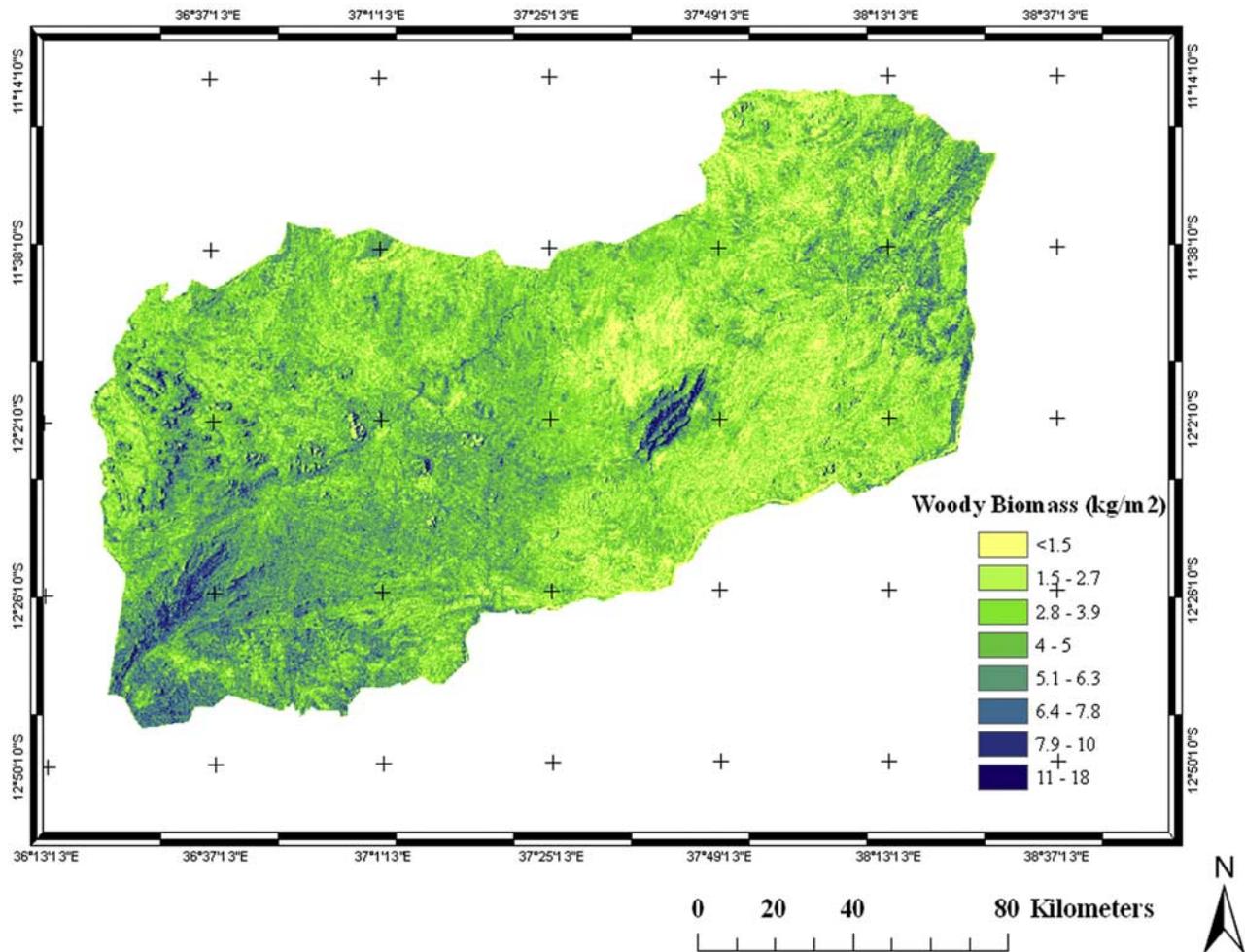


Figure 4. Spatial distribution of biomass within the Niassa Reserve derived from RADARSAT backscatter (C-band, 5.7 cm wavelength) and ETM+ derived SR. The regression model is: Biomass (kg m^{-2}) = $-5.19 + 0.074 * \text{RADARSAT} + 1.56 * \text{SR}$; $r^2 = 0.55$; $p < 0.0001$.

influence of radar fading. Spectral information collected within each window includes RADARSAT backscatter and ETM+ derived SR (equation (2)) and NDVI (equation (3)) data. Plots within burned (class 9) and shaded (class 10) areas were eliminated from the data set. This reduced the number of usable plots to 39. We re-examined the relationships (Spearman correlation) between spectral and field data, and selected the more strongly correlated variables for the prediction model.

[37] Optimum multiple regression models were developed to predict biomass and LAI from the spectral data, using a jackknife stepwise procedure in SAS 9.1. The jackknife procedure randomly removes one observation at a time to produce the regression model [Sokal and Rohlf, 2003] with the best coefficient of determination and the least error. The stepwise process enters each independent variable, evaluates the differences in mean and the correlation to those variables already entered in the process and eliminates redundant variables.

2.4.3. Determinants of Biomass and LAI

[38] We investigated the relationship between satellite derived aboveground biomass and LAI (dependent variables) and prevailing environmental and disturbance condi-

tions (independent predictors) at the plot and landscape-levels using a one-way analysis-of-variance (ANOVA). The idea behind this analysis is that the controls over woodland structure and functioning may vary according to the scale of observation. At the plot level, Worldclim MAP, land cover, 5-year fire frequency, elephant density, and soil nitrogen, phosphorous and organic matter were analyzed as predictors of biomass and LAI. At the landscape-level, the same predictors with the exception of the soil predictors were analyzed. For this analysis, a subsample of spatially disparate pixels across the gradient was used. Fire frequency was used as the classifying variable. Additionally, a Tukey - Kramer statistical test was performed to detect biomass, LAI and soil differences among plots.

3. Results

3.1. Land Cover Map

[39] The land cover map suggests that 82% of the reserve is woodland. Low and medium-density woodlands occupy the lowland areas. High-density woodlands are located on the slopes of the Mecula and Jao mountains in the central portion of reserve, and along the mainstreams in the form of

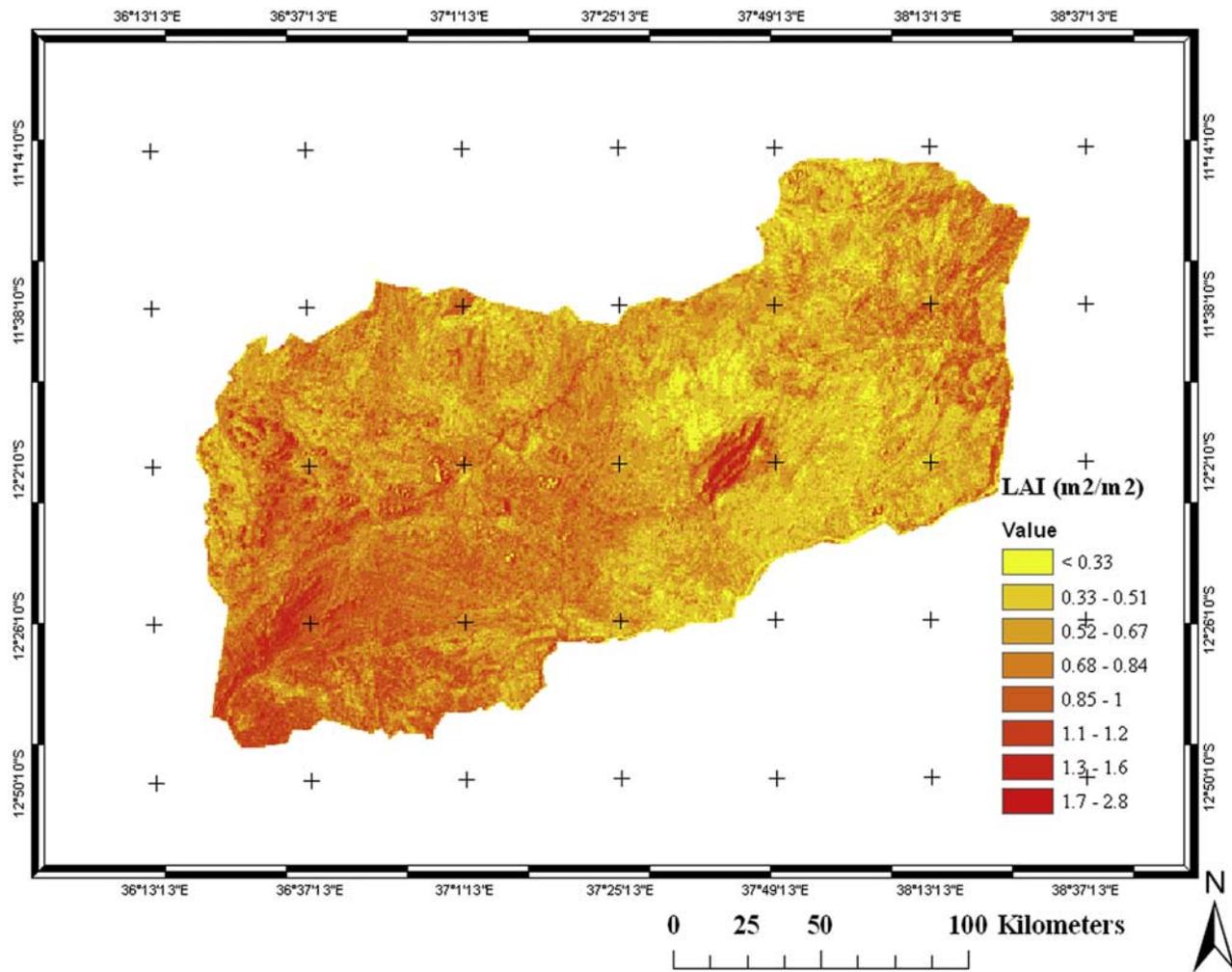


Figure 5. Spatial distribution of LAI within the Niassa Reserve derived from RADARSAT backscatter (C-band, 5.7 cm wavelength) and ETM+ derived SR. The regression model is: $LAI (m^2 m^{-2}) = -0.66 + 0.01 * RADARSAT + 0.22 * SR$; $r^2 = 0.45$; $p < 0.0001$.

riverine forests. Mountain forests cover 0.6% of the reserve and are restricted to the very top of the mountains. Wooded grasslands compose 7% of the total area and are located in the southeastern portion of the reserve (brown color in Figure 3). The remaining 10% corresponds to the other land cover classes (burned areas, clouds, shades and *inselbergs*).

[40] The vegetation map produced with the decision rule procedure had an accuracy of 72%. This represents an improvement comparatively to the map produced by using only the maximum likelihood classification method (which had an accuracy of 60%).

3.2. Relationship Between Field and Remote Sensing Data

[41] The best correlations between field measurements of biomass and the remote sensing data sets were found with the radar backscatter measurements ($r_{biomass} = 0.65$ and $r_{LAI} = 0.57$; $p < 0.0001$). Similar results with other C-band systems have been observed over woodlands in Australia [Cronin *et al.*, 2000]. However, a higher correlation was observed for woodlands in the Amazon Basin by using the L-band (23.5-cm) from JERS-1 ($r = 0.82$) [Saatchi *et al.*, 2007].

Table 3. Biomass, Carbon Stock Density, and LAI per Vegetation Type in Niassa Reserve

Vegetation Type	Biomass \pm Stdev ($kg ha^{-1}$)	Carbon Stock Density (50% of Biomass) ($MgC ha^{-1}$)	LAI \pm Stdev ($m^2 m^{-2}$)
High density woodlands	5.19 ± 2.84	35	1.13 ± 0.42
Medium density woodlands	3.9 ± 1.9	19.5	0.76 ± 0.4
Low density woodlands	2.3 ± 1.5	10.5	0.5 ± 0.21
Wooded grasslands	2.58 ± 1.65	12.9	0.48 ± 0.24
Mountain forests	13.5 ± 4.3	67.5	2.2 ± 0.4

Table 4. Tukey-Kramer Statistic Test at the 5% Level of Significance to Test for Differences in Vegetation Structural Parameters and Soil Nutrients Among Plots^a

Fire Frequency (year ⁻¹)	N	Biomass ± Stdev (kg m ⁻²)	LAI ± Stdev (m ² m ⁻²)	SP ± Stdev (mg 100 ⁻¹)	SOM ± Stdev (%)	SN ± Stdev (%)
0	5	8.99 ± 4.3(a)	1.41 ± 0.4(a)	2.21 ± 2.10(a)	2.25 ± 0.74(a)	0.09 ± 0.03(a)
1	11	5.46 ± 2.0(b)	0.88 ± 0.4(a)	2.00 ± 2.00(a)	1.28 ± 0.66(a)	0.05 ± 0.03(b)
2	10	5.46 ± 1.8(b)	0.88 ± 0.4(a)	2.36 ± 2.33(a)	1.71 ± 0.81(a)	0.07 ± 0.03(ab)
3	14	4.83 ± 1.9(b)	0.81 ± 0.4(a)	1.30 ± 1.64(a)	1.29 ± 0.56(a)	0.05 ± 0.02(b)
4	7	4.86 ± 2.5(b)	0.84 ± 0.4(a)	2.04 ± 2.52(a)	1.32 ± 0.41(a)	0.05 ± 0.02(b)
5	3	5.82 ± 1.2(b)	0.93 ± 0.2(a)	1.9 ± 1.45(a)	1.54 ± 0.38(a)	0.06 ± 0.006(b)

^aLAI, leaf area index; SN, soil nitrogen; SP, soil phosphorous; SOM, soil organic matter; Stdev, standard deviation.

[42] SR has the second best correlation ($r_{\text{biomass}} = 0.36$ and $r_{\text{LAI}} = 0.40$; $p < 0.0001$), and NDVI produced the lowest correlation ($r_{\text{biomass}} = 0.30$ and $r_{\text{LAI}} = 0.35$; $p < 0.0001$). The low correlations with vegetation indices may be related to their high sensitivity to greenness, density and seasonality. For this time of the year (beginning of the dry season) the vegetation indices carry more information about the woody vegetation. However, much of the grass and herbaceous understory are still green, consequently affecting the values for NDVI and SR.

[43] The stepwise jackknife technique produced the following best regression models for biomass and LAI predictions:

$$\text{Biomass}(\text{kg m}^{-2}) = -5.19 + 0.074 \cdot \text{RADARSAT} + 1.56 \cdot \text{SR};$$

$$r^2 = 0.55; p < 0.0001 \quad (4)$$

$$\text{LAI}(\text{m}^2 \text{m}^{-2}) = -0.66 + 0.01 \cdot \text{RADARSAT} + 0.22 \cdot \text{SR};$$

$$r^2 = 0.45; p < 0.0001 \quad (5)$$

3.3. Spatial Distribution of Biomass, LAI, and Carbon Stock Density

[44] The biomass and LAI maps produced from equations (4) and (5) are shown in Figures 4 and 5. The mean biomass and LAI for the entire Niassa Reserve are estimated to be $7.02 \pm 5.5 \text{ kg m}^{-2}$ and $1.13 \pm 0.81 \text{ m}^2 \text{m}^{-2}$, respectively. Based on the coefficient of 50%, the mean carbon stock density for the entire Niassa Reserve is estimated at 35 MgC ha^{-1} . At the plot level, the carbon densities were estimated at $28.4 \pm 2.55 \text{ MgC ha}^{-1}$, ranging from 5.3 MgC ha^{-1} in very disturbed plots to 80.8 MgC ha^{-1} in undisturbed plots around the main camp site. Even though the latter is an outlier for this area, it is found in plots that have been protected from fire for the last 9 years.

[45] The biomass and LAI for the entire Niassa Reserve range between 1.5 and 18 kg ha^{-1} and 0.33 and $2.8 \text{ m}^2 \text{m}^{-2}$, respectively (Figures 4 and 5). The lower end values are mostly found over wooded grasslands, where the low tree density explains the small values. There seems to be an overestimation of the higher value of 180 Mg ha^{-1} observed for the top of the Jao and the Mecula mountains. As a consequence this value should be used with caution.

[46] The average biomass, carbon and LAI stocks per vegetation class are presented in Table 3. About 80% of the reserve is covered by low, medium and high density miombo woodlands, which make up to 45% of the total biomass and have a mean LAI of $0.79 \pm 0.13 \text{ m}^2 \text{m}^{-2}$. The highest mean biomass and LAI values are found in

the mountain forests (biomass = $13.5 \pm 4.3 \text{ kg m}^{-2}$ and LAI = $2.2 \pm 0.42 \text{ m}^2 \text{m}^{-2}$), while the lowest values are found in the wooded grasslands (biomass = $2.58 \pm 1.65 \text{ kg m}^{-2}$ and LAI = $0.48 \pm 0.24 \text{ m}^2 \text{m}^{-2}$).

3.4. Determinants of Biomass and LAI

3.4.1. Landscape Level

[47] At the landscape level, the General Linear Model (GLM) explains 28% and 27% of the overall variation in biomass and LAI, respectively. The GLM reveals that at the 5% cut-off level, MAP ($F_{\text{biomass}} = 13.91$; $F_{\text{LAI}} = 13.62$; $p = 0.0002$) and vegetation type ($F_{\text{biomass}} = 10.25$; $F_{\text{LAI}} = 10.13$; $p < 0.0001$) alone are able to explain the variation in biomass and LAI. Fire frequency ($F_{\text{biomass}} = 2.26$; $p = 0.0459$; $F_{\text{LAI}} = 2.34$; $p = 0.0395$) and elephant density ($F_{\text{biomass}} = 1.50$, $p = 0.2207$; $F_{\text{LAI}} = 1.52$; $p = 0.2176$) proved to be not statistically significant when considered separately but significant when interacting with MAP and vegetation cover ($F_{\text{LAI}} = 5.67$; $F_{\text{biomass}} = 5.67$; $p < 0.0001$).

3.4.2. Plot Level

[48] At the plot spatial scale, the GLM explain 69% and 53% of total variation in biomass and LAI, respectively. At a 5% level of significance, the small-scale variation in biomass within Niassa Reserve is primarily explained by fire frequency ($F = 4.56$; $p = 0.003$), followed by vegetation type ($F = 3.82$; $p = 0.006$), and the interaction among elephant density, fire frequency and the nitrogen content of soils ($F = 3.64$; $p = 0.008$). MAP no longer has a significant effect at this scale. Similarly, the effect of elephant density alone on biomass was not statistically significant ($F = 0.29$; $p = 0.59$). LAI is explained by the single effect of vegetation density ($F = 2.66$; $p = 0.033$).

[49] The Tukey-Kramer statistical test at a 5% level of significance shows that biomass and soil nitrogen are significantly greater in plots that did not burn between 2001 and 2005 compared to the other levels of fire frequency (Table 4). LAI does not differ significantly between plots with different fire frequencies. These results confirm that at any particular place within Niassa Reserve, fire frequency strongly influences the biomass but not the LAI of these woodlands. Elephants did not have statistically significant effect on either biomass or LAI, which is probably due to the low animal densities in the area.

4. Discussion

[50] C-band RADARSAT (5.7 cm wavelength) and ETM+ derived SR provide a fairly good surrogate of woody biomass within the Niassa Reserve. Even though C-band SAR has been proved to saturate at a biomass of 5 kg m^{-2}

and above [Dobson *et al.*, 1992; Harrell *et al.*, 1995], we found good relationships between field and C-band data. According to Harrell *et al.* [1995] this relationship is usually improved when surface moisture conditions are minimized. In this study, both RADARSAT and field data were collected during the dry season.

[51] The predictive regression models explained 55% and 45% of the variation in biomass and LAI data, respectively. The resultant biomass and LAI 30 m resolution maps for the year 2004 allow the discussion of three crucial ecological issues: (1) spatial distribution of biomass and LAI; (2) carbon stock density; and (3) determinants of biomass and LAI.

[52] 1. Spatial distribution of biomass and LAI: Quantification of spatial distribution of biomass and LAI over large and remote areas provides a good understanding of ecosystem processes [Chapin *et al.*, 2002]. This is particularly important for Niassa Reserve, a 23,000 km² conservation area, which apart from being remote and large has limited data.

[53] The 30 m resolution land cover map revealed that the eastern Niassa Reserve is dominated by medium to low density vegetation, while the west is mostly covered by medium to high density woodlands (Figure 3). G. C. Craig and D. St. C. Gibson (unpublished data, 2004) observed that in the southwest portion of the reserve there are patches of tropical forest with evergreen canopies and lianas. The reason associated with this gradient is the higher concentration of population (4,000 people were estimated in 1999) in the east. People use fire as the main tool for hunting, honey collection and to a lesser extent agriculture (only around the Mecula village). Thus, it's not surprising that fire is one of the key determinants of biomass in this study.

[54] Despite some disparity in the maps, the mean biomass (23 Mg ha⁻¹ to 51.9 Mg ha⁻¹) within lowland miombo classes, concur well with other results for southern Africa and savannas worldwide. For instance, field measurements throughout southern Africa report biomass ranges from 22 Mg ha⁻¹ in dry miombo [Guy, 1981; Chidumayo, 1997] to 144 Mg ha⁻¹ in very wet mature miombo in the north of the miombo region [Malaisse and Strand, 1973]. Brown and Gaston [1981] estimated a mean biomass for the open and closed woodlands of Mozambique between 46.6 – 58.6 Mg ha⁻¹ and for southern Africa a mean of 67 Mg ha⁻¹. Similarly, Chapin *et al.* [2002] found that data from Saugier *et al.* (2000) indicate that tropical savannas and grasslands of the world have a biomass of 57 Mg ha⁻¹.

[55] LAI estimations across the miombo region are, in general, scarce. Furthermore, LAI is expected to be highly variable across the region due to the influence of fire and herbivory. Fuller *et al.* [1997] and Caylor and Shugart [2004] estimated woody LAI in two different sites of miombo woodlands in Zambia at 2.10 to 2.64 m² m⁻². These miombo woodlands are wet as opposed to the miombo in Niassa Reserve.

[56] Further validation of LAI and biomass maps, especially against independent data, is highly recommended in the near future. Moreover, improvement using a radar L-band (23.7 cm wavelength) is also recommended. L-band captures signals from stems/boles in addition to the top of canopy and saturates at higher values of biomass (80 Mg ha⁻¹) than does the C-band (50 Mg ha⁻¹) [Lucas *et al.*, 2004]. Thus, it

may provide a more accurate estimation of total biomass (S. Saatchi, personal communication).

[57] The results from this study provide, however, useful information to make inferences about the carbon balance and ecosystem dynamics for this area. Another use of these maps is to provide the base information for management decisions including zoning and definition of priority areas for conservation.

[58] 2. Carbon stock density: Considering the conversion coefficient of biomass of 50%, the carbon stock density (35 MgC ha⁻¹) agrees well with the stocks reported for the miombo region, which vary from 11 (biomass of 22 Mg ha⁻¹) in dry miombo to 72 MgC ha⁻¹ (biomass of 144 Mg ha⁻¹) in wet miombo. This indicates that even though there are ongoing modifications on vegetation structure and composition as a result of disturbances [Ribeiro *et al.*, 2008], the carbon stocks within Niassa Reserve are still preserved.

[59] The carbon stock density at the plot level (although not representative of the entire Niassa Reserve) reveal a much higher variability in carbon stock (5.3 to 80.8 MgC ha⁻¹), which seems to be well correlated to the level of plot protection from disturbances, especially fire. However, at the landscape level the variability is not always clear. This indicates that the interpretation of the biomass and LAI maps should consider that dynamics at small-scales are highly variable and dependent on particular site conditions. The lower carbon stocks in disturbed plots observed in this study are not surprising for the miombo region and for the savannas in general. For example, Trapnell [1959] and Scholes [1996] suggest that the carbon uptake in savanna woodlands is reduced by frequent fires. Scholes and Andrae [2000] state that the amount of CO₂ emitted from vegetation fires in southern Africa may represent up to 20% of the regional net primary production. Thus, an exclusion or small alteration of the fire frequency could have significant consequences for the carbon stock [Scholes, 1996]. However, within the Niassa Reserve, a reduction in fire frequency will be hardly achieved in the near future and thus, other strategies should be explored.

[60] 3. Determinants of biomass and LAI: MAP seem to be the explaining factors for biomass and LAI increase from east to west. But, disturbances especially fires, cause abrupt rather than gradual changes in biomass along the MAP gradient. Elephant effects are, however, less evident that is probably due to the low animal densities (0.3 animals km⁻²). Nonetheless, the ongoing interactions at the plot level reveal that elephants are an important driver of this system. For instance, we previously found that field biomass and LAI are negatively correlated with fire and elephants [Ribeiro *et al.*, 2008] and the correlation between fire frequency and elephant density is considerable ($r = 0.61$, $p = 0.03$) (Ribeiro and Shugart, unpublished).

[61] One interesting finding of this study is the interaction between elephant, fire frequency, and soil nitrogen at the plot level and that soil nitrogen and biomass are higher for unburned plots. These results bring about several hypothesis of the elephant-fire interaction in relation to soils and vegetation. One such hypothesis would be that when fire is eliminated, there is an increased input of nitrogen to the soil (which would be otherwise lost by volatilization from

fires). Higher soil nitrogen may provide elephants with higher quality food, increasing browsing [Jachman and Bell, 1985; Holdo, 2003]. For example Bell and Jachman [1984] found significantly higher elephant browsing in unburned plots (29.2%) than in burned plots (21.7%). However, increased browsing under a fire-free environment may allow for some level of woody vegetation recovery from damage by elephants. This may ultimately lead to higher woody biomass of unburned plots as opposed to the burned ones. This hypothesis should be further studied through both theoretical and empirical methods.

[62] Considering the increasing elephant population of 0.03 animals km⁻² year⁻¹ and a planned culling of 12 animals per year (Chande, personal communication), an addition of about 678 animals yr⁻¹ is expected. This means that, in 15 years there will probably be an elephant density of 1 animal km⁻², with higher densities expected in the eastern Niassa Reserve. Densities above 1 animal km⁻² are reported elsewhere in southern Africa to cause significant effects on vegetation [Guy, 1989; Ben-Shahar, 1998; Baxter and Getz, 2005; Chafota, unpublished data] (among others). We recommend further studies on elephant population dynamics including aspects of elephant movements within the reserve and, feeding and reproductive behaviors.

[63] Overall, the patterns of vegetation-environment-disturbance interactions found in this study conform with recent findings that African savannas with more than 650 mm year⁻¹ of rainfall are mostly “disturbance driven” ecosystems in which, rainfall (750 mm year⁻¹ in Niassa Reserve) is sufficient to maintain a higher woody biomass stock but fire and/or herbivory are required to maintain varied ratios of trees and grasses [D’Odorico et al., 2006; Sankaran et al., 2006], which imply varied vegetation stable states.

[64] Previous studies in miombo woodlands, and African savannas in general, have pointed to the existence of multiple stable states [Lawton, 1978; Dublin et al., 1990; Van Langevelde et al., 2003; Baxter and Getz, 2005; Van de Koppel and Prins, 2005]. The different stable states correspond to varied vegetation characteristics including species composition, biomass and tree density, and are caused by fire and maintained by elephants (and their interaction with other herbivores). For example, Starfield et al. [1993] suggested a transition in escarpment woodlands of the Zambezi Valley, from *Brachystegia boehmii*-dominated woodland to grassland and bushland dominated by *Combretum apiculatum*, caused by the combination of elephants and fire.

[65] The large-scale increase in biomass and LAI from east to west of Niassa Reserve reveal that most probably the eastern part is in a different stable state than the western. This is further confirmed by small-scale observations that biomass stocks differ significantly between unburned and burned plots. In addition, previous results for the miombo woodlands in Niassa Reserve reveal a varied species composition according to the level of disturbance in the plots [Ribeiro et al., 2008].

5. Conclusions

[66] The results of the present study reveal that remote sensing data from C-band RADARSAT and ETM+ derived

SR are fairly good surrogates of biomass and LAI within Niassa Reserve. Further improvement is recommended by testing the maps against independent data and using a longer wavelength radar L-band (23.7-cm wavelength).

[67] Our results support the hypothesis that large-scale variations in biomass and LAI in these miombo woodlands is primarily determined by precipitation, but fires and elephants also play a key role. At a plot spatial scale, woody biomass reflects the effects of disturbances, especially fire frequency. This confirms the hypothesis that the different scales of observations reflect differentiated relationships. The current results also reveal that in general, the miombo within the Niassa Reserve sustains average carbon stock for African savannas.

[68] The outputs from this study allow an improved understanding of the fundamental nature of this ecosystem and, to infer future changes. For instance, changes in the climatic pattern (5–15% reduction in precipitation is predicted for southern Africa [Chidumayo, 2005]), may affect the fire regime (for example, increase fire frequency). This associated with the envisaged increasing elephant and human populations may impose accentuated decrease in woody biomass and LAI in the future. These aspects should, however, be further investigated through theoretical models. Finally, information generated by this study should be integrated into the existing strategic management plan for the Niassa Reserve to fully achieve conservation objectives.

[69] **Acknowledgments.** The authors would like to thank the Sociedade para a Gestão e Desenvolvimento da Reserva do Niassa (SGDRN), especially Anabela Rodrigues and Baldeu Chande; financial assistance from the Bureau of Educational and Cultural Affairs of the United States Department of State to H. H. S. of the University of Virginia, a Faculty Development Grant from the Office of the Vice-Provost for Faculty Affairs, University of Virginia, to R. A.-W., the Department of Environmental Sciences Jefferson Conservation Scholarship to N. S. R.; the International Union for Conservation Nature (IUCN-Mozambique); the Faculdade de Agronomia e Engenharia Florestal, Universidade Eduardo Mondlane, and the field survey team: Cândida Zita, Zachary Manis, Mbumba Marufu, Paulo Chaleta, Rogerio, and Ermelindo.

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