



Identifying *Dicymbe corymbosa* Monodominant Forests in Guyana Using Satellite Imagery

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ABSTRACT

The ectomycorrhizal (EM) canopy tree *Dicymbe corymbosa* (Fabaceae subfam. Caesalpinioideae) forms monodominant forests in the Pakaraima Mountains of western Guyana. Like other tropical monodominants, *D. corymbosa* has several life-history traits that promote conspecific clumping, in contrast to density-dependent recruitment limitations characterizing most tropical trees. *Dicymbe corymbosa* forests, occurring in Guyana as patches within a largely non-EM mixed-species forest matrix, are important habitats for a diverse assemblage of EM fungi. Ground-based studies have not adequately determined the regional extent of *D. corymbosa* forests, nor are they practical due to the rugged, remote nature of the Pakaraima Mountains. We assessed the suitability of Landsat satellite imagery for mapping regional distribution of *D. corymbosa* forests in Guyana's Upper Potaro River Basin. Supervised image classification was performed on images from August 1989 (Landsat-5 TM) and October 1999 (Landsat-7 ETM+). In situ forest reference data were used to quantitatively assess accuracy of output classification maps. Classification performed well in distinguishing monodominant from mixed-species forests. For both images, *D. corymbosa* forest class accuracy was good (1989 user's accuracy = 89.8%, $K_{hat} = 0.74$; 1999 user's accuracy = 80.7%, $K_{hat} = 0.59$). The resulting output classification maps will be useful for planning fungal surveys and ecological studies in forests of the Pakaraima region. Classification of Landsat images may be effective for identifying monodominant forests in other remote regions of the tropics.

Key words: Caesalpinioideae; ectomycorrhizal fungi; Guiana Shield; Landsat imagery; monodominance; Neotropics; remote sensing.

DOMINANCE OF TROPICAL RAIN FORESTS BY A SINGLE SPECIES OF CANOPY TREE (monodominance) is a phenomenon of interest to tropical ecologists (Connell & Lowman 1989, Torti *et al.* 2001, Henkel 2003). Monodominance, occurring when over 60 percent of the number of canopy individuals, basal area, or both consist of a single tree species on well-drained soil, may result from life-history traits of the dominant tree species that alter the understory environment, promote self-persistence and recruitment, and lead to clumped distributions, such as the ectomycorrhizal (EM) habit, mast fruiting, limited dispersal, shade tolerance, and reiteration (Connell & Lowman 1989, Hart *et al.* 1989, Torti *et al.* 2001, Henkel *et al.* 2005, Mayor & Henkel 2006, Woolley *et al.* 2008). Monodominant forests allow study of ecological processes circumventing those leading to the typically high tree species diversity in tropical rain forests (Connell and Lowman 1989, Hart 1990, Torti *et al.* 2001, Leigh *et al.* 2004, McGuire 2007).

Monodominance has been documented in the Paleo- and Neotropics, but the phenomenon is not uniformly distributed. Caesalpinoid legumes (*e.g.*, *Gilbertiodendron dewevrei*) form extensive monodominant stands across portions of the Congo Basin (Torti *et al.* 2001). In lowland tropical Asia certain dipterocarps (*e.g.*, *Dryobalanops aromatica*) achieve monodominance (Whitmore 1984, Richards 1996). Monodominance is less well known in the Neotropics, where the only well-documented examples of persistent dominance (*e.g.*, overstory dominance with ample regeneration of the dominant species, unrelated to edaphic influence, flooding, or

succession) involve the caesalpinoids *Peltogyne gracilipes* in northern Brazil (Nascimento & Villela 1997) and *Dicymbe* spp. in Guyana (Zagt 1997, Henkel 2003). Of interest is the fact that most tropical monodominant forests are dominated by tree species that are EM, a root symbiosis otherwise poorly represented in the tropics (Alexander & Lee 2005).

The EM canopy tree *Dicymbe corymbosa* Spruce *ex* Benth. achieves dominance levels among the highest recorded for upland monodominant species in the Neotropics. In the Pakaraima Mountains of western Guyana, *D. corymbosa* comprised 63–95 percent of the basal area in stands ranging from one to several hectares (Henkel 2003). In these stands, the species dominated all levels of forest strata due to reiteration and persistence of mature individuals as well as high recruitment of shade-tolerant seedlings and saplings (Henkel *et al.* 2005, Woolley *et al.* 2008). In the Upper Ireng and Upper Potaro River Basins EM fungi appear largely restricted to *Dicymbe* stands (Henkel 1999; Henkel *et al.* 2002, 2006; Fulgenzi *et al.* 2007). The spatially limited, site-specific distribution of EM fungi in an otherwise non-EM forest matrix suggests that *Dicymbe* forests may be the primary habitats for these obligately symbiotic fungi in Guyana.

Despite the emerging importance of *Dicymbe* forests, ground-based observations have been inadequate for determining their distribution (Fanshawe 1952, Richards 1996, Henkel 2003), nor are monodominant forests in the Pakaraima Mountains region represented on existing vegetation maps of Guyana (*i.e.*, country-scale maps produced using a combination of ground, soil, and remotely sensed data; Huber *et al.* 1995, Guyana Forestry Commission & H. ter Steege 2001). Several factors suggest satellite remote

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sensing may be a useful tool for examining these unusual tropical forests.

Remote sensing can be a cost-effective solution for determining land cover in inaccessible tropical regions where ground-based data are difficult to obtain (Clark *et al.* 2005). Spectral reflectance data from remote optical sensors are useful in extracting information about target vegetation (Cohen & Goward 2004, Boyd & Danson 2005). This technology has been applied to tropical forests to detect changes in phenology, type, and extent of vegetation (Green *et al.* 1994, Bohlman *et al.* 1998, Carreiras *et al.* 2006, Cayuela *et al.* 2006); investigate forest structure, succession, community composition, and species diversity (Vieira *et al.* 2003, Gillespie *et al.* 2004, Salovaara *et al.* 2005, Palace *et al.* 2008); document anthropogenic and natural disturbance (Skole & Tucker 1993, Read *et al.* 2003, Souza *et al.* 2005); and create land cover maps (Mayaux *et al.* 1998, Eva *et al.* 2004). Remote sensing can be a powerful technique to generalize from traditional site-specific plot studies to landscape, regional, and global scales (Foody *et al.* 2003, Clark *et al.* 2005).

Remotely sensed data from Landsat satellites have been used to map forests in tropical regions, although difficulties in discriminating distinct forest types persist because high plant diversity, structural heterogeneity, and cloud cover introduce complexity into radiance signals (Asner 2001, Foody *et al.* 2003, NASA 2003, Cohen & Goward 2004, Powell *et al.* 2004, Thenkabail *et al.* 2004, Salovaara *et al.* 2005, Carreiras *et al.* 2006, Cayuela *et al.* 2006, Fuller 2006, Zhang *et al.* 2006). In addition to its relatively low cost, Landsat imagery has a globally comprehensive data-acquisition policy, centralized, searchable online data bases, and 30-m spatial resolution across six optical bands (Fuller 2006). Landsat's spectral resolution is well-suited for vegetation classification as it includes near-infrared (NIR) and shortwave-infrared (SWIR) portions of the electromagnetic spectrum (NASA 2003). These bands are most effective in separating spectra of tropical canopy tree species (Cochrane 2000, Clark *et al.* 2005).

In order to identify a specific plant community in satellite imagery, target vegetation must have a unique spectral signature within the context of its surroundings (Lillesand *et al.* 2004, Clark *et al.* 2005, Zhang *et al.* 2006). This spectral signature is dependent on the chemical and structural properties of plant tissues, the physiognomic structure of the vegetation, and numerous other factors (Lillesand *et al.* 2004). Successful differentiation of vegetation type classes is generally determined by the degree of spectral variation within classes (intra-class) and between classes (inter-class; Clark *et al.* 2005, Zhang *et al.* 2006). Given these parameters, *D. corymbosa* stands in western Guyana may have a high probability of classification success due to their uniformity of crown structure, leaf composition, and vertical stratification, in contrast to the surrounding heterogeneous forest matrix (Henkel 2003, Woolley *et al.* 2008).

Here we examine the utility of Landsat satellite imagery for identifying *D. corymbosa* monodominant forests in Guyana's Upper Potaro River Basin. Specifically, we asked: Can supervised image classification of Landsat-5 TM and Landsat-7 ETM+ data allow us to distinguish monodominant *Dicymbe* stands from other forest types in the Pakaraima Mountain region? If successful, this

approach could potentially be used in the future to develop distribution estimates of *D. corymbosa* and other ecologically important monodominant forests in the tropics.

METHODS

STUDY AREA.—Our work was conducted in the central Pakaraima Mountains of western Guyana, an area thought to encompass the geographical distribution center of *D. corymbosa* (Fanshawe 1952, Henkel 2003; Fig. 1). The central Pakaraimas are blanketed with dense primary forest, predominantly of the seasonal evergreen *Eschweilera–Licania* association, with an elevational range of 700–2200 m (Fanshawe 1952). Limited small-scale mining and slash-and-burn agriculture have occurred in portions of the region; however, these activities have not caused visible changes in regional forest structure. Primary stands dominated by *D. corymbosa* have been noted within hilly, intermountain valleys of the Upper Potaro, Mazaruni, and Ireng River Basins (Myers 1936, Fanshawe 1952, Henkel 2003). These stands vary in size from roughly one to several hectares, and have relatively well-defined boundaries with the surrounding, diverse, mixed-species forest matrix that lacks *D. corymbosa* (Fanshawe 1952, Henkel 2003, Henkel *et al.* 2005). Stands dominated by the non-EM *Micrandra glabra* Schultes (Euphorbiaceae) and *Micrandra spruceana* Schultes occur in extensive contiguous patches on poorly drained sandy soils overtopping hardpan or shatterrock (Fanshawe 1952). Additionally, the EM tree species *Dicymbe alstonii* Sandw., *D. jenmanii* Sandw., and *Aldina insignis* (Benth.) Endl. occur as scattered individuals or small groves in the mixed forest matrix (Henkel *et al.* 2002). A 200-km² study site within the Upper Potaro Basin was chosen to examine the utility of Landsat imagery for identifying *D. corymbosa* monodominant forests. Vegetation within this area has been virtually unchanged by anthropogenic activity, and topographic variation within the intermountain valleys containing *D. corymbosa* occurs at a relatively fine scale, ca 0–30 m. For further details of climate, geology, and soils see Henkel (2003), Henkel *et al.* (2005), and Mayor and Henkel (2006).

REMOTELY SENSED DATA.—A digital elevation model (DEM) of the three-arcsecond (ca 90 m) Shuttle Radar Topography Mission (SRTM) finished C-band sensor data for the central Pakaraima Mountains region was downloaded from the Global Land Cover Facility of the University of Maryland (GLCF; <http://glcf.umi.acs.umd.edu>). Data were referenced to horizontal datum WGS84, vertical datum MSE WGS84 EGM96 geoid (Slater *et al.* 2006). These data were projected to Universal Transverse Mercator, zone 20 N and datum WGS 1984. The SRTM DEM was used in the preclassification masking process to remove areas clearly outside of the elevational range of *D. corymbosa*. Because of its coarse pixel size relative to the fine-scale variation in vegetation and topography across the study site, SRTM elevation data were not utilized in the final supervised classification.

Two Landsat satellite images (170 × 183 km) encompassing the Upper Potaro Basin study area were obtained from the

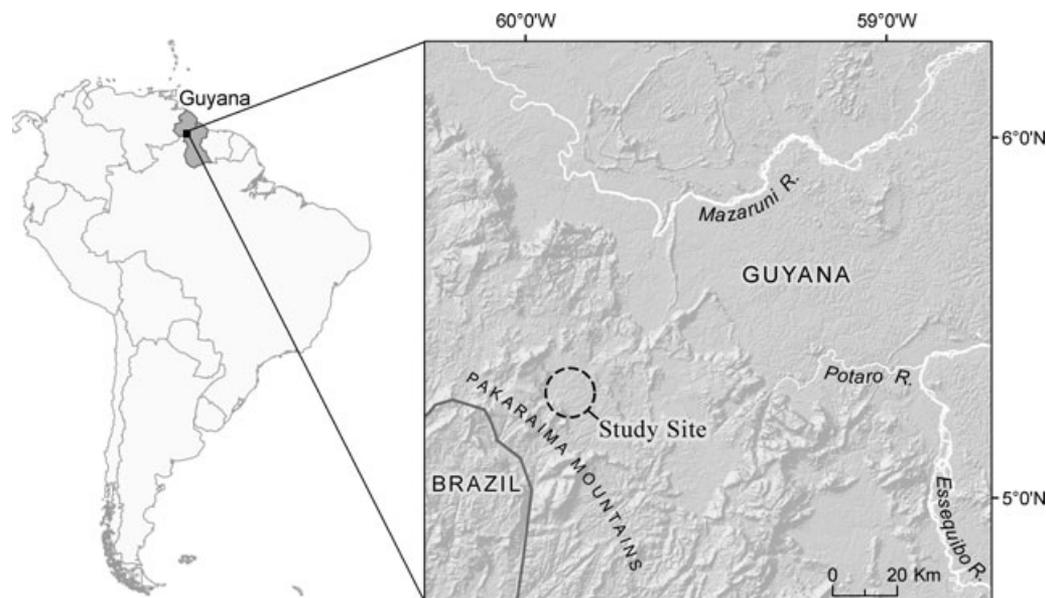


FIGURE 1. Study site showing position of Guyana in South America and topography of the Pakaraima Montane region.

GLCF (<http://glcf.umiacs.umd.edu>). Satellite data consisted of one Landsat-7 ETM+ scene (path 232, row 056, WRS-2) acquired on 16 October 1999, and one Landsat-5 TM scene (path 232, row 056, WRS-2) acquired on 9 August 1989. Each image was acquired during the dry season and selected for low (< 10%) cloud cover over the study area. Both images were used in the forest classification process, with the assumption that tree species distributions had not changed significantly to the present. Spectral resolution of the imagery is 0.45 to 2.35 μm with seven bands spanning the blue to mid-infrared portion of the electromagnetic spectrum (NASA 2003). Bands 1–5 and 7 were included in the classification process. Spatial resolution (pixel size) of the imagery is 28.5 m (NASA 2003). Images were orthorectified and coregistered by EarthSat (GLCF 2007), then projected in Universal Transverse Mercator, zone 20 N and datum WGS 1984. Imagery from the two dates was processed separately, so atmospheric corrections were unnecessary (*i.e.*, digital number reflectance values did not have to be normalized; ERDAS IMAGINE 2005). Topographic correction was not performed because the 90-m resolution of available raster elevation data was too coarse to capture topographic variation across the study site. ERDAS Imagine Software version 9.1 was used for analysis of satellite imagery data (ERDAS IMAGINE 2005).

PRELIMINARY DATA PROCESSING.—Preliminary supervised classification of Landsat images was used to develop an effective stratified sampling regime for wider-scale field data collection and accuracy assessment. Supervised classification incorporates *a priori* knowledge from field sampling into the classification process (through the definition of training areas) and relates measured spectral reflectance properties directly to known vegetation cover. For each predetermined category, training areas are identified on the image and delineated so their spectral properties can be examined.

Classification of the remainder of the image is based on values defined via these training sets (Lillesand *et al.* 2004). Preliminary supervised classification was carried out using previously collected data sets compiled from eight 1-ha forest inventory plots of known structure and tree species composition (Henkel 2003, Henkel *et al.* 2005, Woolley *et al.* 2008) and additional transect point surveys. This work was conducted during June–August 2006 within a 5-km radius of a permanent base camp located along the Upper Potaro River at 5°18'04.8" N, 59°54'40.4" W, at 710–750 m asl. Forest data were simplified for classification, and field sites were assigned to one of three classes: (1) *D. corymbosa* dominant (> 60% of stems \geq 30 cm dbh; diameter at 1.37 m above the ground) to monodominant (> 80% of stems \geq 30 cm dbh); (2) *Micrandra* dominant (> 60% stems \geq 30 cm dbh); or (3) mixed-species forest lacking *D. corymbosa* and *Micrandra* spp., with no clearly dominant canopy tree species. Field sites that did not fit these classes were excluded from the classification data set. We utilized this three-class forest composition data set, Global Positioning System (GPS) data, and topographic maps to digitize polygons around areas of known forest types in a Geographic Information System (GIS; Environmental Systems Research Institute 2006). The polygons digitized were subsequently used as training areas for preliminary supervised classification of Landsat images. The output classification was used to identify a suitable pool of sampling targets (*i.e.*, contiguous forest patches > 5 ha) for a second phase of fieldwork from which to collect representative ground data over a broader area for subsequent remote sensing analysis. The latitude and longitude of selected target patches' weighted internal centroids were calculated in a GIS and then uploaded to a handheld GPS (Garmin GPSMap76).

Fieldwork for the second phase of *D. corymbosa* classification and accuracy assessment was conducted during January 2007, within a 10-km radius of a camp located *ca* 3 km south of the

TABLE 1. Characteristics of forest classes and subclasses used in vegetative classification for the Upper Potaro River Basin, Guyana.

Class	Description	Subclass	Description
DCF	<i>Dicymbe corymbosa</i> dominant ^a to monodominant ^b , <i>Dicymbe altsonii</i> absent, present, or codominant	DCD	<i>D. corymbosa</i> dominant
		DCD	<i>D. corymbosa</i> dominant
		DCM	<i>D. corymbosa</i> monodominant
		DCDADC	<i>D. corymbosa</i> dominant, <i>D. altsonii</i> present to moderately codominant.
		DCDACM	<i>D. corymbosa</i> dominant to monodominant, <i>D. altsonii</i> present to strongly codominant.
MF	<i>Micrandra</i> sp. dominant ^a	MGD	<i>Micrandra glabra</i> dominant
		MSD	<i>Micrandra spruceana</i> dominant
MX	Mixed-species forest lacking <i>D. corymbosa</i>	MXR	Mixed-species riverine, lowland association
		MX	Mixed-species upland forest

^a $\geq 60\%$ stems ≥ 30 cm dbh; ^b $\geq 80\%$ stems ≥ 30 cm dbh.

Upper Potaro River at $5^{\circ}17'22.6''$ N, $59^{\circ}52'23.9''$ W, ca 8 km east of the base camp described above. From the base camp, patches of target vegetation were located via a compass and GPS wherein a minimum of three point locations were randomly chosen at which to assess forest composition. Each point was located at least 60 m into a contiguous forest type and 100 m from other survey points. Four experienced tree spotters estimated and recorded the relative abundance of canopy tree species (≥ 30 cm dbh) within a 15 m radius of the GPS survey point. In total, 182 new survey points were assessed within the study area, bringing our total number of usable forest survey points to 224, when combined with previously collected data (Fig. 2). Vegetation and coordinate data for each location were added to a GIS database, and, for classification purposes, all survey points were assigned to one of eight predefined subtype classes as given in Table 1.

CLASSIFICATION PROCEDURE.—To improve vegetation classification accuracy, 1989 and 1999 imagery areas unsuitable for target vegetation were excluded from the image classification process (Tottrup 2004, ERDAS IMAGINE 2005). SRTM data were used to eliminate areas where elevation exceeded 1000 m, a conservative estimate of *D. corymbosa*'s upper elevation range (Henkel *et al.* 2002). Nonforest savanna, scrubland, water, clouds, and shadows were excluded from consideration using preliminary unsupervised classification of each image. Unsupervised classification is a purely statistical method and incorporates no *a priori* knowledge of target characteristics into the classification process. Digital values from combinations of spectral bands are used to identify inherent groupings in the image data (Lillesand *et al.* 2004). For each image, classes representing nonforest areas were combined with areas of unsuitable elevation, and the resultant pixels were masked during subsequent classification procedures (ERDAS IMAGINE 2005). Forest survey points occurring within masked areas of a given image were excluded from the training and reference data sets used in classification and accuracy assessment.

In keeping with our objectives, we chose a final classification scheme identifying: (1) *D. corymbosa* dominant and monodominant forest; (2) *Micrandra* dominant forest; and (3)

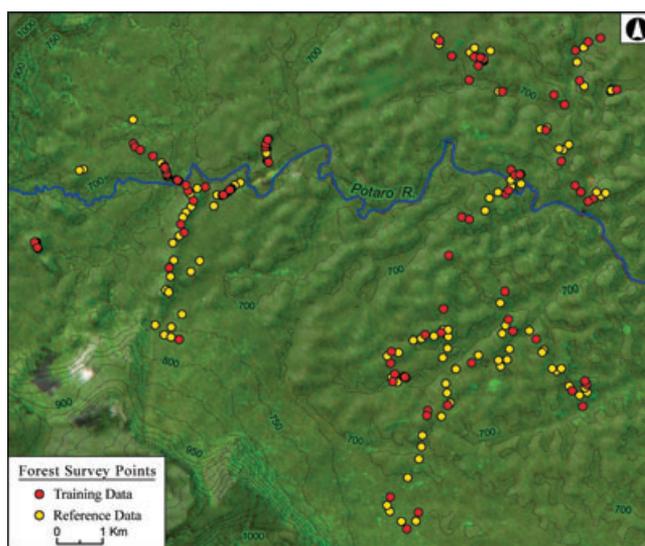


FIGURE 2. Distribution of the 224 forest survey points used for training supervised classification (40% of total; $N = 81$ for 1989; $N = 69$ for 1999) and as reference data in accuracy assessment (60% of total; $N = 122$ for 1989; $N = 103$ for 1999). Not all points are visible at the given map scale. Due to areas obscured by clouds all 224 points were not used in analyses of each image. Forest assessment points for the study site in western Guyana are shown on a color composite (bands 5, 4, and 3 allocated to red, green, and blue channels, respectively) Landsat-5 TM satellite image acquired on 9 August 1989.

mixed-species forest lacking *D. corymbosa*, serving as an 'other' forest class. Several subclasses existed within each parent class (Table 1) and were retained in order to achieve maximum spectral separability between classes (Lillesand *et al.* 2004). Subclasses were pooled postclassification. Forty percent of forest survey points from each subclass were randomly selected to train the supervised classification process ($N = 81$ for 1989; $N = 69$ for 1999); the remaining sixty percent were set aside for accuracy assessment ($N = 122$ for 1989; $N = 103$ for 1999). Figure 2 shows the distribution of

all training and reference points used in analysis. To accommodate the area covered by a forest survey and GPS error, all pixels within 30 m of training points were extracted from an image to generate class-specific spectral signatures (ERDAS IMAGINE 2005). A transformed divergence calculation was used to determine spectral separability between forest cover classes and as a guide to either aggregate or discard classes (ERDAS IMAGINE 2005). A maximum likelihood supervised classification was subsequently performed on both Landsat images using spectral signatures of the retained classes. Output thresholds were set at $\alpha = 0.05$ to exclude pixels that did not fit well in the given classes.

THEMATIC ACCURACY ASSESSMENT.—The output classification map generated from remotely sensed data was compared with ground reference data to assess accuracy (Foody 2002, Powell *et al.* 2004). To accomplish this, sixty percent of the ground survey points in each forest class were excluded from supervised classification training and used in accuracy assessment. Classification accuracy was ultimately assessed using 134 independent reference points. To examine relationships between classification and reference data, error matrixes were generated for each classification map and the following statistics were calculated: (1) errors of omission; (2) errors of commission; and (3) K_{hat} , an estimate of the conditional Kappa coefficient expressing the proportional reduction in accuracy, when random chance agreement is removed (Congalton & Green 1999). ‘User’s accuracy’, the probability that a pixel classified on the image actually is that land cover type on the ground, was selected as the accuracy assessment parameter with the greatest utility for future use of this approach for field survey design (Congalton & Green 1999). Also in keeping with the purpose of the study, accuracy assessment focused on successful classification of single-species dominant forest classes (Foody 2002).

RESULTS

The classification error matrices for the 1989 and 1999 images show a good agreement between the classified maps and reference

data for the *D. corymbosa* and *Micrandra* forest classes (Tables 2 and 3). The K_{hat} values for the *D. corymbosa* class were 0.735 and 0.587 for the 1989 and 1999 images, respectively, indicating the classifications were 73.5 and 58.7 percent correct with chance agreement discounted. The *Micrandra* forest class had the highest class accuracy, with K_{hat} values of 0.841 (1989) and 0.948 (1999). For both image dates, the *D. corymbosa* class had lower errors of commission (10.2% for 1989; 19.3% for 1999) than errors of omission (41.3% for 1989; 23.6% for 1999). Classification of the 1989 image correctly identified 58.7 percent of the *D. corymbosa* forest present (‘producer’s accuracy’). The probability of a pixel labeled as *D. corymbosa* on the classified image actually being *D. corymbosa in situ* was 89.8 percent (user’s accuracy; Congalton & Green 1999). Producer’s accuracy for the 1999 image was 71.4 percent and user’s accuracy was 80.7 percent. Low K_{hat} values for the mixed-species forest class (0.221 for 1989; 0.347 for 1999) reflect high omission and commission errors, which are to be expected for such a diverse class. The most common misclassification was *D. corymbosa* forest as mixed-species forest.

The classification output maps indicate *D. corymbosa* is locally prevalent on a variety of soil types across the Upper Potaro study area; its stands are interspersed with patches of mixed-species forest. *Micrandra*-dominated forest is present in more internally homogeneous swaths north of the Potaro River (Fig. 3).

DISCUSSION

CLASSIFICATION OF FOREST TYPES.—Supervised classification of Landsat imagery performed well in distinguishing forest types dominated by a single tree species from mixed-species forest. We achieved user’s accuracies of 80–90 percent for *D. corymbosa*-dominated stands and 87–96 percent for *Micrandra*-dominated stands. These accuracies are good given that > 85 percent accuracy is often set as an upper target for less complex land cover classes (Foody 2002). *Dicymbe corymbosa* forest was more accurately identified (89.9% user’s accuracy) using the Landsat-5 TM scene (9 August 1989) than the Landsat-7 ETM+ scene (80.7%; 16 October 1999). This

TABLE 2. Error matrix for maximum-likelihood supervised classification of Landsat-5 TM scene (path 232, row 056, WRS-2) acquired on 9 August 1989. Forest classes for the Upper Potaro River Basin (Guyana) study site include: (1) *Dicymbe corymbosa* forest (dominant and monodominant); (2) *Micrandra*-dominant forest; and (3) mixed-species forest lacking *D. corymbosa*.

Classification data	Reference data				User’s accuracy (%)	Error of commission (%)	K_{hat}
	DCF	MF	MX	Total			
<i>Dicymbe corymbosa</i> forest (DCF)	44	0	5	49	89.8	10.2	0.735
<i>Micrandra</i> forest (MF)	2	20	1	23	87.0	13.0	0.841
Non-DCF, mixed-sp. forest (MX)	29	2	19	50	38.0	62.0	0.221
Total	75	22	25	122			
Producer’s accuracy (%)	58.7	90.9	76.0				
Error of omission (%)	41.3	9.1	24.0				

TABLE 3. Error matrix for maximum-likelihood supervised classification of Landsat-7 ETM+ scene (path 232, row 056, WRS-2) acquired on 16 October 1999. Forest classes for the Upper Potaro River Basin (Guyana) study site include: (1) *Dicymbe corymbosa* forest (dominant and monodominant); (2) *Micrandra*-dominant forest; and (3) mixed-species forest lacking *D. corymbosa*.

Classification data	Reference data				User's accuracy (%)	Error of commission (%)	K_{hat}
	DCF	MF	MX	Total			
<i>Dicymbe corymbosa</i> forest (DCF)	42	1	9	52	80.7	19.3	0.587
<i>Micrandra</i> forest (MF)	1	25	0	26	96.2	3.8	0.948
Non-DCF, mixed-species forest (MX)	12	1	12	25	48.0	52.0	0.347
Total	55	27	21	103			
Producer's accuracy (%)	71.4	92.6	57.1				
Error of omission (%)	23.6	7.4	42.9				

likely resulted from significantly less cloud cover in the Landsat-5 TM scene, which allowed more survey data to be incorporated as training input for the 1989 classification, yielding a higher user's accuracy.

The most common misclassification was *D. corymbosa* forest incorrectly classified as mixed-species forest (Tables 2 and 3). This misclassification may have arisen from: (1) our combining multiple types of non-*D. corymbosa*, mixed-species forest into two general categories (Table 1) creating high spectral variation within the class, and/or (2) relatively low spectral separability (*i.e.*, shown by low transformed divergence values) between *D. corymbosa* and mixed-species forest classes. Spectral reflectance of monodominant forests is likely influenced by within-stand uniformity of crown structure, leaf composition, and vertical stratification, allowing it to be discriminated from structurally complex, species diverse forests with high epiphyte loads (Henkel 2003). In addition, *D. corymbosa*'s reiterative stem growth and minimal horizontal branching may inhibit canopy liana development, thus reducing spectral variation of within-stand canopy reflectance in contrast to liana-rich, mixed-species forests (Richards 1996, Henkel 2003, Clark *et al.* 2005, Woolley *et al.* 2008). The *Micrandra* forests, which are also dominated by a single canopy tree species, have a SWIR spectral signature indicative of high water content (Mayaux *et al.* 2000, Lillesand *et al.* 2004). This suggests that elevated soil moisture and/or frequent inundation likely contribute to the high spectral separability and resulting excellent classification accuracies of *Micrandra* forests.

Comparison of our results with other published research is challenging because remote-sensing studies in the tropics often focus on mapping broad primary and secondary forest cover categories, with little fine-scale differentiation of forest types (Huber *et al.* 1995, Hansen *et al.* 2000, Mayaux *et al.* 2000, Vieira *et al.* 2003, Eva *et al.* 2004, Stibig *et al.* 2004, Thenkabail *et al.* 2004, Joshi *et al.* 2006). Difficulties for comparison also arise when studies lack detailed information on vegetation class definitions, sampling design, and individual class accuracy assessment (Foody 2002, Powell *et al.* 2004, Salovaara *et al.* 2005). In some cases, we found that our *Dicymbe* and *Micrandra* forest class accuracies were

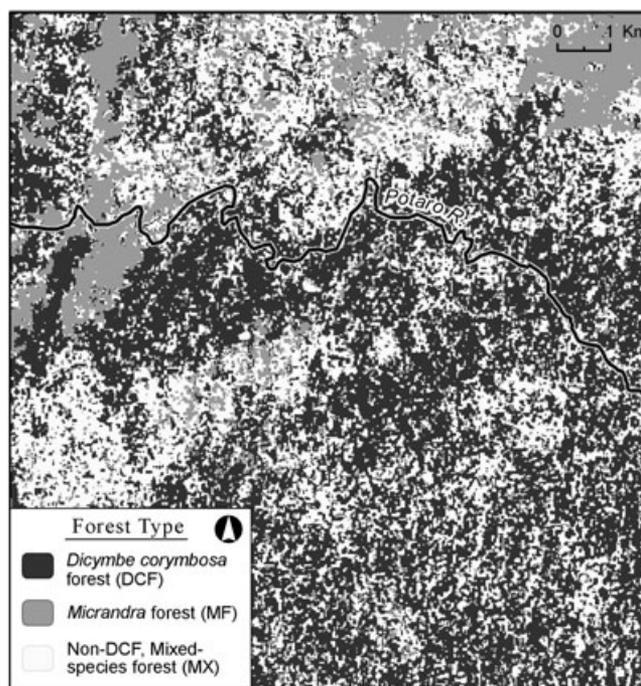


FIGURE 3. Thematic map showing predicted forest distribution for the Upper Potaro River Basin study site in western Guyana. Supervised classification output for 16 October 1999 Landsat-7 ETM+ scene is shown. Cloud covered areas were filled with classification output from the Landsat-5 TM image acquired on 9 August 1989. Dark grey areas represent *Dicymbe corymbosa* dominant and monodominant forest, medium grey depicts *Micrandra* dominant forest, and light grey indicates mixed-species forest lacking *D. corymbosa*.

comparable to those obtained for evergreen broadleaf tropical forests in South America (Hansen 2000) and India (Joshi *et al.* 2006). Using Landsat ETM+ and elevation data from the Peruvian Amazon, Salovaara *et al.* (2005) attempted to differentiate three floristically defined types of closed-canopy primary lowland tropical forest, with user's accuracies ranging from 48.0 to 94.6 percent. Our accuracies

for *Dicymbe* and *Micrandra* forest classes exceeded those of a number of studies that, utilizing multispectral sensor data, could not accurately separate various primary tropical evergreen forests from mixed deciduous, flood plain, semi-evergreen, degraded primary, and late secondary successional forests (Foody & Hill 1996, Mayaux 2000, Stibig *et al.* 2004, Thenkabail *et al.* 2004, Carreiras *et al.* 2006). Conversely, as with our *Micrandra* forests, both Hill (1999) and Mayaux *et al.* (2000) found that low diversity, closed-canopy swamp forests could be differentiated by spectral reflectance.

DISTRIBUTION.—Our classification map and field data indicate that *D. corymbosa* monodominant forests occur most frequently within the study area south of the Potaro River on ironstone hills and low-lying alluvial sands, indicative of the broad edaphic amplitude of the species (Fig. 3; Fanshawe 1952, Henkel 2003). The results are consistent with previous suggestions that *D. corymbosa* forests are prevalent over a 40-km stretch from the Upper Potaro River south to the Upper Ireng River Basin (Fanshawe 1952, Richards 1996, Henkel *et al.* 2005). Our estimation of *D. corymbosa* distribution within the study area is likely conservative as classifications of both the 1989 and 1999 images had lower errors of commission (producer's accuracy) than of omission (user's accuracy). Consequently, areas identified as *D. corymbosa* monodominant have a high probability of being correct, but some stands of the class were likely missed.

Our *D. corymbosa* classification likely defines the core areas of EM fungal habitat in the study area; however, EM fungi are not entirely restricted to *D. corymbosa* stands. In particular, EM fungi may occur in specific locales within the mixed forest matrix in association with the congeneric EM tree *D. altsonii* (Henkel *et al.* 2002). Over the course of our fieldwork *D. altsonii* was found to occur in small groves of moderate conspecific density within local areas of mixed-species forest and in some cases as a codominant with *D. corymbosa*. In these cases we could not separate *D. altsonii* from *D. corymbosa* or mixed-species forest by spectral reflectance. This lack of discrimination may have resulted from: (1) our small *D. altsonii*-containing forest sample size; (2) the potential complexity and variability of *D. altsonii* forest types; and (3) the physiognomy and structural characteristics of *D. altsonii*, which does not dominate the forest's vertical strata through stem reiteration to the same degree as *D. corymbosa* (Zagt 1997, Henkel *et al.* 2002, Woolley *et al.* 2008). *Dicymbe altsonii* may act as locally restricted, low-density host reservoir for EM fungi within an otherwise non-EM mixed species forest and may provide connectivity for EM fungal dispersal between *D. corymbosa* stands (Henkel *et al.* 2002).

Our classification map also shows large swaths of *Micrandra*-dominated forest extending north from the Upper Potaro River. Little work has been conducted on these forests, which may be dominated either by *M. glabra* or *M. spruceana* on shallow, poorly drained sandy soils, and have blackwater drainage systems (Fanshawe 1952). While this study focused on *D. corymbosa*, our methodology identified *Micrandra*-dominated forests accurately. As an example of Neotropical heath forests *Micrandra* systems could serve in regional investigations of these unique communities (Janzen 1974, Whitmore 1990).

Our use of supervised classification of Landsat imagery to accurately identify *D. corymbosa*- and *Micrandra*-dominated stands is particularly promising given persistent difficulties in differentiating primary tropical forest subtypes with remote sensing (Foody & Hill 1996, Mayaux 2000, Thenkabail *et al.* 2004). Nonetheless, analytic refinements might improve future classification results. In particular, image segmentation, multivariate analysis, and preclassification image smoothing have been shown to increase Landsat classification accuracies for tropical forests (Hill 1999, Tottrup 2003). Hyperspectral sensors, which give detailed reflectance information for > 50 narrow spectral bands (spanning the visible, NIR, and SWIR spectra), show great promise for detailed mapping of tropical forests (Cochrane 2000, Thenkabail *et al.* 2004, Clark *et al.* 2005, Zhang *et al.* 2006). Thenkabail *et al.* (2004) compared Landsat ETM+ image analysis with hyperspectral (Hyperion) data and found that hyperspectral analysis allowed separation of complex tropical moist forests with much higher class accuracy (96% vs. 42%). However, high acquisition costs, current lack of operating platforms, the advanced data storage and processing capacity necessary for analysis, and its limited geographic and temporal coverage indicate that the use of hyperspectral data is not currently viable for most studies (Fuller 2006, Zhang *et al.* 2006). Landsat data offer affordability and availability, a globally comprehensive acquisition policy, and a historic time series, making it an attractive choice for most tropical studies (Cohen & Goward 2004, Fuller 2006). However, the newest Landsat satellite (Landsat-7 ETM+) malfunctioned in May 2003, ending over 30 yr of continuous Landsat series data acquisition (Leimgruber *et al.* 2005). Thus, researchers seeking recent satellite data may have to turn to other medium resolution sensors, such as SPOT or IRS satellites (Carreiras *et al.* 2006, Joshi *et al.* 2006, Short 2006) for which low-cost global imagery may be less readily available (Leimgruber *et al.* 2005).

FUTURE APPLICATIONS.—Our study is the first to identify upland tropical monodominant forests using remotely sensed data. This approach should be useful in identifying sites for system-specific ecological studies and EM fungal surveys. Additionally, given availability of training data and proper preprocessing of Landsat imagery (Bruce & Hilbert 2004), this technique shows potential to estimate the broader regional distribution of *D. corymbosa* forests, and help guide conservation planning and studies involving regional-scale processes contributing to monodominance, such as mast fruiting (*e.g.*, Henkel *et al.* 2005). High classification accuracy for *Micrandra*-dominated forests offers a relatively straightforward, inexpensive means of gaining a better understanding of this understudied association. We suggest that supervised classification of Landsat imagery may be applicable to mapping monodominant forests elsewhere in the Neotropics as well as tropical Africa and Asia.

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