WETLANDS, Vol. 16, No. 4, December 1996, pp. 477–487

CHARACTERIZATION OF WETLAND PLANT STRESS USING LEAF SPECTRAL REFLECTANCE: IMPLICATIONS FOR WETLAND REMOTE SENSING

John E. Anderson[1], and James E. Perry[2]
[1] *U.S. Army Corps of Engineers*
Alexandria, VA 22315

[2] *Virginia Institute of Marine Science*
Gloucester Point, VA 23062

Abstract: Spectral measurements were recorded for leaves from two monospecific stands of *Acer rubrum* in an attempt to characterize leaf reflectance at different stages of flooding. The stands occupied two different soil types possessing different soil moisture regimes. Leaves were excised from different parts of the trees, and their reflectance properties were measured with a hand-held spectroradiometer recording from 400 to 900 nanometers in 3-nm increments. Soil redox potentials were recorded at the sites in an attempt to characterize stress as a function of the soil reducing conditions. Spectral curves, reflectance peaks, soil moisture observations, and redox potentials were plotted and analyzed to document the conditions of the trees during a two-and-a-half month period in the early local growing season. Compared to non-flooded trees, spectral measurements for flooded trees showed elevated reflectance in both the green spectral region at 550 nm as well as the near infrared region at 770 nm. In addition, the reflectance measurements were strongly related ($r \geq 0.80$) to redox potentials recorded during the same period. The results indicated that spectrally detectable changes in visible and near infrared leaf reflectance may be more influenced by prolonged flooding than saturation. This suggests that where remote sensing is used for wetland mapping, there may be optimal times to spectrally separate stands of forested wetlands during the growing season.

INTRODUCTION

Many facultative wetland tree species occur in monospecific stands and occupy landscape positions containing combinations of upland, transitional, or wetland (hydric) soil units. These sites are delineated on visible and near infrared imagery on the basis of differences in spectral reflectance, which is a function of leaf canopy characteristics (Carter 1982). The reflectance properties of the living leaf, in the photographic spectrum, incorporate energy ranging from the blue (400 nanometers) to far-red and near infrared (710 to 780 nanometers) regions (Hale and Orcutt 1987). Because of these properties, most wetland mapping incorporates the use of remote sensing in the form of satellite data, color infrared aerial photography, and more recently, as high-resolution, multispectral videography (Carter 1982, Tiner 1990, Sersland et al. 1995).

Spectral reflectance data and imagery are increasingly being used to monitor wetland ecosystems (Jensen et al. 1983). Reflectance spectra can be recorded simply by taking photographs (reflected visible or infrared light) or by using a spectroradiometer to measure the wavelength response as a count of photons absorbed or reflected by an object. During growth and senescence, plant spectral responses are governed by changes in photochemical pigments (chlorophyll), leaf anatomy and morphology, water content, and stress (Gates et al. 1965, Jackson, 1986, Rock et al. 1988, Carter 1993, Peñuelas et al. 1993).

Flooding has long been documented to be a severe physiological stress for many trees. Under strongly reduced conditions, such as are found in flooded environments, the redox potential can fall to low levels, causing the transformation of metals and nutrients. This transformation can govern the availability of plant nutrients to vegetation exposed to flooding (Hale and Orcutt 1987). For example, Hsiao (1976) indicate that (depending on hydrologic regime) plants undergo biophysical changes in both leaves and stems during the growing season to cope with flooding and the resulting anaerobiosis. In facultative species subjected to flooding, Kozlowski and Pallardy (1979) discovered premature closing of leaf stomates, which reduces stomatal conductance and translocation. Flooding stress has also been shown to govern physical, chemical, and morphological changes in wetland plants. For example, Coutts and Phillipson (1978) and Coutts (1981) have described the following symptoms associated with flooding stress in plants: chlorosis, drooping petioles, leaf epinasty, hypertrophy (swelling), and wilting. In flood-intolerant plant species, ethylene production facilitated the collapse and disintegration of cell walls and reduction of leaf structure (Kawase 1981). These responses may be detected from the spectral properties of affected wetland vegetation.

Spectral reflectance measurements have been used effectively to evaluate vegetation type and condition as well as provide baseline data on the selection of wavebands for remote sensing systems. Carter (1993) and Carter and Miller (1994) used spectral measurements, waveband selection, and digital imagery to characterize a variety of plant stresses as changes in visible and near infrared reflectance. Studies by Hoque et al. (1992) identified specific narrow wavebands to observe forest damage using canopy reflectance. Murtha (1982) documented the use of remote sensing to identify specific spectral responses of stressed vegetation. Changes in visible and near infrared leaf reflectance were also observed by Satterwhite and Anderson (unpublished data 1993) in a controlled study to evaluate nutrient and water stress. In geobotanical studies, Carter et al. (1992) and Milton et al. (1989) presented results on changes in leaf reflectance due to nutrient and metals stress.

In wetland mapping, the use of spectral reflectance measurements in conjunction with imagery data has been applied since the early 1970s. Carter and Anderson (1978) used field spectral measurements of individual plant species to assist in the mapping of various wetland environments. In studies using the spectral data available from Landsat Thematic Mapper, Gammon et al. (1979) mapped wetland vegetation of the Great Dismal Swamp along the Virginia and North Carolina border based on plant reflectance characteristics.

While the spectral reflectance signatures of many wetland plants can facilitate the easy detection and separation of community boundaries, subtle reflectance differences associated with stress may require a seasonal approach (Anderson 1995). Depending on the extent of flooding during the growing season, when the canopy is in full leaf-out, discrimination between flooded and non-flooded areas within forested wetlands can prove difficult (Porter 1992). Improved mapping of forested wetlands during the growing season may benefit from an approach based on recorded seasonal changes in the leaf reflectance properties of flooding-stressed vegetation.

The objective of this research was to characterize the visible and near-infrared leaf spectral reflectance response of a facultative wetland plant species exposed to flooding stress and falling redox potential. The 400 to 900 nm bandpass was selected because it is the spectral region where most remote sensing systems used in wetland mapping operate. Additionally, this region includes the action spectrum of vegetation that incorporates both chlorophyll and structural responses and has also been found to be the most useful for characterizing plant stress (Carter 1993). This research sought to demonstrate whether or not there are optimal times during the growing season to delineate wetlands using imagery or sensitive spectral detection instruments. The hypothesis of this research is that, in facultative wetland plants, spectral reflectance provides an indication of stress imposed by flooding and the subsequent falling redox potential. This response may allow for the improved delineation of wetland areas cloaked within monospecific stands of predominantely facultative vegetation.

METHODS

A wetland area bordering the Rappahannock River near Fredericksburg, Virginia (Figure 1) was selected for this study. This area was colonized by an almost monospecific stand of the facultative wetland species *Acer rubrum* (L.) (red maple) averaging 13.4 cm diameter at breast height (dbh) with dense canopies. The area was divided into two sites characterized by two different and distinct hydric soil units. Visual observation and soil redoxymorphic characteristics were used to categorize each soil type and hydrologic influence. The wet site, which lay along a stream tributary, was semi-permanently flooded and had standing water periodically throughout the growing season. This site contained Cartecay-Wehadkee local hydric soils units, consisting of deep, poorly-drained soils formed in loamy alluvium of the Piedmont Province. The dry site was temporarily flooded and not subject to total seasonal inundation. This site contained Congaree local hydric soils units and was characterized by deep, well-drained sloping soils along a stream flood plain. (Soil Conservation Service 1980).

Leaves and reflectance measurements were collected weekly for 10 weeks during April, May, and early June 1994. This time-frame allowed for measurements to be recorded before, during, and after spring flooding events. Two 30-m sampling transects were established in the wetland, one transect in each of the wet and dry sites. Twenty-five trees were sampled at random each week along each of the transects.

Spectral reflectance analysis was used to record the specific response wavelengths characteristic of green vegetation. These included both the visible reflectance characteristics of cholorophyll pigments (400–760 nm) and the near infrared reflectance representing leaf structure (760–900 nm). The spectral reflectance for

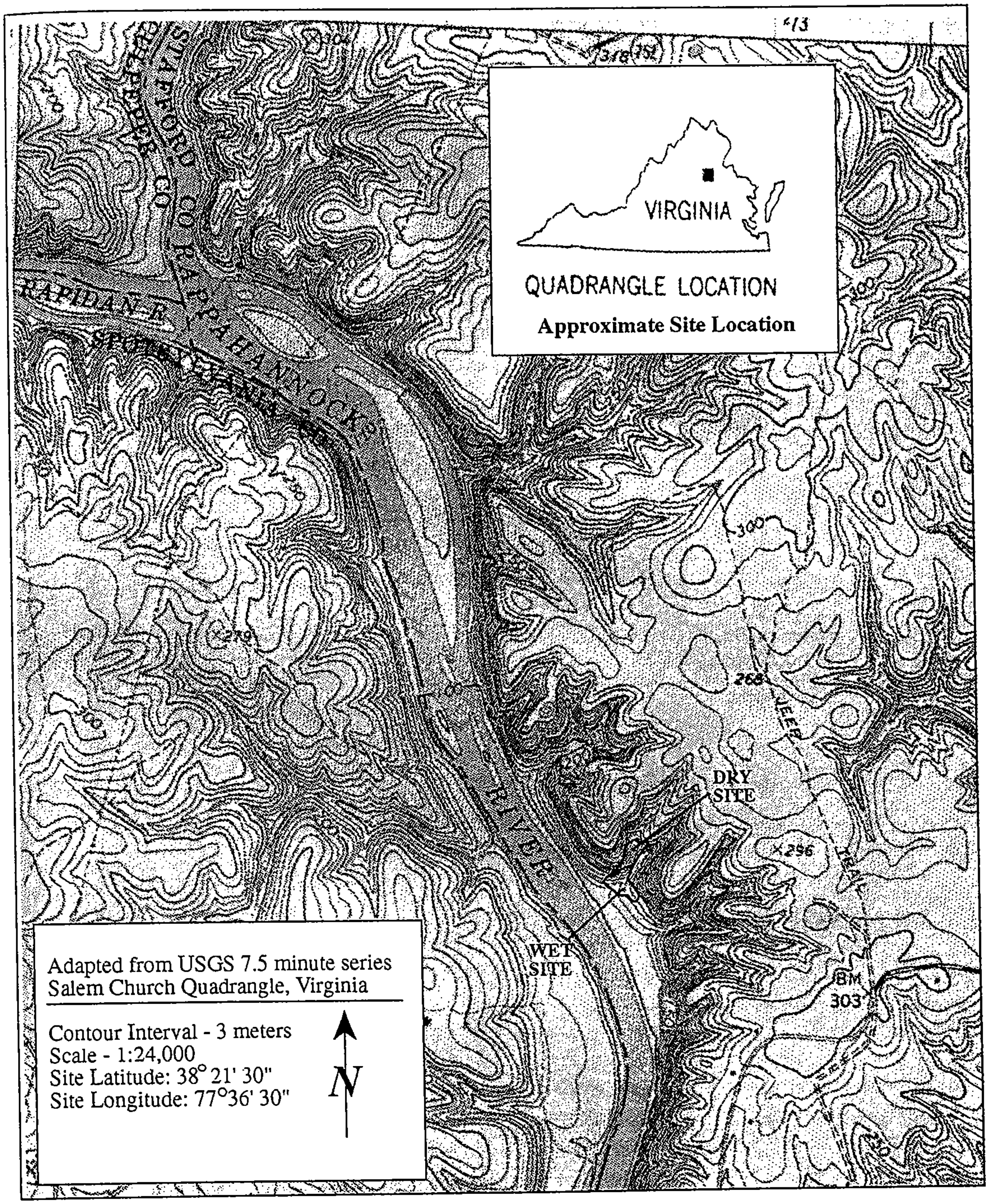

Figure 1. Location map of the study site along the Rappahannock River.

selected wetland plants, acquired prior to this experiment, are illustrated in Figure 2. Many of the features associated with the spectral response of leaves can be influenced by subtle, physiological changes exhibited by plants under stress (Goetz et al. 1985, Rock et al. 1988). These wavelengths provide the most information regarding plant cholorophyll pigment reflectance and structure reflectance (Gates et al. 1965, Rossotti 1983, Hale and Orcutt 1987, Carter 1993).

Leaf spectra were recorded using an Analytical Spectral Devices (ASD) PS II field spectroradiometer recording in 3-nm increments and incorporating a 5-degree field-of-view collimator. This provided an 8-cm-diameter field-of-view at a distance of 1 m from the leaf samples. Individual leaf samples were arranged facing up to fill the field-of-view. Using a bubble level, the radiometer was positioned at a nadir viewing angle in relation to the samples. Three spectra

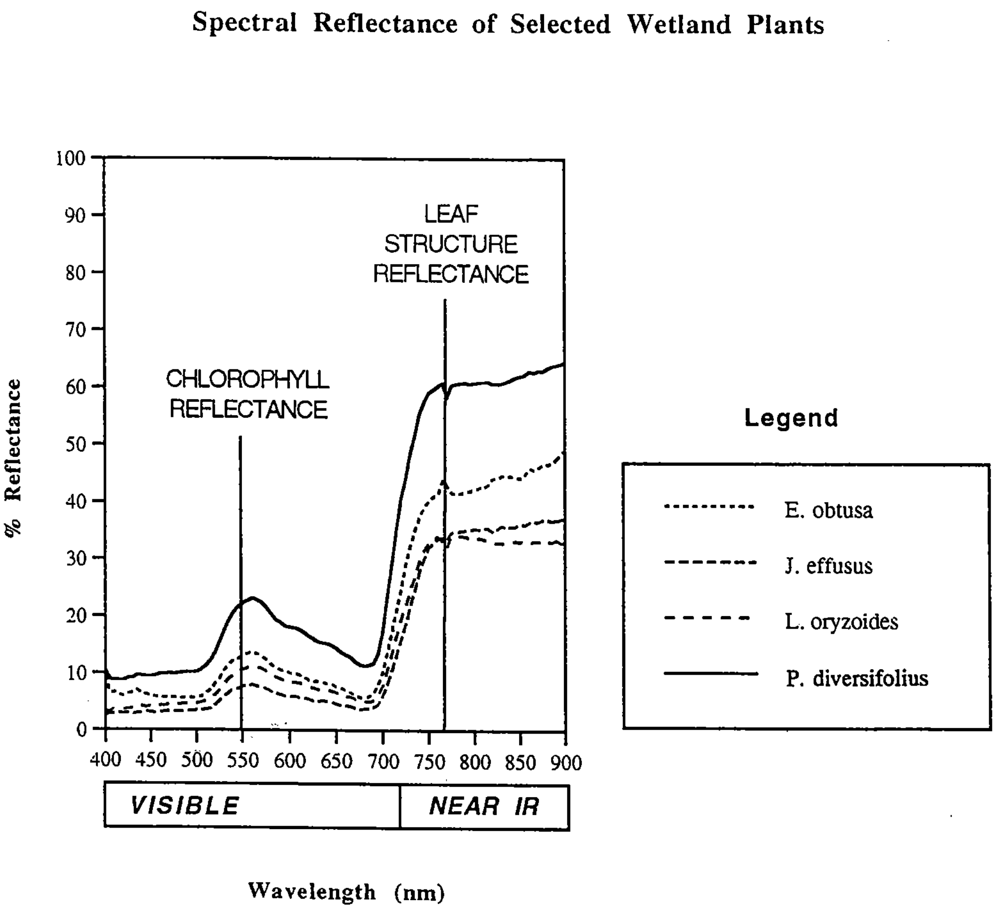

Figure 2. Spectral reflectance measurements for *Eleocarus obtusa* (Willd.), *Juncus effusus* L.), *Leersia oryzoides* (L.), and *Potamogeton diversifolius* (Raf.) collected during the growing season.

were recorded and averaged from leaf mosaics made from 8 to 10 leaves excised from different portions of the tree canopy. This allowed measurements to be obtained from sunlit and shaded leaves. All measurements were taken as close to local (solar) noon as possible to permit optimal lighting conditions. Procedures for obtaining leaf spectra followed those established by Satterwhite and Henley (1991). All measurements were referenced to a Spectralon halon reflectance standard.

For this experiment, redox potential (Eh) was used as a surrogate indicator of stress. The redox potential describes the condition of soils whereby the availability of oxygen and cation exchange capacity are altered due to a positive or negative electric potential (Ponnamperuma 1972, Wetzel 1983). It must be stressed that while these measurments provide insight to saturated or flooded conditions of soils, there does not exist a widely accepted method to measure and interpret soil redox potentials (Cogger et al. 1992). For this experiment, *in situ* redox measurements were made using a pH-mV meter with a calomel reference electrode and platinum electrodes following the methods of Cogger et al. (1992). Measurements recorded in millivolts (mV) were made in soils at the base of each of the sampled trees. All readings were corrected for the potential of the reference electrode by adding +244 mV to each reading. Probes were left to equilibrate in the soil prior to measurement. All weekly recorded measurements for the wet and dry sites were averaged.

Statistical analysis using a t-test determined whether significant differences between the pre- and post-saturation/inundation reflectance values of the wet and dry sites existed. In addition, second order polynomial regression was used to examine the cause-and-effect relationship between changes in the visible and near infrared reflectance (dependent variables) and the redox potential (independent variable) within each site. All analyses were performed using JMP SAS* and Statmost* statistical software.

RESULTS

Reflectance values of *A. rubrum* leaf specimens were not significantly different between the wet and dry sites during the first three weeks of April 1994

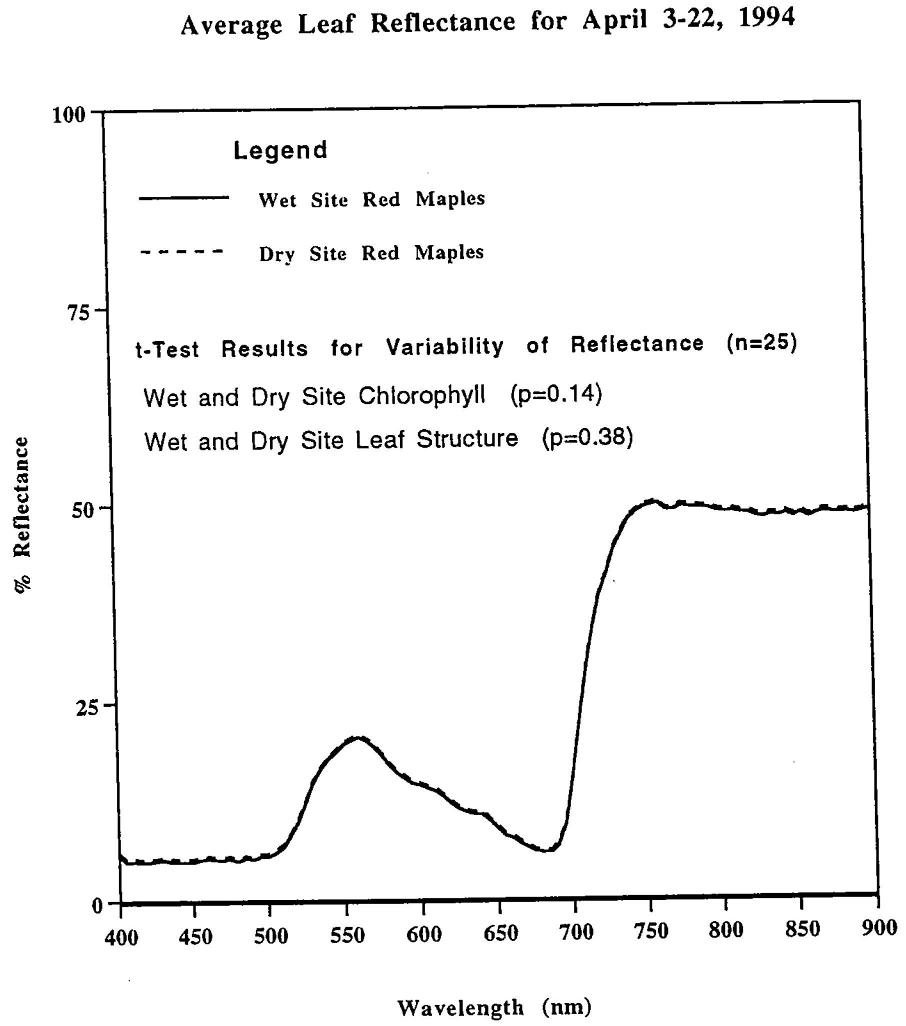

Figure 3. Average leaf spectral reflectance measurement for *Acer rubrum* (L.) collected during the April 3–22, 1994 sampling period.

(Figure 3). At this time, wet site soils were saturated and the dry site was moist. The trees were in full leaf-out and leaves were green and turgid and showed no apparent visible signs of stress.

During late April and early May, the wet site became completely surface-inundated and remained flooded until the beginning of the final three weeks of the experiment. Compared to the dry site leaves, wet site leaves showed a detectable increase in leaf reflectance in the visible region at 550 nm which is characteristic of the onset of chlorosis (Figure 4). In addition, there was also a measured increase in the near-infrared reflectance at 770 nm for wet site leaves as well as a subtle shift to shorter wavelengths (Figure 4). For this sampling period, the reflectance measured for wet site leaves was significantly greater than the reflectance measured at the dry site ($p \leq 0.007$). As the experiment progressed, the redox potential fell sharply at the wet site over a period of 5 weeks but began to rebound during the last four weeks of the sampling period (Figure 5). In contrast, redox potentials at the dry site were consistently positive and more stable, even during saturation (Figure 5). Redox measurements recorded in wet site flooded soils during this sampling period were at their lowest point for the experiment, while leaf reflectance was at its highest (Figure 6). Also during this sampling period the dry site, which became saturated but not inundated, had more stable redox potentials and lower leaf reflectance when compared to the wet site leaves (Figure 6).

Reflectance results from the final sampling period, recorded from the end of May through the second week of June, showed a decrease in values from the previous sampling period in both the visible and near infrared reflectance peaks for wet site leaves (Figure 7). For this final period, there was no statistically significant difference ($p \geq 0.09$) between wet and dry site leaf reflectance measurements. Redox potentials and

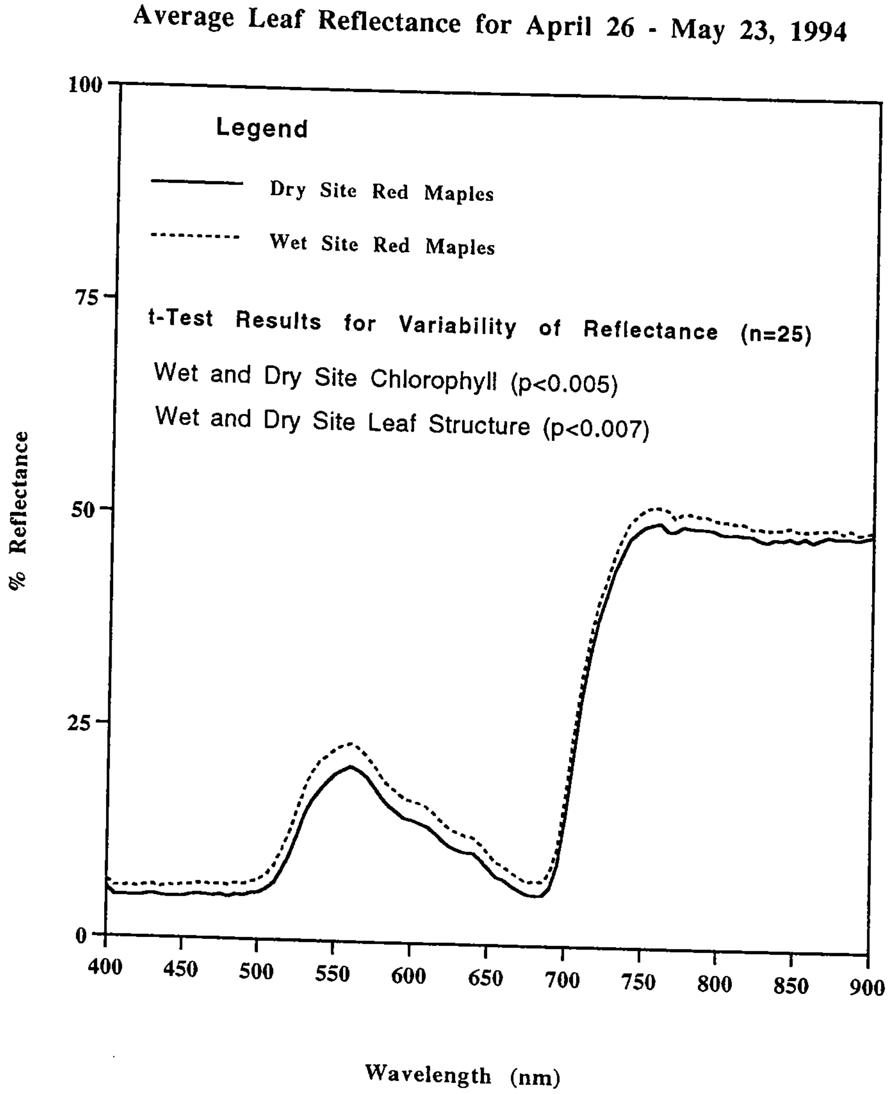

Figure 4. Average leaf spectral reflectance measurement for *Acer rubrum* (L.) collected during the April 26–May 23, 1994 sampling period. Evidence of stress is observed in an elevated reflectance at 550 nm and the shift at 770 nm for wet site specimens.

soil moisture conditions recorded for this period, presented in Figure 6, illustrate lowered reflectances for the wet site and virtually no change in reflectance at the dry site.

During the first three weeks of April, when no change in reflectance was detected, redox potentials at the wet site were negative and characteristic of reduced conditions (Mitsch and Gosselink 1986). T-test results for the wet site soil redox measurements showed that there was no significant difference ($p = 0.2$) between redox measurements obtained for the first three weeks (during saturation) and the next four weeks (during flooding) of the experiment (Table 1). However, redox measurements for the wet site were significantly lower ($p = 0.0001$) during flooding than those measurements recorded during the final three weeks of drying (Table 1).

Second order, polynomial regression analyses demonstrated a relationship ($r \geq 0.88$) between redox potential and leaf reflectance changes observed in the visible and near infrared for both the wet and dry sites (Figures 8 and 9). To further explore the strength of the relationship between flooding stress and reflectance at the wet site, measurements obtained during the first three weeks of saturation were excluded from the regression. For these wet site trees, a stronger relationship resulted ($r \geq 0.89$) between the leaf reflectance and redox potentials.

DISCUSSION

During the early part of the 1994 growing season, two forested wetlands dominated by *A. rubrum* were used to assess changes in leaf reflectance as it related

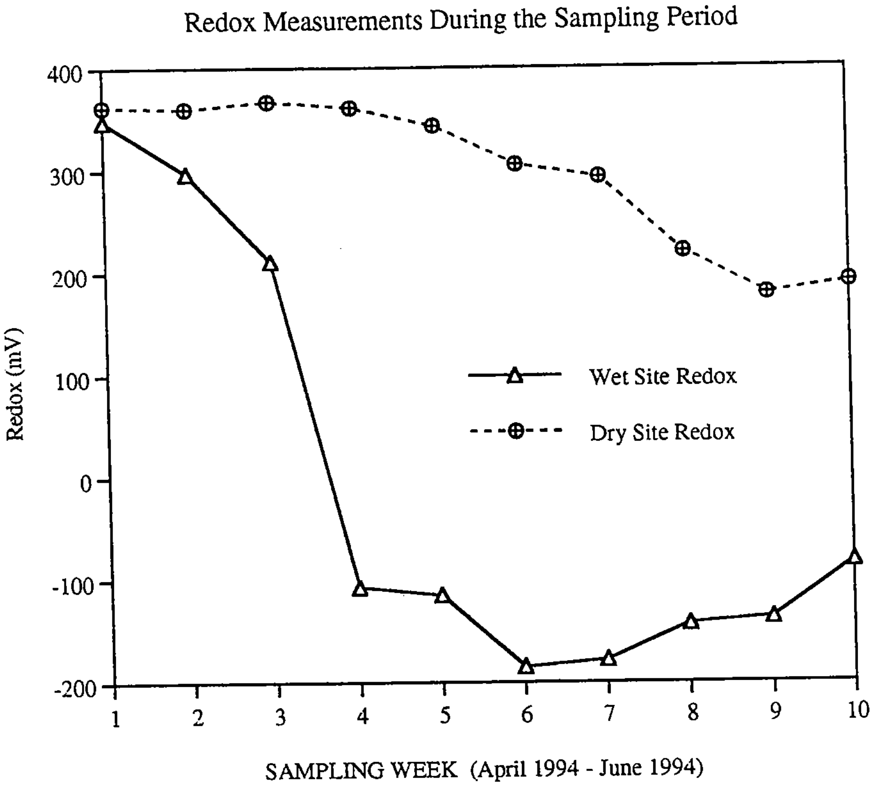

Figure 5. Redox mesurements recorded during the entire ten week sampling period showing the sharp five week drop (in mV) for redox potentials at the wet site.

to flooding. Due to different soil and hydrologic regimes, the study area was divided into a dry site and a wet site. As a surrogate measure of stress, soil redox potentials were monitored at each site and used to derive relationships with the measured spectral reflectance.

The results demonstrated that leaves associated with trees occupying the wet site showed a biophysical response during flooding. This response was manifested spectrally as an increased reflectance in the visible and near infrared portion of the spectrum during the May–June sampling period. This spectral response indicated that wet site trees did not show stress until the flooding became prolonged and the redox potential fell to its lowest point. This condition may indicate a lag-time in the biophysical response of flooding stressed trees. Of the symptoms associated with flooding stress on vegetation, a detectable chlorotic condition developed in wet site leaves. These findings seem to be consistent with research performed by Carter (1993) and Carter and Miller (1994) on spectral reflectance and plant stress. Their research has demonstrated significant changes can be observed in reflectance spectra when plants are under stress.

Initial spectral measurements obtained in April and final measurements recorded in June did not show significant differences between wet and dry site leaf reflectance. Reflectance curves generated for leaves obtained from each of these sites followed the typical trends of healthy green vegetation as established by Gates et al. (1965) and Collins (1978). However, regression analysis revealed a relationship between the changing visible and near infrared reflectance and soil redox potential for both sites during the course of the experiment. A stronger relationship was demonstrated for wet site measurements obtained during flooding by excluding measurements recorded during the saturation. This suggests that the reduced conditions associated with flooding had a greater influence on leaf reflectance than the reduced conditions associated with saturation.

Detectable reflectance differences recorded between the wet and dry site leaves were greatest during the May–June sampling period when the site was flooded and the redox potentials were at their lowest. Elevated leaf reflectance detected at 550 nm indicated the onset of chlorosis (Coutts and Phillipson 1978, Coutts 1981, and Carter and Miller 1994). Additionally, the increase in reflectance at 770 nm and a subsequent shift to shorter wavelengths were consistent with theories and observations related to delayed plant growth and maturity (Collins 1978). This four-week period would seem to offer the best opportunity to observe the spectral differences in these forested wetlands using a re-

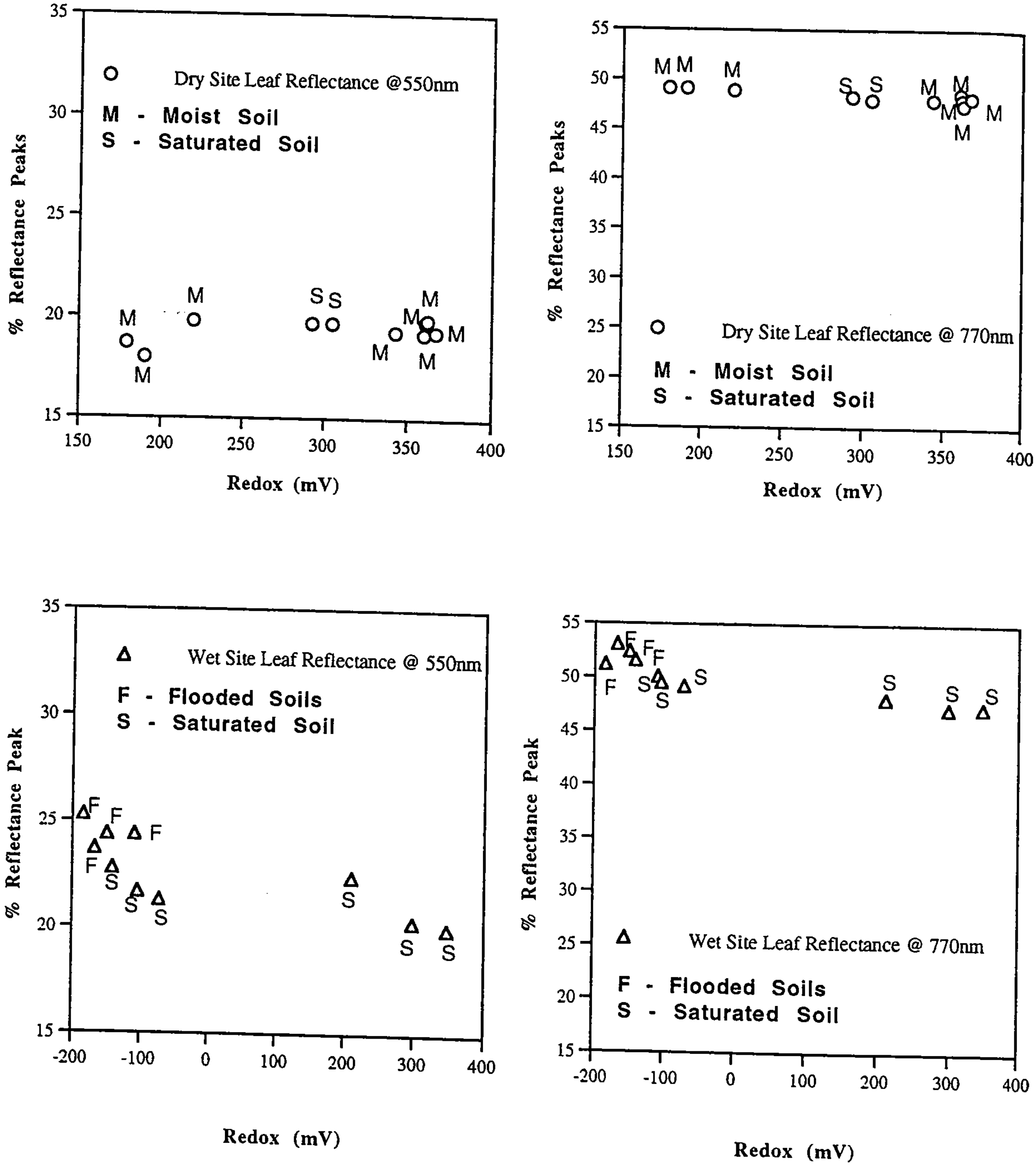

Figure 6. Dry site and wet site leaf reflectance, soil moisture, and redox measurements plotted to show the differences observed and measured in trees occupying both sites.

mote sensing system recording in the visible and near infrared wavelengths.

While detectable differences were measured with a spectroradiometer, this is not to suggest that these differences could be observed using broad band, remotely sensed imagery such as that represented by conventional aerial photography and satellite data. However, these differences may be detectable using narrow band remote sensing, which allows spectral data to be recorded in discrete wavelengths less than 10 nm wide. For example, recent research by Carter and Miller (1994) describes the use of narrow band imagery for characterizing subtle changes in plant reflectance in response to a host of stress agents. Using narrow band filters and video cameras, their research found that ratio techniques, applied to specific visible and near infrared spectral bands, allowed stress to be detected in the imagery. These spectral regions were identified as being the most responsive to unfavorable growing conditions.

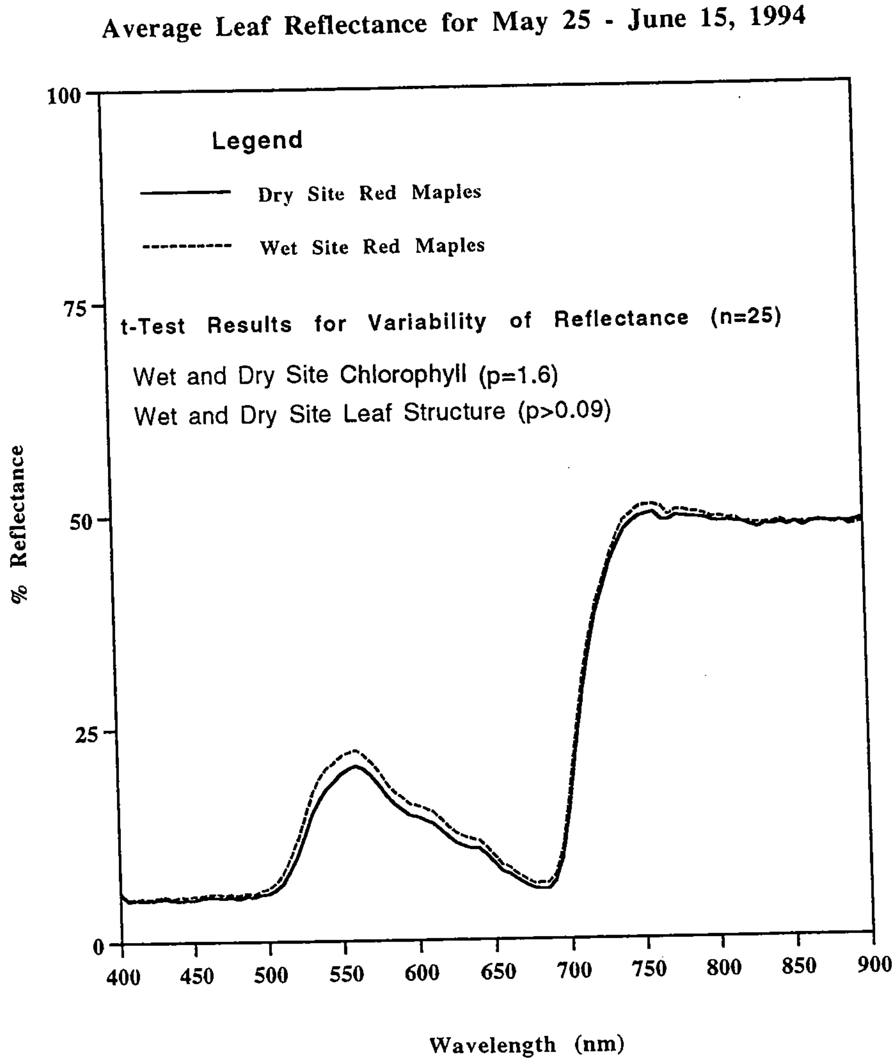

Figure 7. Average leaf spectral reflectance measurement for *Acer rubrum* (L.) collected during the May 25–June 15, 1994 sampling period. The elevated reflectance at 550 nm and the shift at 770 nm for wet site specimens, observed during the previous sampling period, has dropped indicating a rebound or physiological adjustment. Also during this period, water levels dropped and the wet site became drier.

Table 1. Results of t-tests computed on redox potentials recorded for wet site soils during saturation and flooding.

Saturated Conditions (First 3 weeks) and Flooded Conditions (Second 4 weeks)

t	Tabulated t	C.L.	p
−10.5138	2.0150	95%	0.0001

Flooded Conditions (Second 4 weeks) and Saturated Conditions (Final 3 weeks)

t	Tabulated t	C.L.	p
1.2791	2.0150	95%	0.2570

Baseline data collected on growing conditions and the spectral reflectance properties of forested wetlands may permit a seasonal remote sensing strategy to be designed. Using a detection system that incorporates filtered fore optics, centered at specific visible and near infrared response wavelengths, the characterization of forested wetlands may be improved. Recent advances in aerial video imaging and digital multispectral video already make it possible to selectively control the acquisition of image data in discrete narrow bands. These compact technologies allow for the flexibility to quickly deploy a remote sensing system when opportunities are limited to observe specific phenomena.

The implications for wetland mapping could be significant if seasonal relationships are recorded for various plant communities. The ability to improve the de-

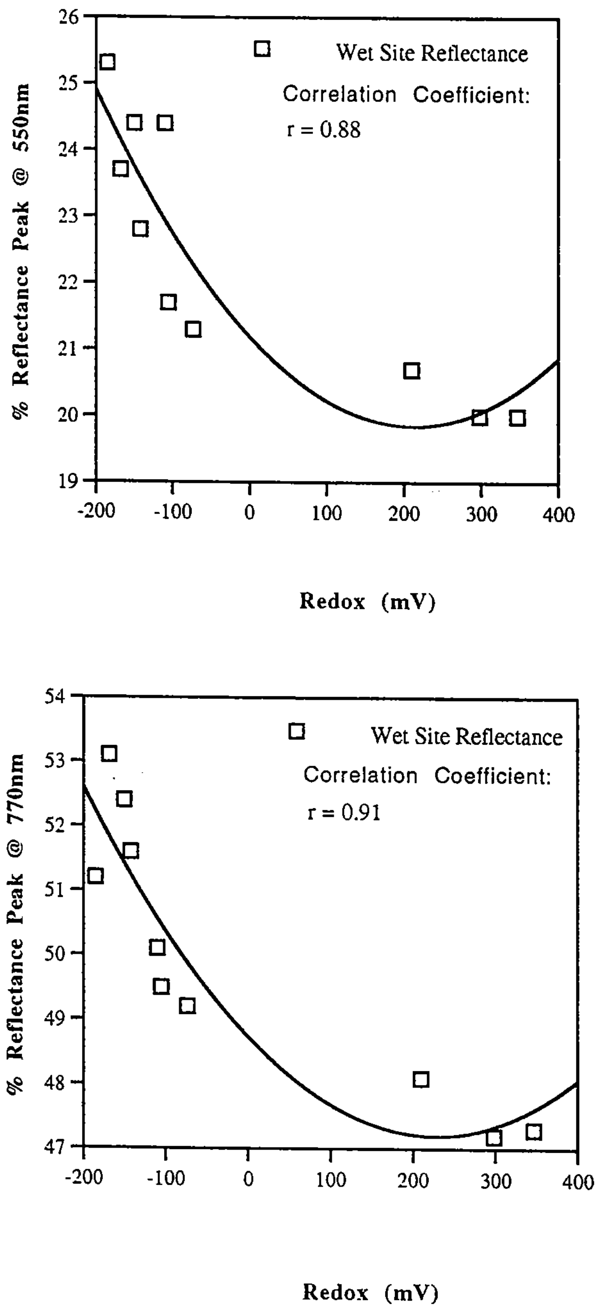

Figure 8. Regression analysis showing the relationship (r ≥ 0.88) between spectral reflectance measurements recorded for wet site *Acer rubrum* (L.) and falling redox potentials.

tection of wetlands within monospecific vegetation stands could help improve the accuracy of many wetland map products, including the NWI. Carter (1982) suggested that improved spatial and spectral resolution will facilitate mapping of wetlands of less than 4 ha. Known seasonal spectral reflectance signatures and the ever improving spatial and spectral resolution of aerial photography and high resolution videography should make this possible.

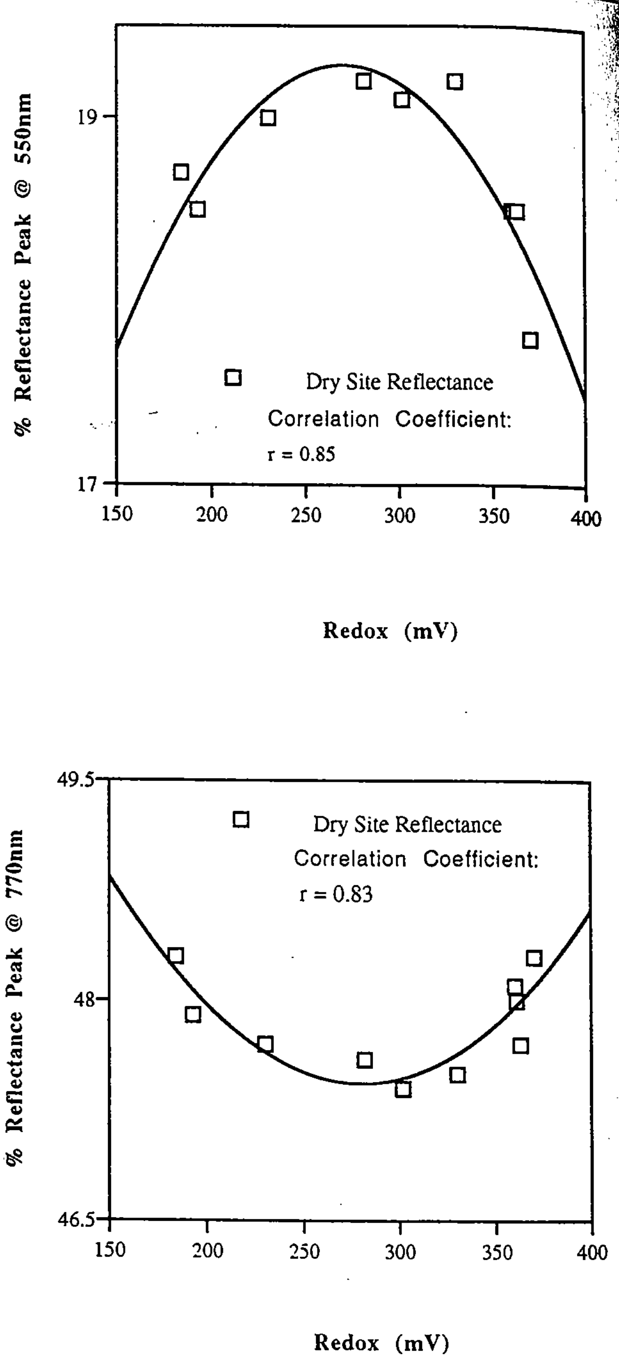

Figure 9. Regression analysis showing the relationship (r ≥ 0.83) between spectral reflectance measurements recorded for dry site *Acer rubrum* (L.) and redox potentials.

LITERATURE CITED

Anderson, J.E. 1995. Spectral signatures of wetlands plants (350–900 nm). U.S. Army Corps of Engineers Topographic Engineering Center, Alexandria, VA, USA. TEC Report #0068.

Campbell, J.B. 1987. Introduction to Remote Sensing. The Guilford Press, New York, NY, USA.

Carter, G., R.J. Mitchell, A.H. Chappelka, and C.H. Brewer. 1992. Response of leaf spectral reflectance in loblolly pine to increased atmospheric ozone and precipitation acidity. Journal of Experimental Botany 43:577–584.

Carter, G. 1993. Responses of leaf spectral reflectance to plant stress. American Journal of Botany 80:239–243.

Carter, G. and R. Miller. 1994. Early detection of plant stress by digital imaging within narrow stress-sensative wavebands. Remote Sensing Environment 50:295–302.

Carter, V. 1982. Applications of remote sensing to wetlands. p. 284–300. *In* C. Johannson and J. Sanders (eds.) Remote Sensing for Resource Management. Soil Conservation Society of America. Ankeny, IA, USA.

Carter, V. and J. Anderson. 1978. Interpretation of wetlands imagery based on spectral reflectance characteristics of selected plant species. p. 580–595. *In* Proceedings, 38th Annual Meeting of the American Society of Photogrammetry. Falls Church, VA, USA.

Cogger, C.G., P.E. Kennedy, and D. Carlson. 1992. Seasonally saturated soils in the Puget Lowland II. measuring and interpreting redox potentials. Soil Science 154:50–58.

Collins, W. 1978. Remote sensing of crop type and maturity. Photogrammetric Engineering and Remote Sensing 44:43–55.

Coutts, M.P. 1981. Effects of water logging on water relations of actively growing and dormant Sitka spruce seedlings. Annual Botany 47:747–753.

Coutts, M.P. and J.J. Phillipson. 1978. Tolerance of tree roots to water logging, New Phytologist 80:63–69.

Gammon, P., V. Carter, and W. Rohde. 1979. LANDSAT digital classification of the vegetation of the Great Dismal Swamp with an evaluation of classification accuracy. p. 87–97. *In* Satellite Hydrology Proceedings, Pecora V Symposium. American Water Resources Association. Minneapolis, MN, USA.

Gates, D.M., H.J. Keegan, J.C. Schleter, and V.R. Weidner. 1965. Spectral properties of plants. Applied Optics 4:11–20.

Goetz, A.F.H., G. Vane, J.E. Solomon, and B.N. Rock. 1985. Imaging spectrometry for earth remote sensing. Science 228:1147–53.

Hale, M.G. and D.M. Orcutt. 1987. The Physiology of Plants Under Stress. John Wiley & Sons,New York, NY, USA.

Hoque, E., P. Hutzler, and H. Hiendl. 1992. Reflectance, colour, and histological features as parameters for the early assessment of forest damage. Toxicology and Enviromental Chemistry 27:209–215.

Hsiao, T.C. 1973. Plant responses to water stress. Annual Review of Plant Physiology 24:519–570.

Iarig, D. and A. Strobel, Jr. 1974. Soil Survey of Stafford and King George Counties. United States Department of Agriculture, Soil Conservation Service Washington, DC, USA.

Jackson, R. 1986. Remote sensing of biotic and abiotic plant stress. Annual Review of Phytopathology 24:265–287.

Jensen, J.R., E.J. Christiansen, and R. Sharitz. 1983. Nontidal wetland mapping in South Carolina using multi-spectral scanner data. Remote Sensing Environment 16:1–12.

Kawase, M. 1981. Effects of ethylene on aerenchema development. American Journal of Botany 68:651–658.

Koslowski, T.T. and S.G. Pallardy. 1979. Stomatal responses of *Fraxinus* pennsylvanica seedlings during and after flooding. Physiology of Plants 46:155–158.

MacMannon, M. and R.M.M. Crawford. 1971. A metabolic theory of flooding tolerance; the significance of enzyme distribution and behavior. NewPhytology 10:299–306.

Milton, N., C.M. Ager, B.A. Eisworth, and M.S. Power. 1989. Arsenic- and selenium-induced changes in spectral reflectance and morphology of soybean plants. Remote Sensing Environment 30: 263–269.

Mitsch, W. and J.G. Gosselink. 1986. Wetlands. Van Nostrand Rhinehold, New York, NY, USA.

Murtha, P. 1982. Detection and analysis of vegetation stress. p. 151–158. *In* C. Johannson and J. Sanders (eds.) Remote Sensing for Resource Management. Soil Conservation Society of America. Ankeny, IA, USA.

Peñuelas, J., I. Filella, C. Biel, L. Serrano and R. Savé. 1993. The reflectance at the 950–970 nm region as an indicator of plant water status. International Journal of Remote Sensing 14:1887–1905.

Ponnamperuma, F.N. 1972. The chemistry of submerged soils. Advanced Agronomy 24:29–96.

Rock, B.N., T. Hoshizaki, and J.R. Miller. 1988. Comparison of in situ and airborne spectral measurements of the blue shift associated with forest decline. Remote Sensing Environment 24:109–127.

Rossotti, H. 1983. Colour: Why the World Isn't Grey. Princeton University Press, Princeton, NJ, USA.

Satterwhite, M.B. and J.P. Henley. 1989. Hyperspectral signatures (400 to 2500 nm) of vegetation, minerals, soils, rocks, and cultural features: laboratory and field measurements. U.S. Army Engineer Topographic Laboratories, Fort Belvoir,VA, USA. ETL Report #0573.

Sersland, C.A., C.A. Johnston, and J. Bonde. 1995. Assessing wetland vegetation with GPS-linked, color video image mosaics. p. 53–62. *In* Paul Mausel (ed) ASPRS 15th Biennial Workshop on Videography and Color Photography in Resource Assessment, ASPRS, Terre Haute, IN, USA.

Sokal, R.S. and F.J. Rohlf. 1990. Biometry. W.H. Freeman and Company, New York, NY, USA.

Tiner, R.W., Jr. 1990. Use of high-altitude aerial phtography for inventorying forested wetlands in the United States. Forest Ecology Management 33–34:593–604.

Wetzel, R.G. 1983. Limnology. Saunders College Publishing, Fort Worth, TX, USA.

Manuscript received 7 July 1995; revisions received 2 February 1996 and 7 May 1996; accepted 28 July 1996.