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LARGE-SCALE PATTERNS OF FOREST SUCCESSION AS DETERMINED BY REMOTE SENSING¹

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Abstract. The spatial pattern of and the transition rates between forest ecological states were inferred for $\approx 260\,000$ pixel-sized (3600 m^2) landscape units using satellite remote sensing. Transition rates were estimated from 1973 to 1983 Landsat images of the study area, classified into ecological states associated with forest succession. The effects of classification error on transition rate estimates were modeled and error adjustments made.

Classification of the 1973 and 1983 Landsat images of the 900 km^2 study region required a relatively small set of ground-observed and photo-interpreted plots in 1983, with a total area of just 1.62 km^2 . An innovative technique for correcting multiyear Landsat images for between-image differences in atmospheric effects and sensor calibration, permitted classification of the 1973 Landsat image using 1983 ground observations. Given current Landsat data, and ground observations in one year, this technique would permit monitoring of forest succession and dynamics for nearly a 20-yr period.

Results of applying these techniques to a forest ecosystem showed that during the 10-yr observation period it was patchy and dynamic. For both a wilderness and a nonwilderness area in the study region, sizeable values of transition rates were observed and over half of the landscape units were observed to change state; however, a Markov analysis, using the observed transition probabilities, suggests that at the regional level neither the wilderness nor the nonwilderness areal proportions of ecological states are undergoing rapid change.

Key words: biosphere; ecosystem dynamics; global change; landscape ecology; long-term ecological research; stability; succession.

INTRODUCTION

Improved understanding of the interaction between land-surface vegetation and climate has been of increasing interest in the past decade. Of particular importance are the implications of climate change to forested ecosystems, implications for: (1) global biogeochemical cycles, particularly carbon and nitrogen (Pastor and Post 1986, Wofsy et al. 1988, Harmon et al. 1990), (2) the hydrological cycle (Running and Coughlan 1988), and (3) the surface energy balance (Sellers et al. 1988). Also of interest are the impacts of human activities on: (1) terrestrial vegetation (Guppy 1984), (2) atmospheric trace gas composition (Harris

et al. 1988), and (3) species extinction (Soulé 1986). Such changes have been hypothesized to exert global effects on the climate and composition of terrestrial ecosystems within the next few decades (MacCracken and Luther 1985).

Investigations of these issues require observations and modeling of phenomena operating at a variety of temporal and spatial scales across regional and global landscapes. Long-term ecosystem studies, which require field observations in multiple years, also require continuity in personnel and equipment and are often prohibitively expensive. Extending ecosystem studies from local to regional scales has been hampered by the difficulty of observing the spatial patterns and the long-term dynamics of disturbance and plant succession at the larger scales. While it is possible to characterize average conditions of natural landscapes with sparse ground-based sampling, ground-based techniques are

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inadequate to characterize the spatial patterns of successional states over a large landscape (Lieth and Whittaker 1975). Typical ground plots cover 100 m², and require on the order of 10–50 h of labor to locate, visit, and measure. Sampling even a modest 2% of a study area (20 plots/km²) is impractical for regional survey.

The purpose of this study was to develop and demonstrate the use of satellite remote sensing to characterize the spatial patterns and long-term changes in a forest at spatial scales ranging from 0.3 to 3000 km² and at temporal scales equal to the satellite period of record. Specifically, 1983 ground and aircraft observations were used to relate spectral measurements from a 1983 Landsat 4 satellite image to ground-observed ecological states of a forested ecosystem (clearing, regeneration, deciduous, deciduous/conifer mix, and conifer). Previous applications of satellite remote sensing of vegetation have been generally restricted to land cover classifications such as hierarchical Anderson-level associations (Anderson et al. 1971). Later investigations extended the satellite-based classifications to a framework of somewhat more ecologically meaningful relationships, such as age-dependent timber harvest classes (Beaubien 1979, Horler and Ahern 1986). In this paper we define ecological states, based on the species composition and age structure of landscape elements, and show that they are associated with distinct patterns of reflected light, or spectral "signatures." Based on these spectral "signatures" the 1983 Landsat image was then classified into these ecological states. The 1983 Landsat 4 ecological state "signatures" were then used to classify a 1973 Landsat 1 image over the same area into the same ecological states; to do this it was necessary to develop a technique to adjust the 1983 Landsat signatures for radiometric differences between the images, i.e., sensor differences (the 1973 Landsat 1 satellite carried a different sensor than the 1983 Landsat 4 satellite), atmospheric differences, and growing season differences. By looking at pixel-by-pixel differences in the ecological states of the landscape between 1973 and 1983, we calculated rates of change in the forested ecosystem due to natural and anthropogenic disturbance, as well as natural succession. The rates of succession and disturbance so obtained, are potentially useful inputs to regional and even global-scale biogeochemical, hydrological, and energy cycle studies of the types cited above. For instance, the forest carbon flux model of Harmon et al. (1990), in order to compute the carbon flux for a forest ecosystem, requires landscape-level data on age distribution, species composition, cause of disturbance (fire, windthrow, logging, urbanization), and rotation interval. As another example, the simple biosphere model of Sellers et al. (1986) requires data on species composition and age structure of surface vegetation to compute surface-atmosphere transfer rates for heat, moisture, and radiation.

STUDY AREA

The study was conducted in the Superior National Forest (SNF), including the protected wilderness of the Boundary Waters Canoe Area (BWCA), in northeastern Minnesota. (We will refer to the BWCA portion of our study area as "wilderness" and the portion of the SNF outside of the BWCA as "nonwilderness.") We selected boreal forests for study because they are of great extent and importance globally. Boreal forests are a major source of commercial timber and are believed to be one of the major reservoirs of the earth's organic carbon (Lieth and Whittaker 1975, Botkin and Simpson 1990), and thus play an important role in the dynamics of the biosphere. They are currently subject to rapidly accelerating management and development. We chose the SNF as a study site because the vegetation is comparatively well known (Heinselman 1973, 1981, Grigal and Ohmann 1975, Ohmann and Grigal 1979), and because we believed that northern Minnesota, in particular, and the boreal forest, in general, are well suited for remote sensing, due to the taxonomic simplicity of boreal forests, relatively flat terrain, and high proportion of cloud-free days in comparison to tropical rain forests, which are also of great interest to earth systems science.

Several dozen tree species occur in the SNF, but landscape dominants are few. Upland areas are forested except for recently disturbed areas and scattered rock outcroppings. Early successional stands on uplands are dominated by aspens (*Populus* spp., primarily *P. tremuloides* and *P. grandidentata*) on relatively mesic sites and jack pine (*Pinus banksiana*) on shallow, dry soils. Following classical concepts of ecological succession, in upland stands succession in the SNF has been believed to proceed towards dominance by conifers including balsam fir (*Abies balsamea*) and black and white spruce (*Picea mariana* and *P. glauca*). White and red pine (*Pinus strobus* and *P. resinosa*) can be locally dominant but constitute a small proportion of total landscape cover. Extensive acidic peatlands range from open shrublands to dense stands of black spruce mixed in open stands with tamarack (*Larix laricina*).

Several investigators have described community patterns as controlled by soil, slope, aspect, and successional history (Heinselman 1973, Ohmann and Grigal 1979, Swain 1980). Grigal and Ohmann (1975) constructed a detailed vegetation classification for a region that included our study area. Fire is the dominant natural disturbance in upland stands, with a previously estimated average return time of slightly less than 100 yr (Heinselman 1973). Extensive windthrow, insect outbreaks, and drought also cause significant disturbance. Logging is an important disturbance in the SNF, while logging has not been permitted in the BWCA since 1978, when that area became a legally designated wilderness. The natural fire cycle in both

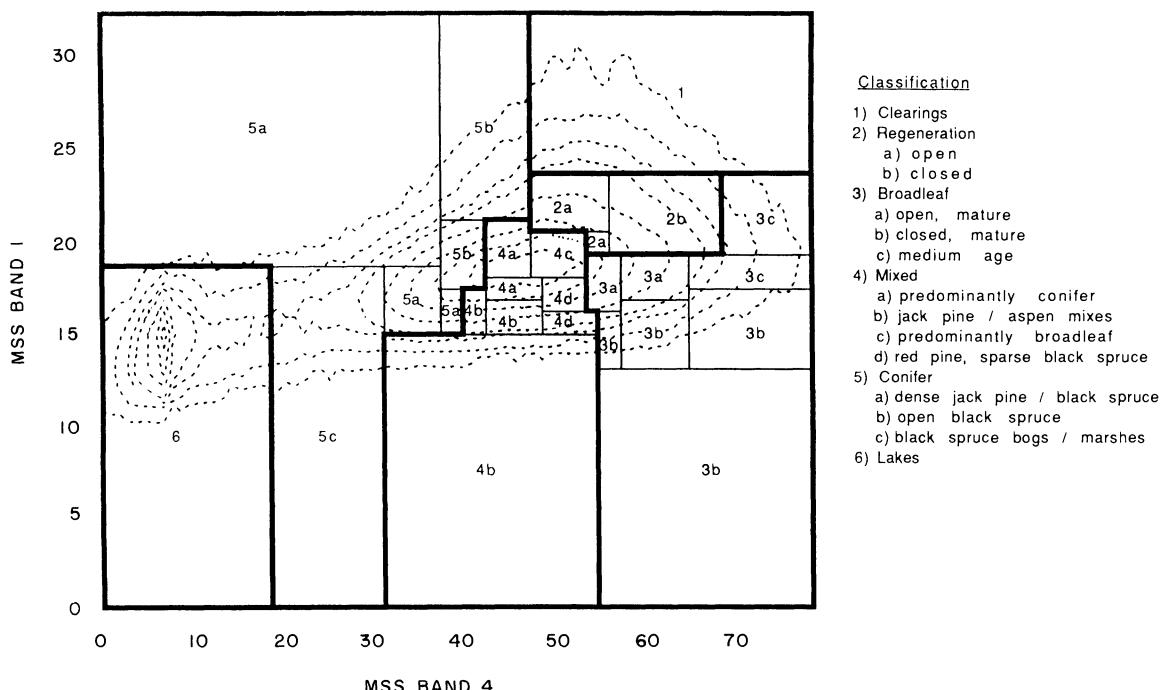


FIG. 1. Scatterplot showing correspondences between ecological states and reflected light intensity as measured in July 1983 by Landsat-4 MSS in wavelength band 4 (near-infrared, 0.8–1.1 μm) and band 1 (visible light near the green peak, 0.5–0.6 μm). The boxes define correspondences of spectral regions with ecological states. The units on each axis are digital counts (0–256) proportional to radiance as recorded by the Landsat MSS. Box boundaries were determined as described in the text (*Methods: Decision regions . . .*). The isopleths shown are regions of constant numbers of pixels. The interior isopleths enclose the higher abundances of pixels. For example, the innermost isopleths are >400 pixels. Fourteen ecological states were distinguishable in the July 1983 Landsat-4 MSS imagery. These states (clearings, lakes, and the 12 ecological states with lower case alphabetical designations) are represented in the scatterplot with lighter bordered boxes. In the June 1973 Landsat-1 MSS imagery, it was necessary to combine some of the 1983 states as shown by the boxes with darker borders. The six final states (clearings, regeneration, broadleaf, mixed, conifer, and lakes) were used to classify both the 1983 and 1973 Landsat images.

areas has been altered by fire suppression since ≈ 1900 . However, the $\approx 94\,000$ ha study area include a 6000 ha area that burned in 1971 (Ohmann and Grigal 1979).

METHODS

Analysis of remote-sensing imagery

In simplest terms, the observational methods consist of (1) obtaining remote sensing images of a scene in two or more years, (2) using field observations or aerial photos from one of the years to determine the ecological states of ground plots, (3) determining the geographic coordinates of the image pixels and locating the pixels corresponding to the ground plots ("training pixels"), (4) adjusting the images for atmospheric, sensor, and growing season differences between dates, and (5) computing the spectral characteristics of the ecological states, and based on these characteristics, computer classifying the remaining image pixels into ecological states.

Landsat Multispectral Scanner (MSS) data (≈ 60 m resolution) were acquired for 3 July 1973 and early 18

June 1983 over the study area long the Echo Trail north of Ely, Minnesota (acquisition dates for the 2 yr were chosen to be as similar as possible to minimize changes in reflectance due to growing season differences). Three sections of the imagery (>2800 km^2) were analyzed, each section composed of a 512×512 array of MSS picture elements ("pixels," which we will also refer to as "landscape elements"). The central 512×512 section (≈ 940 km^2), roughly evenly divided between wilderness and nonwilderness, was used to compare the two management regimes. Classification of the image pixels into ecological states was accomplished using supervised classification; specifically, the statistical distributions of the Landsat radiometric measurements from the training pixels for each ecological state were used to define unique "decision" regions for the states, regions within a two-dimensional Cartesian space of Landsat band 1-band 4 measurements (Fig. 1). Classification of a nontraining pixel is accomplished by assigning to it an ecological state label corresponding to the decision region that contains its band 1-band 4 value pair. See Haralick and Fu (1983) for more details on this technique.

Decision regions: association of ecological states with spectral signatures

To characterize the ecological states spectrally, two types of "training" sites, consisting of a range of ecological states, were located within the study area. The first type, ground observations acquired for an earlier study in 1983 (K. W. Woods, *personal observation*), consisted of 98 circular plots (60 m in diameter) consisting of aspen, jack pine, and lowland spruce stands. Within each 60 m diameter stand, canopy and understory composition (basal area for canopy species and per cent cover for both) data were measured in 1983 within five circular plots, 8 m in radius: one at the center and four contiguous to it, to the north, south, east, and west. The second type of ground site consisted of 50 plots, which we selected specifically for this remote sensing study, based on photo-interpretation of aerial photography and high-resolution (≈ 12 m pixel size) digitally generated imagery; the imagery was acquired on 23 September 1983 from an aircraft-borne camera and multispectral scanner, the thematic mapper simulator, which measures reflected light in the same wavelength bands as the Thematic Mapper on the Landsat satellite. These plots were described by dominant species and extent of forest canopy cover.

All plots were then located in the aircraft, and MSS satellite imagery and spectral "signatures" of the sites (average radiance for each band over a nine-pixel square centered on the site) were extracted. A scatterplot, with MSS band 1 (0.5–0.6 μm) counts on one axis and MSS band 4 (0.8–1.1 μm) counts on the other (counts are digitized sensor voltages, proportional to radiance), was constructed (Fig. 1). Bands 2 and 3 were not used because infrared band 3 was highly correlated with infrared band 4, and visible light band 2 was highly correlated with visible light band 1. Signatures of training sites with the same ecological state tended to "cluster," i.e., group within local regions of the scatterplot. Different ecological states fell mostly into distinct regions.

The spectral differences between these regions or states were a result of (1) between-species differences in leaf optical properties and morphology, (2) differences in crown closure, and (3) understory leaf properties of open canopies (Butera 1985, Shen et al. 1985, Badhwar et al. 1986, Li and Strahler 1986). As can be seen in Fig. 1, at one extreme, closed black spruce and jack pine (class 5), which have highly light-absorbing needles and dense branch structures, are highly absorbing in both the visible (bands 1 and 2) and the infrared bands (3 and 4) of MSS, leading to low reflectance. At the other extreme, clearings (class 1), i.e., rock outcrops, grassy areas, and unforested boglands with low leaf area, are highly reflective in both the visible and infrared bands. For regeneration states (class 2), i.e., cleared areas covered by low shrubs and young trees, increased leaf area results in decreased visible

reflectance. As deciduous shrubs and young trees grow to mature deciduous stands (class 3), further increases in leaf area and shadowing from branches leads to further reductions in the visible reflectances. The near infrared and visible reflectance of mixed deciduous/conifer stands (class 4) decreases as a result of the low reflectance conifers.

As shown in Fig. 1, rectangles were used to delineate the different regions or states. Where confusion existed, i.e., where regions overlapped on the scatterplot, the rectangular decision boundaries were selected to minimize the probability of misclassification of the training pixels (following Moik 1980). The resulting "decision regions" are used for supervised classification of the entire 1983 Landsat image and the 1973 Landsat image, adjusted for sensor, atmospheric, and seasonal differences between acquisitions.

Radiometric rectification of the 1973 image to the 1983 image

In order to use the decision regions of the ecological states determined in the 1983 image, for classification of the 1973 image, radiometric adjustment of the 1973 image to the 1983 image was necessary, in part because atmospheric effects on reflected light can differ between dates, but also because the MSS instrument on Landsat 1 had a different calibration from the MSS on Landsat 4. We refer to this technique as "radiometric rectification." Additional detail can be found in Hall et al. (1987, *in press*). In summary, this technique involved three steps: (1) finding radiometric "control" elements in the two images, i.e., "bright" landscape elements, rock outcrops and roads, and "dark" landscape elements, deep, clear water bodies; (2) estimating the parameters of a linear relationship, band by band, between the radiance values of the radiometric "controls." Since the reflectance of these control elements changes little with time, the relationship between them contains the information specifying the atmospheric and sensor differences between images; (3) multiplying the 1973 Landsat radiometric data by the relationship determined for the controls to radiometrically rectify the 1973 to the 1983 image.

Adjustments for seasonal differences in reflectance

Following radiometric rectification of the two images, 1973 Landsat radiances were further adjusted for differences in reflectance characteristics of the ecological states induced by growing season differences between 1973 and 1983. At the time of the 3 July 1973 acquisition, 677 growing degree-days (average temperature minus 4.4°C; see Allen 1976) had accumulated since 1 January of that year, by 18 June 1983, only 267. To account for these differences, we used the fact that a sequence of five Landsat images acquired during the growing season of 1976 showed that the reflectances

of ecological states in this region have nearly the same variation with accumulated growing degree-days, including nutrient-deficient bogs. Since these bogs changed little in structure or successional state over the 10-yr period, any change in the reflectance of them between the 1973 and 1983 acquisition dates resulted primarily from seasonal differences; thus, seasonally induced reflectance changes in an ecological state could be approximated by those observed for bogs.

Spectral separability of the ecological states

The ecological states in the 1973 MSS data were not as distinct as in the 1983 data because of the poorer radiometric quality of the sensor. For example, in the 1983 imagery, jack pine could be distinguished from other conifers and several types of nonforest vegetation were separated, but these distinctions could not be made in the 1973 imagery. Classes with poor separability in 1973 were combined in both the 1973 and 1983 classifications, and each pixel in each image was then classified according to the decision regions set in band 1–band 4 space, leading to the six classes shown in Fig. 1 and listed in Table 2. These classes did not provide a perfect ecological classification. For instance, jack pine stands, which are early successional, were lumped with relatively stable upland spruce-fir and bog-conifer forests. Open and sparsely forested sphagnum bogs were confused to some extent with clearing, regeneration, and deciduous. Upland clearings produced by very recent disturbance were generally not distinguishable from barren rock outcrops. Nonetheless, although some successional trends are confounded, these classes were ecologically functional for a study of succession.

Rates of change at the landscape unit level

Following radiometric rectification and phenology adjustment of the 1973 Landsat radiances, each pixel in the 1973 and the 1983 images was classified into the ecological states. The classified images were then spatially registered using an algorithm that matches ground control points between images (roads and rock outcrops). The classified images were then used to tabulate changes of landscape elements between ecological states on a pixel-by-pixel basis. From this, a transition matrix T was created, which provided direct measures of rates of change in successional states over the 10 yr for each landscape unit. The a th row and b th column of T is the proportion of pixels in the scene that were in the a th ecological state in 1973 and the b th ecological state in 1983. Each diagonal element of T , $a = b$, is a retention frequency, i.e., the proportion of landscape elements in a state that remained in or returned to the same state between 1973 and 1983. Each off-diagonal element, $a \neq b$, is a transition frequency, i.e., the rate at which landscape elements in a given state changed to other states during the 10-yr period.

Rates of change at the regional level

It is of some interest to investigate the implications of the current transition rates at the landscape unit level for rates of change of the areal proportions P_c of ecological states at the regional level. For instance, do the currently observed rates of deforestation from logging suggest significant rates of decline in the area covered by mature forest stands?

If the climate and anthropogenic influences that affect transition rates are nearly constant for future observation periods, the “steady-state” value of the areal proportions of ecological states can be calculated by solving the eigenvector equation,

$$\mathbf{P} = \mathbf{T}\mathbf{P}. \quad (1)$$

Recent reviews of such models for vegetation dynamics can be found in Usher (1981) and Hulst (1979). We can also calculate the number of observation periods, m , to reach “steady state.” Clearly an assumption of a constant transition matrix is unrealistic over long time periods; however, if m is small, then \mathbf{P} is approximately correct and $\mathbf{P} - \mathbf{P}_c$ provides a first-order approximation to the implications of current management and environmental conditions on near-term rates of change of ecosystem states at the regional level. As stated by Rosswall et al. (1988), the Markov model “... remains remarkably useful as a first approximation to changes taking place from one state to another when only the probabilities of the transitions can be estimated.”

Recurrence times for ecological states

From the transition matrices it is possible to estimate the recurrence time, $\langle T_r \rangle$, the average number of years for a landscape element to return to a given state once it had left that state, and the occupancy time, $\langle T_o \rangle$, the average time a landscape element remained in a state. The total cycle time, $\langle T_c \rangle$, is the expected time for a landscape element to enter a state, leave that state, and return, so that $\langle T_c \rangle = \langle T_o \rangle + \langle T_r \rangle$.

Assuming that the entire set of landscape units obeys a Markov process, the average occupancy time, $\langle T_o \rangle$, is $10/(1 - P_{bb})$, i.e., 10 yr (the length of our observational interval) times the expected number of “steps” a landscape unit will remain in step b , where P_{bb} is the measured retention probability. The recurrence time, $\langle T_r \rangle$, is $10(1 - P'_b)/(P_b(1 - P_{bb}))$, i.e., 10 times the expected number of steps out of state b during one cycle. P'_b is the Markov projection of steady-state areal proportion for the b th state (Emlen 1985).

Transition matrix error model

Remote-sensing classification is not perfect. Misclassification of ecological states can arise in one of three ways: (1) misclassification of pixels with spectral values near the decision boundaries of Fig. 1 where

TABLE 1. Transition matrices showing changes in ecological state in wilderness and surrounding nonwilderness areas of a northern Minnesota forest, as calculated from satellite images. Diagonal elements are retention frequencies; off-diagonal elements are transition frequencies; upper off-diagonal transitions are successional and lower off-diagonal transitions are disturbance.

A) For an area of 534 km², with 148 406 landscape elements, in the protected wilderness of the Boundary Waters Canoe Area.

| 1973 state | 1983 state | | | | | |
|--------------|------------|--------------|-----------|-------|---------|-------|
| | Clearings | Regenerating | Broadleaf | Mixed | Conifer | Other |
| Clearings | 17.09 | 45.54 | 16.72 | 15.2 | 5.22 | 0.12 |
| Regenerating | 4.55 | 30.83 | 16.93 | 37.27 | 10.03 | 0.36 |
| Broadleaf | 1.12 | 19.72 | 47.06 | 27.61 | 4.16 | 0.28 |
| Mixed | 0.52 | 6.81 | 11.28 | 58.11 | 22.55 | 0.72 |
| Conifer | 1.04 | 4.37 | 1.81 | 31.02 | 57.8 | 3.93 |
| Other | 0.53 | 3.14 | 3.19 | 8.6 | 13.38 | 71.06 |

B) For an area of 409 km², with 113 738 landscape elements, in the multi-use Superior National Forest (nonwilderness) near the Boundary Waters Canoe Area.

| 1973 state | 1983 state | | | | | |
|--------------|------------|--------------|-----------|-------|---------|-------|
| | Clearings | Regenerating | Broadleaf | Mixed | Conifer | Other |
| Clearings | 20.66 | 47.09 | 9.97 | 17.47 | 4.64 | 0.12 |
| Regenerating | 8.18 | 36.39 | 13.71 | 32.71 | 8.84 | 0.14 |
| Broadleaf | 5.74 | 26.67 | 34.4 | 28.68 | 4.33 | 0.12 |
| Mixed | 5.89 | 13.46 | 8.19 | 51.12 | 21.01 | 0.31 |
| Conifer | 5.65 | 10.28 | 1.79 | 31.02 | 53.87 | 1.66 |
| Other | 3.36 | 16.58 | 12.86 | 23.88 | 16.22 | 26.88 |

two ecological states can have the same spectral characteristic; (2) misclassification of "mixed" pixels, i.e., pixels that fall on the boundary between two dissimilar patches; and (3) misclassification of misregistered pixels, i.e., pixels that shift ground locations between acquisitions (registration accuracy is better than ± 0.5 pixel).

Misclassification of a pixel at one or both dates can affect the estimates of transition probabilities by creating an erroneous observation of no transition between dates when, in fact, there was one (Type I error) or by creating an erroneous observation of a transition between dates when, in fact, there was none (Type II error). Fortunately, these errors are, to some degree, offsetting; Type I errors cause underestimates of the transition probabilities; Type II errors overestimate the transition probabilities. The Appendix gives a derivation for the error in the transition probability estimates as a function of observed classification likelihoods. Note that in the Appendix we calculate an "adjusted" transition probability matrix, based on the classification likelihood estimates. If the estimated classification likelihoods themselves were error free, then the "adjusted" transition probability matrix could be considered to represent the "true" values for transition probabilities. However, the classification likelihood estimates are not error free, since they are based on a sample only and therefore will not be totally representative of the classification likelihoods for the entire scene. They represent the best estimates of classification likelihoods that can be obtained with the currently available data.

RESULTS AND DISCUSSION

Rates of change at the landscape unit level

Table 1 shows the transition matrices for the wilderness (Table 1A) and nonwilderness (Table 1B), as calculated from the 1973 and 1983 Landsat images. The diagonal elements of the matrices are *retention* frequencies, indicating stability; the off-diagonal elements, *transition* frequencies, show dynamic change. The transition frequencies are further divided into "successional" transitions (changes in state typically associated with ecological succession) and "disturbance" transitions (changes counter to typical successional trends). In just 10 yr, 1973–1983, over half the landscape elements changed state in both the wilderness and nonwilderness areas. The diagonal elements in Table 1 show that the wilderness changed slightly less than the nonwilderness, but at the spatial scale of the landscape elements, both the managed and wilderness areas were quite dynamic.

As the diagonal elements of Table 1 also show, the mature states, such as conifer, were more stable than earlier successional states such as regeneration. In addition, there was a strong successional direction to the transitions, i.e., the predominant transitions were from an earlier to a later state (upper off-diagonals). An examination of the upper off-diagonals of Table 1 shows that in either the wilderness or nonwilderness the primary succession pathway (defined by the largest transition probabilities) is from clearings to regeneration to broadleaf to mixed to conifer. This result is consistent with ecological expectations of succession. In gen-

eral, the disturbance transition frequencies (lower off-diagonals) were small, with the exception of broadleaf to regeneration and conifer to mixed transitions.

Comparison of transition frequencies inside and outside of the protected wilderness provides a quantitative measure of the effects of recent human activities in the Superior National Forest. The magnitudes of the upper off-diagonals between the wilderness and nonwilderness are roughly the same, indicating that the succession processes are operating at about the same rate in both areas. Disturbance rates, i.e., transitions from conifer, mixed, broadleaf, and regeneration to clearing, are as expected much higher in the nonwilderness than in the wilderness and are concentrated in logged areas as shown in Fig. 2.

Spatial patterns of ecological states

Fig. 2 shows the spatial pattern of ecological states in 1973 and 1983 (classification images) and an image of ecological state transitions between these two dates. As explained in Fig. 2, this particular state transition image is color coded to emphasize the spatial patterns of natural succession, regeneration, and disturbance. In the classification images, we see that in both 1973 and 1983 the scene is composed of a range of ecological states, from early to late succession.

The classification images also suggest that ecological states are grouped into large homogeneous areas, as opposed to a random spatial pattern; for example, in both years, conifers form a band extending northeast from the largest lake in the image. However, we have calculated the average patch size for the ecological states, using the algorithm developed by Burrows (1988), and have found that they are quite small, ranging from ≈ 1 to 10 ha. For vegetated ecological states, i.e., regeneration, broadleaf, mixed, and conifer, the average patch sizes are roughly the same for the wilderness and nonwilderness regions (regeneration and broadleaf ≈ 1 ha, mixed ≈ 3.6 ha, and conifer ≈ 3 ha). For the clearings or deforested areas, the nonwilderness average patch size is almost double that of the wilderness (≈ 10 vs. 5 ha), indicating that the logging patterns in the SNF create much larger clearings than those generated by natural disturbance in the wilderness. Larger clearings increase habitat fragmentation, which has been observed by Wilcox et al. (1986) to decrease faunal species diversity in temperate forests.

As might be expected, the spatial structure of the state transition map reflects differences between the wilderness and nonwilderness areas, in terms of anthropogenic disturbance and fire. Disturbance transitions from vegetative states to clearings (red pixels labeled deforested classes in Fig. 2) form small and widely scattered patches in the wilderness area but occur in large contiguous patches in the nonwilderness, indicating the aftermath of logging. One exception to this pattern in the wilderness is the large contiguous area of deforestation occurring near the bottom right center

of the change image; a subsequent visit to this area showed this to be a tract that was logged in the mid-1970s (C. Jarvis, *personal communication*). Landscape elements that make the transition from clearings to regeneration (yellow) are also more widely scattered in the wilderness area than in the nonwilderness. The extensive yellow area of regeneration from clearings in the upper center of the change image is recovery of the forest from the 1971 Little Sioux forest fire (Ohmann and Grigal 1979).

Regional-level proportions of ecological states

As shown in Table 2, in both the wilderness and nonwilderness, early successional ecological states (clearings and regeneration) occupy a sizeable portion of the landscape in both years. We should not be surprised at this large proportion of early succession in the nonwilderness ($\approx 30\%$ in both 1973 and 1983), where logging operations are widespread. But in the wilderness area, where human disturbance has been less pronounced for the last 40 yr, $\approx 15\%$ of the landscape is still in early succession, likely a residual from logging or a result of natural disturbance such as tree mortality, windthrow, or fire. The estimate in Table 2, that 2% of the wilderness is in clearings, is reasonably consistent with computer simulations of forest growth in the northern hardwood forests of New England (Botkin et al. 1973), which suggest that $\approx 1\%$ of the landscape would be in very early stages of succession, even in old-age stands.

There may also be differences in the dynamics and long-term composition between the wilderness and nonwilderness areas as suggested by observed differences in the areal proportions of ecological states between the two regions. Clearings and regeneration occupied a larger portion of the nonwilderness area than the wilderness, while broadleaf, mixed, and conifer states occupied less.

To the degree that the effects of current climate and human activities on ecosystem transition rates are reflected in the pixel-level transition rates, we should be able to assess longer term rates of change in the regional landscape cover implied by current conditions using a Markov analysis (as described in *Methods: Rates of change at the regional level*). Such an analysis, based on the transition rates of Table 1, yielded the projected steady-state values of the regional-level proportions of the ecological states shown in Table 3. In both the wilderness and nonwilderness areas, projections show that at the landscape level, currently observed proportions of ecological states are near projected future values and would attain these values in only three, 10-yr increments from 1983. Thus, if current climate and human activities imply significant changes in the overall composition of the landscape cover, the Markov analysis did not detect such a trend.

Regarding this conclusion, two cautions are warranted. Because the satellite data record is short com-

TABLE 2. Percent of land area by class.*

| Ecological state class | 1973 | | 1983 | |
|------------------------|------------|---------------|------------|---------------|
| | Wilderness | Nonwilderness | Wilderness | Nonwilderness |
| Clearings | 3.91 | 8.95 | 1.93 | 7.35 |
| Regeneration | 11.2 | 15.2 | 13.4 | 22.2 |
| Broadleaf | 22.6 | 17.9 | 20.8 | 13.6 |
| Mixed | 37.9 | 33.5 | 40.6 | 35.4 |
| Conifer | 24.3 | 21.5 | 26.2 | 21.5 |

* Water and clouds are omitted; hence some columns do not sum to 100%.

pared to the time scales over which forested ecosystems respond to climate change, transition probability estimates based on the existing satellite record may not capture the total effect of current climate trends, particularly if these effects are nonlinear. Second, even in the absence of secular climate change, we cannot be certain that our sample is extensive enough to provide representative estimates of the frequency of disturbance events such as fire and logging. Additional studies are required to ascertain the effects of time interval between acquisitions and the spatial extent of the Landsat data on transition probability estimates.

It should also be borne in mind that current values of transition probabilities do not reflect future climate trends. Manabe and Wetherald (1986) predict that a doubling of atmospheric CO₂ by the middle of the next century will increase average temperatures by 10°C in the region of the Superior National Forest. As indicated by paleoclimatological studies such as those by Solomon and Webb (1985), Davis (1981), Davis and Botkin (1985), and Davis et al. (1986), a climate change of this magnitude would clearly affect the composition of the boreal forest biome.

Recurrence times

From the transition matrices we calculated the recurrence times (Table 4). This calculation requires the assumption that the transition processes are Markovian and that the transition probabilities are time invariant, assumptions not likely to be met exactly (Botkin and Sobel 1975).

Values of the average recurrence time, $\langle T_r \rangle$, the average occupancy time, $\langle T_o \rangle$, and the total cycle time, $\langle T_c \rangle$, are very similar between wilderness and nonwilderness areas for the later successional states, but $\langle T_o \rangle$ and $\langle T_c \rangle$ are very different for the disturbance states (clearing and regeneration). The expected occupancy time, $\langle T_c \rangle$, increases with time since disturbance in both the wilderness and nonwilderness areas; this is consistent with the slower turnover expected for late successional stages.

The average expected recurrence time for clearings is ≈800 yr in the wilderness area, but <200 yr in the nonwilderness area. The recurrence time for regenerating stands is twice as long in the wilderness as outside it. Recurrence times for late successional stages are

shorter within the wilderness than outside. These differences reflect the effect of human land use outside the wilderness, where there is clearing from logging. Other studies of the Superior National Forest and similar ecosystems suggest that prior to European settlement an area burned on the average slightly more frequently than once a century (Lafond and Ladoceur 1968, Heinselman 1973, Laframboise 1975, Boudoux 1978, Gerardin 1980, Cogbill 1982). In presettlement times, average recurrence times varied with site conditions. Peatlands dominated by black spruce (*Picea mariana*) experienced fires at ≈150–200 yr intervals, while upland jack pine barrens on sand plains had fires as frequently as every 15–30 yr (Heinselman 1981). The difference between our calculated values and historical values from other studies appears to be a consequence of the lack of fire during the study interval, 1973–1983, possibly reflecting the impact of intentional fire suppression in the 20th century. The impact of recent human activities, including logging, is suggested by differences in recurrence time, $\langle T_r \rangle$, for clearing and regeneration classes inside and outside of the wilderness; smaller values (shorter recurrence time) in the nonwilderness area are a consequence of logging.

Error model

As discussed in *Methods: Transition matrix error model*, we have developed a first-order error model (Appendix) for the transition probabilities, based on estimates of the classification likelihood matrix (Table 5). As can be seen from Table 5, the frequencies of correct classification (diagonal elements) are reasonably high, ranging from 0.80 to 0.96. The largest errors result from confusion of conifers with mixed states ($C = 0.138$) and regeneration with clearings ($C = 0.118$). The lowest probability of correct classification is for conifers ($C = 0.793$). This is largely a result of poor separability in the Landsat 1 MSS, requiring that we combine dense jack pine, as well as open and closed black spruce bogs into the conifer class, as shown in Fig. 1. The confusion of conifers with clearings arises from confusion of sparse black spruce bogs (having a sphagnum moss background) with grassy, cleared areas. As discussed in *Methods: Transition matrix error model* and shown in the Appendix, misclassifications can lead to detection of transitions between states when

TABLE 3. Markov projections of steady-state areal percentages occupied by ecological states.

| Ecological state class | Wilderness | | | Nonwilderness | | |
|------------------------|------------------|-------------------|---------------------------------------|------------------|-------------------|---------------------------------------|
| | 1983 (% area) | Proj. (% area) | Relative difference (% of 1983) | 1983 (% area) | Proj. (% area) | Relative difference (% of 1983) |
| Clearings | 1.7 | 1.42 | -16.5 | 7.2 | 7.39 | 2.6 |
| Regeneration | 11.9 | 10.9 | -8.4 | 21.6 | 21.7 | 0.5 |
| Broadleaf | 15.8 | 13.9 | -12.0 | 13.2 | 11.0 | -16.6 |
| Mixed | 35.8 | 41.0 | 14.5 | 34.5 | 36.4 | 5.5 |
| Conifer | 23.1 | 27.7 | 19.9 | 20.9 | 22.8 | 9.0 |

there are none (Type 2 errors), and an indication of no transitions when in fact there were (Type 1 errors). The error model of the Appendix quantifies the dependence of these errors in the classification-based transition probabilities on the magnitude of the classification likelihoods and the proportion of the scene classified as in the various ecological states.

Table 6 gives values for "adjusted" transition probabilities and differences from the classification-based transition probabilities of Table 1. Because our error model is first order, and our estimates of classification error based on a sample of sites, one must be careful in placing too much credence on any one error value in Table 6; however, the error terms as a whole suggest how classification error affects the transition probability estimates. For example, in both the wilderness and nonwilderness, the retention probabilities of the adjusted matrices are $\approx 5\%$ smaller on the average than those in the nonadjusted matrices in Table 1. This suggests that when adjusted for classification error, the landscape unit is even more dynamic than shown in Table 1. It is also important to note, in comparing Table 6 with Table 1, that the major successional and disturbance trends, while somewhat different in magnitude, are consistent. For example, as with the nonadjusted transition probabilities, disturbance rates (lower off-diagonals) are still much higher in the nonwilderness than in the wilderness. In addition, as with Table 1, Table 6 shows the wilderness and nonwilderness succession rates (upper off-diagonals) to be roughly the same.

The error model developed here is first order, and ignores the effects of mixed pixels and misregistration between acquisitions. Additionally, it provides only one value for the error magnitudes, based on one estimate of classification likelihoods. To pursue the error modeling further would require substantial effort, involving some rather fundamental, unanswered ques-

tions about errors generated by image processing. A promising approach would be image simulation. Image pairs representing changing landscapes could be simulated with known transition probabilities, including spatial structures incorporating average patch sizes, proportions, etc., of real landscapes. These simulated image pairs could then be sampled at various spatial resolutions to examine the effect of mixed pixels on accuracy. The image pairs could also be misregistered to study the effects on apparent transition probabilities. Clearly, such a study should be done, but is beyond the scope of this investigation.

To examine the effect of the transition probability errors on ecosystem dynamics, we made Markov projections of the ecological state areal proportions for the study area, using the adjusted transition probabilities, for both the wilderness and nonwilderness areas (Table 7). While the projected values of areal proportions using the adjusted transition matrix are somewhat different than those projected from the nonadjusted transition matrix (3.1% average difference for the wilderness, 2.2% average difference for the nonwilderness), the qualitative implication from Markov projections, that current climate and management practice do not imply large rates of change to the ecosystem regional-level composition, remains valid.

CONCLUSIONS

We have developed a remote-sensing tool for ecology that permits one to infer the state of an ecosystem, in years following or preceding that in which ground observations were acquired. By identifying and utilizing reflectance-stable targets (deep lakes and rock outcrops) in two Landsat scenes, we were able to make relative corrections between years in the spectral signatures of ecological states for (1) atmospheric differences between years, without requiring in situ atmospheric observations and (2) differences in charac-

TABLE 4. Recurrence times [(T_r)]. Recurrence time = the average number of years for a landscape element to return to a given state once it had left that state.

| | Clearing | Regeneration | Broadleaf | Mixed | Conifer |
|---------------|----------|--------------|-----------|-------|---------|
| Wilderness | 803 | 113 | 112 | 32 | 61 |
| Nonwilderness | 157 | 57 | 124 | 35 | 73 |

TABLE 5. Likelihoods of correct and incorrect classifications based on satellite remote sensing.*

| Ground-observed states | Classified states | | | | | |
|------------------------|-------------------|--------------|-----------|-------|---------|-------|
| | Clearings | Regeneration | Broadleaf | Mixed | Conifer | Other |
| Clearings | 0.88 | 0.00 | 0.00 | 0.00 | 0.069 | 0.00 |
| Regeneration | 0.118 | 0.882 | 0.00 | 0.095 | 0.00 | 0.00 |
| Broadleaf | 0.00 | 0.059 | 0.957 | 0.048 | 0.00 | 0.00 |
| Mixed | 0.00 | 0.059 | 0.044 | 0.857 | 0.138 | 0.00 |
| Conifer | 0.00 | 0.00 | 0.00 | 0.00 | 0.793 | 0.00 |
| Other | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 |

* Matrix elements $C(a|b)$ are the estimated likelihoods (based on ground-observed patches) of classifying a ground-observed patch (pixel) into ecological state a if ground observations indicated that it was in ecological state b . That is $C(a|b) = n(a|b)/N$ where $n(a|b)$ is the number of patches that ground observation showed to be in ecological states of type b but that were classified as type a , and N is the total number of patches (pixels) in the ground-observed set. The diagonals of the matrix are the estimated likelihoods of correct classification. The off-diagonal elements are the estimated likelihoods of incorrect classification.

teristics of MSS sensors between Landsat 1 through 4. With the 17-yr record now provided by the Landsat sensors, we have a capability to study the dynamics of ecosystems, at regional scales, over ecologically significant time intervals. We have developed a first-order error model that estimates errors in the transition matrix arising from classification error in the ecological states. This analysis needs to be extended, but our first-order calculations show that while the error magnitudes will change some of the details of our results, they will not affect the more general conclusions regarding the dynamics of the ecosystem.

Application of this technique to a forest test site in northern Minnesota shows that at the landscape unit level the forest ecosystem is undergoing rapid change, with roughly one-half the landscape units changing state

in just 10 yr. However, if these large transition rates imply large future changes in the regional composition of the boreal forest, a dynamical analysis using a Markov model does not show it.

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TABLE 6. "Adjusted" transition probabilities and differences from the transition probabilities of Table 1, calculated using Eq. A.5 and the classification likelihoods of Table 5.

A) For an area of 534 km² with 148 406 landscape elements in the protected wilderness of the Boundary Waters Canoe Area.

| 1973 state | 1983 state | | | | | | | | | | | |
|--------------|------------|-------|--------------|-------|-----------|-------|-------|-------|---------|-------|-------|-------|
| | Clearings | | Regeneration | | Broadleaf | | Mixed | | Conifer | | Other | |
| | Prob. | Diff. | Prob. | Diff. | Prob. | Diff. | Prob. | Diff. | Prob. | Diff. | Prob. | Diff. |
| Clearings | 12.0 | 5.08 | 31.7 | 13.9 | 14.2 | 2.52 | 23.0 | -7.78 | 17.8 | -12.5 | 1.37 | -1.25 |
| Regeneration | 4.37 | 0.18 | 26.6 | 4.22 | 18.3 | -1.37 | 39.9 | -2.62 | 10.4 | -0.36 | 0.44 | -0.08 |
| Broadleaf | 1.43 | -0.31 | 19.9 | -0.15 | 44.2 | 2.89 | 29.7 | -2.09 | 4.53 | -0.37 | 0.32 | -0.04 |
| Mixed | 2.3 | -1.78 | 11.8 | -4.95 | 14.0 | -2.74 | 51.1 | 7.01 | 19.8 | 2.71 | 0.99 | -0.27 |
| Conifer | 4.91 | -3.87 | 6.94 | -2.57 | 3.47 | -1.66 | 35.0 | -3.93 | 45.8 | 12.0 | 3.93 | 0.0 |
| Other | 0.92 | -0.39 | 3.79 | -0.65 | 3.81 | -0.62 | 9.8 | -1.2 | 10.6 | 2.81 | 71.1 | -0.04 |

B) For an area of 409 km² with 113 738 landscape elements in the multiuse Superior National forest nonwilderness near to the Boundary Waters Canoe Area.

| 1973 state | 1983 | | | | | | | | | | | |
|--------------|-----------|-------|--------------|-------|-----------|-------|-------|-------|---------|-------|-------|--------|
| | Clearings | | Regeneration | | Broadleaf | | Mixed | | Conifer | | Other | |
| | Prob. | Diff. | Prob. | Diff. | Prob. | Diff. | Prob. | Diff. | Prob. | Diff. | Prob. | Diff. |
| Clearings | 17.0 | 3.66 | 40.3 | 6.79 | 11.6 | -1.63 | 20.7 | -3.25 | 9.86 | -5.22 | 0.37 | -0.25 |
| Regeneration | 8.2 | -0.02 | 33.4 | 3.04 | 15.5 | -1.82 | 34.1 | -1.34 | 8.54 | 0.3 | 0.168 | -0.028 |
| Broadleaf | 5.6 | 0.14 | 26.6 | 0.1 | 33.0 | -1.44 | 30.0 | -1.32 | 4.67 | -0.34 | 0.139 | -0.019 |
| Mixed | 6.82 | -0.93 | 17.7 | -4.24 | 11.1 | -2.92 | 45.4 | 5.7 | 18.4 | 2.59 | 0.421 | -0.111 |
| Conifer | 8.69 | -3.04 | 12.3 | -2.0 | 3.59 | -1.8 | 31.1 | -4.32 | 42.8 | 11.1 | 1.66 | 0.0 |
| Other | 4.07 | -0.71 | 17.3 | -0.72 | 14.4 | -1.48 | 24.2 | -0.34 | 12.9 | 3.37 | 26.9 | 0.0 |

TABLE 7. Projected future values of areal percentages occupied by ecological states using adjusted and nonadjusted transition probabilities.

| Ecological state | Wilderness | | Nonwilderness | |
|------------------|---------------------|----------------------|---------------------|----------------------|
| | Nonadj. (% area) | Adjusted (% area) | Nonadj. (% area) | Adjusted (% area) |
| Clearings | 1.42 | 3.24 | 7.39 | 8.13 |
| Regeneration | 10.9 | 14.6 | 21.7 | 23.5 |
| Broadleaf | 13.9 | 17.2 | 11.0 | 13.9 |
| Mixed | 41.0 | 39.6 | 36.4 | 35.9 |
| Conifer | 27.7 | 20.7 | 22.8 | 17.8 |

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APPENDIX follows on page 640.

APPENDIX

TRANSITION PROBABILITY ERROR MODEL

Let a denote the "true" ecological state and α denote the classified or observed ecological state.

Let $T(a, b)$ denote the joint probability of a landscape unit having "true" ecological state a at acquisition 1 and "true" ecological state b at acquisition 2. Let $T(\alpha, \beta)$ denote the joint probability of classifying an image pixel in ecological state α at acquisition 1 and in ecological state β at acquisition 2.

Let $P_1(a)$ denote the probability of "true" ecological state a at acquisition 1. Let $P_1(\alpha)$ denote the probability of classifying a pixel into ecological state α at acquisition 1.

Let T_{ab} denote the transition probability from "true" ecological state a to "true" ecological state b . Let $T_{\alpha\beta}$ denote the transition probability from classified or observed ecological state α to classified or observed ecological state β .

Then, by the above notation.

$$T_{ab} = T(a, b)/P(a) \quad \text{and} \quad T_{\alpha\beta} = T(\alpha, \beta)/P(\alpha). \quad (\text{A.1})$$

Let $C(\alpha|\beta)$ denote the conditional probability that a landscape unit classified in ecological state β is in "true" ecological state a . The collection $\{C(a|\beta)\}_{a,b}$ forms the classification likelihood matrix (Table 6).

The transition probabilities for the "true" states can be calculated in terms of the transition probabilities for the observed states and the classification likelihood matrix.

$$\begin{aligned} T(a, b) &= T(\alpha, \beta)C(a|\alpha)C(b|\beta) \\ &\quad (\text{term 1}) \\ &+ C(a|\alpha) \sum_{\beta' \neq \beta} T(\alpha, \beta')C(b|\beta') \\ &\quad (\text{term 2}) \\ &+ C(b|\beta) \sum_{\alpha' \neq \alpha} T(\alpha', \beta)C(a|\alpha') \\ &\quad (\text{term 3}) \\ &+ \sum_{\alpha' \neq \alpha} \sum_{\beta' \neq \beta} T(\alpha', \beta')C(a|\alpha')C(b|\beta') \quad (\text{term 4}) \end{aligned} \quad (\text{A.2})$$

Eq. A.2 assumes that the classification likelihood is the same for both acquisitions and that the classification errors are independent between the acquisitions. The terms in Eq. A.2 may be interpreted as follows:

- term 1 = observed transitions from α to β , which were true transitions from a to b ;
- term 2 = observed transitions from α to not β , which were true transitions from a to b ;
- term 3 = observed transitions from not α to β , which were true transitions from a to b ;
- term 4 = observed transitions from not a to not b which were true transitions from a to b .

Eq. A.2 thus accumulates all the true transitions from the four possible classes of observed transitions (correct classification in both years, incorrect classification in year 2, incorrect classification in year 1, incorrect classification in both years).

Eq. A.2 can be simplified as

$$T(a, b) = \sum_{\alpha} \sum_{\beta} T(\alpha, \beta)C(a|\alpha)C(b|\beta). \quad (\text{A.3})$$

Now from Eq. A.1, $T_{ab} \equiv T(a, b)/P(a)$, and $P(a)$ is given by

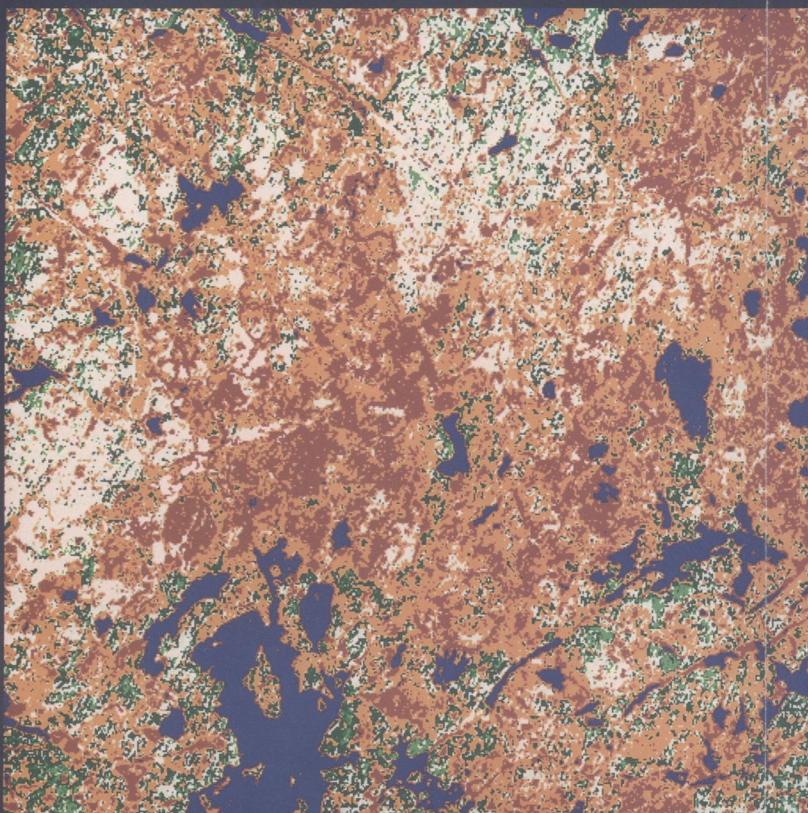
$$P(a) = \sum_{\alpha} C(a|\alpha)P(\alpha). \quad (\text{A.4})$$

The transition probabilities for the true ecological states can be estimated by combining Eqs. A.1, A.2, and A.3.

$$T_{ab} = \frac{\sum_{\alpha} \sum_{\beta} T(\alpha, \beta)C(a|\alpha)C(b|\beta)}{\sum_{\alpha} C(a|\alpha)P(\alpha)}. \quad (\text{A.5})$$

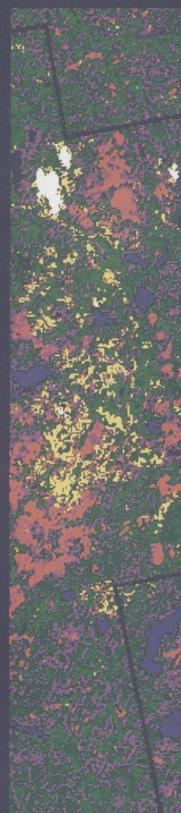
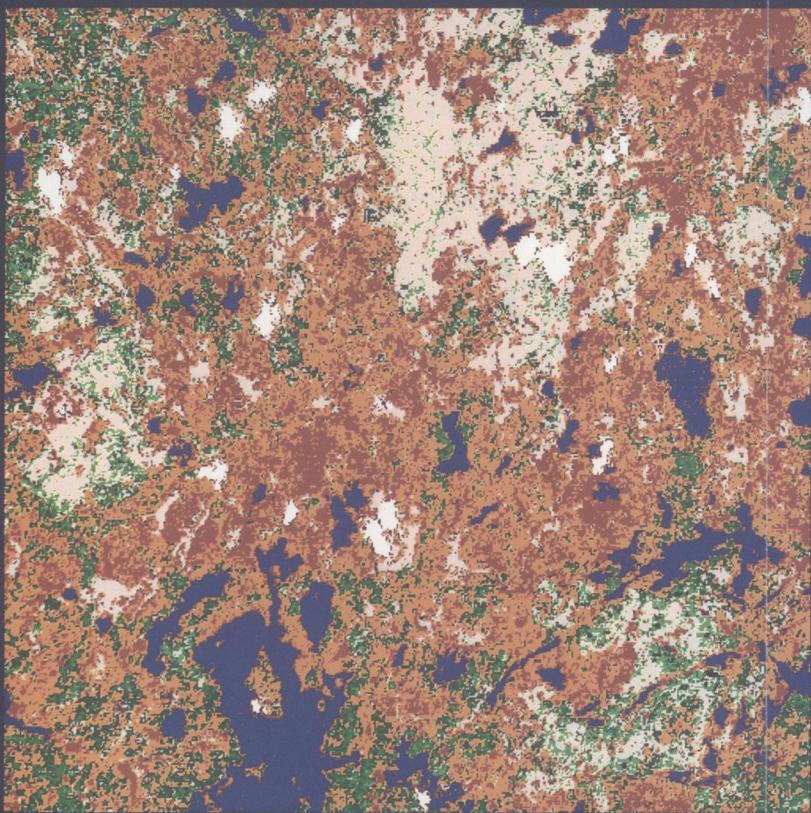
And the difference δe between the "true" and the estimated transition probabilities is given by the difference of the estimated and the true transition probabilities.

$$\delta e = \frac{T(\alpha, \beta)}{P(\alpha)} - \frac{\sum_{\alpha} \sum_{\beta} T(\alpha, \beta)C(a|\alpha)C(b|\beta)}{\sum_{\alpha} C(a|\alpha)P(\alpha)}. \quad (\text{A.6})$$



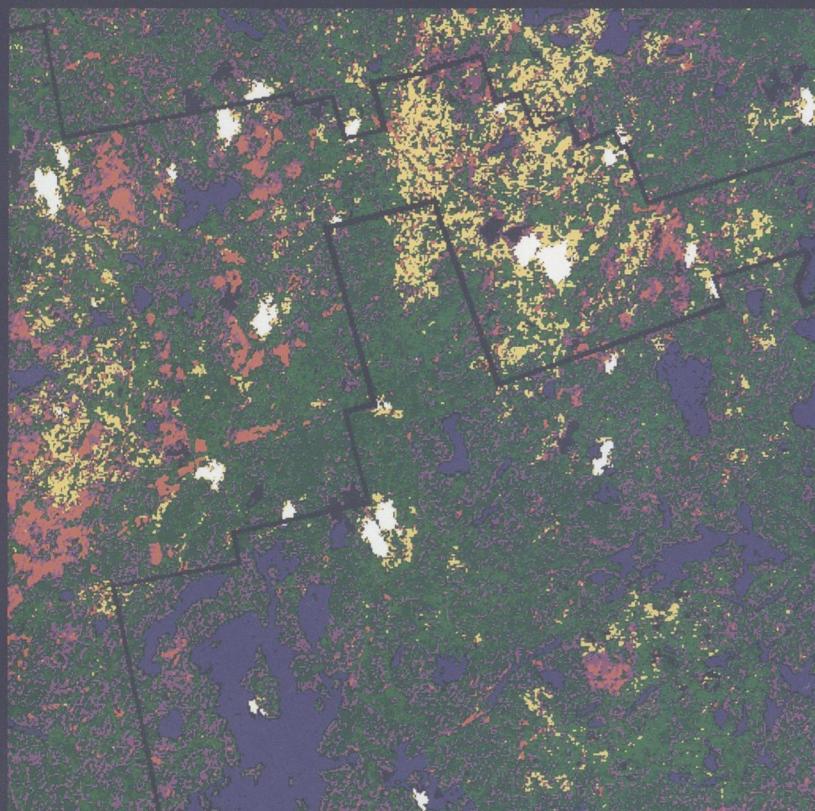
KEY TO CLASS IMAGES

- CLEARING
- REGENERATION
- BROADLEAF FOREST
- MIXED FOREST
- CONIFER FOREST
- WATER
- CLOUDS





| KEY TO CLASSIFIED IMAGES | |
|--------------------------|--|
| CLEARINGS | |
| REGENERATION | |
| BROADLEAF | |
| MIXED | |
| CONIFER | |
| WATER | |
| CLOUDS | |



| KEY TO CHANGE IMAGE DYNAMICS OF THE BOREAL FOREST | |
|--|--|
| UNCHANGED VEGETATION AREAS | |
| NATURAL SUCCESSION AREAS | |
| NATURAL DISTURBANCE AREAS | |
| DEFORESTED AREAS | |
| REVEGETATED AREAS | |
| WATER | |



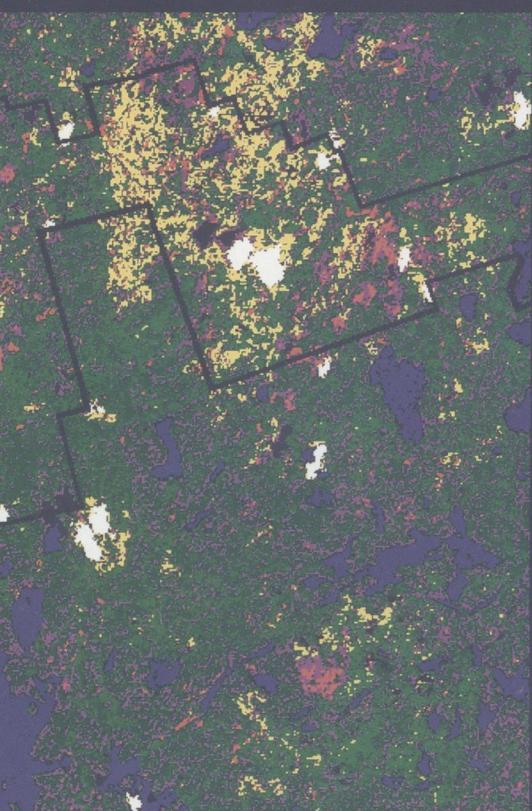
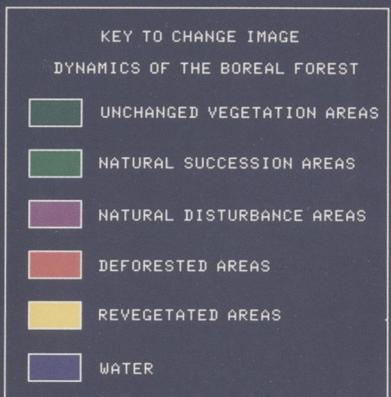
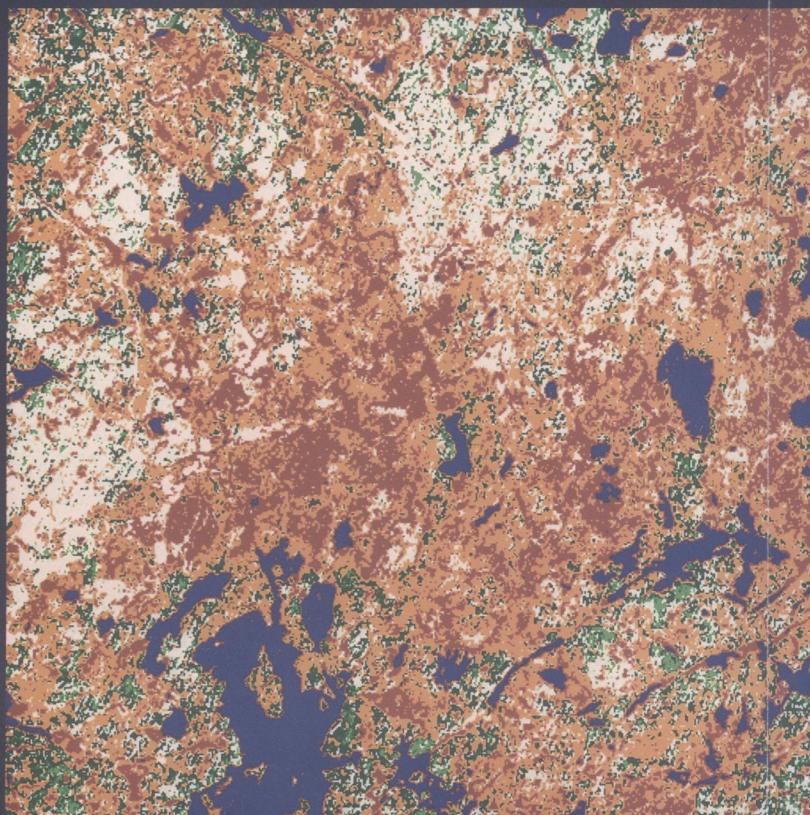


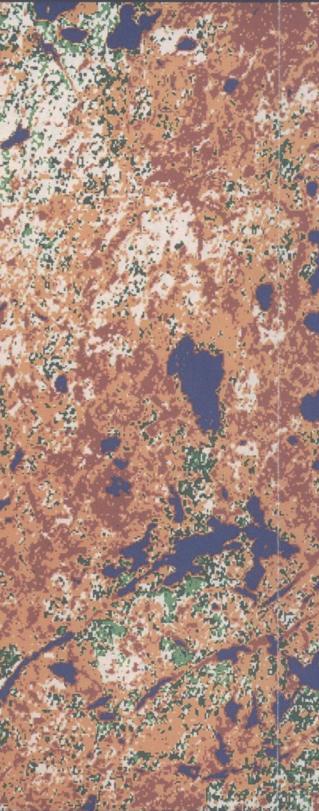
FIG. 2. Geographic patterns of ecological states are shown for 1973 (bottom left) and 1983 (top left). The change in ecological states 1973–1983 is shown in the bottom right image. The color codes for the 1973 and 1983 images are given in the top center; the color codes for the change image are given in top right. Color codes for the change image (bottom right) have been selected to emphasize the spatial patterns of stability, natural succession, regeneration, and disturbance. Landscape elements that remained in the same ecological state in 1973 and 1983 are dark green; landscape elements that changed from clearings in 1973 to regeneration in 1983 are yellow. Deforested areas (from forested in 1973 to clearings in 1983) are orange; other disturbance classes (changing from later to earlier ecological stages in succession) are reddish purple. Natural successional classes, i.e., from earlier to later stages, are lighter green. Clouds, primarily in the 1973 image (and, perforce, in the change image), are white. Black lines mark the borders of the Boundary Waters Canoe Area, which lies in two sections, one extending from the upper edge of the image and the other extending from the center of the image down. The area between the black lines is part of the Su-



KEY TO CLASS IMAGES

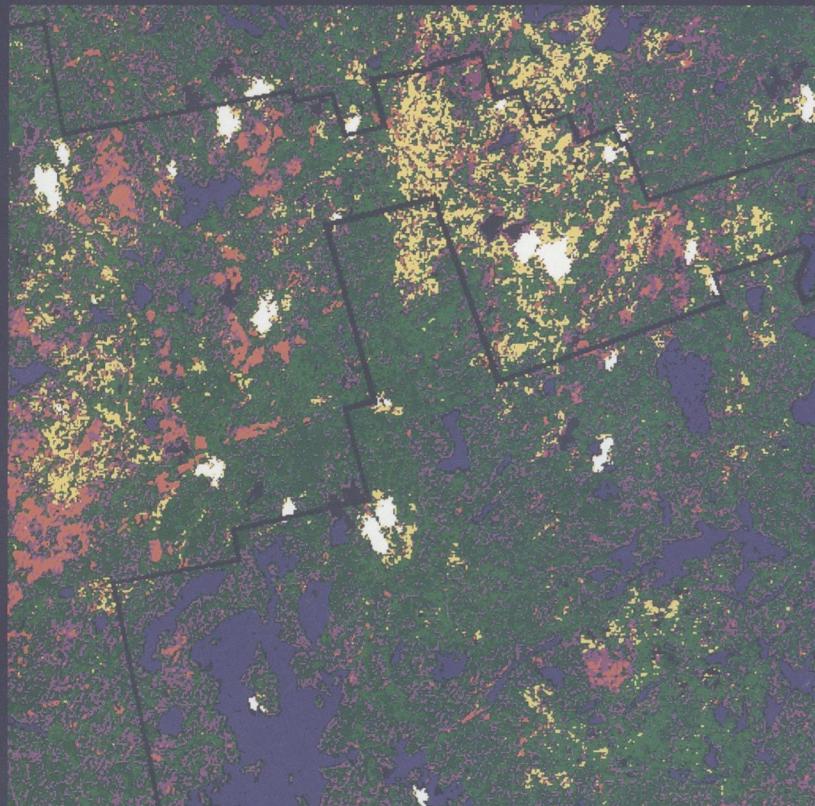
- CLEARING
- REGENERATION
- BROADLEAF
- MIXED
- CONIFER
- WATER
- CLOUDS





| KEY TO CLASSIFIED IMAGES | |
|--------------------------|--------------|
| | CLEARINGS |
| | REGENERATION |
| | BROADLEAF |
| | MIXED |
| | CONIFER |
| | WATER |
| | CLOUDS |

| KEY TO CHANGE IMAGE DYNAMICS OF THE BOREAL FOREST | |
|--|----------------------------|
| | UNCHANGED VEGETATION AREAS |
| | NATURAL SUCCESSION AREAS |
| | NATURAL DISTURBANCE AREAS |
| | DEFORESTED AREAS |
| | REVEGETATED AREAS |
| | WATER |



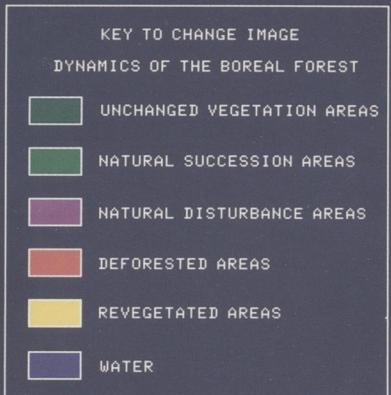


FIG. 2. Geographic patterns of ecological states are shown for 1973 (bottom left) and 1983 (top left). The change in ecological states 1973–1983 is shown in the bottom right image. The color codes for the 1973 and 1983 images are given in the top center; the color codes for the change image are given in top right. Color codes for the change image (bottom right) have been selected to emphasize the spatial patterns of stability, natural succession, regeneration, and disturbance. Landscape elements that remained in the same ecological state in 1973 and 1983 are dark green; landscape elements that changed from clearings in 1973 to regeneration in 1983 are yellow. Deforested areas (from forested in 1973 to clearings in 1983) are orange; other disturbance classes (changing from later to earlier ecological stages in succession) are reddish purple. Natural successional classes, i.e., from earlier to later stages, are lighter green. Clouds, primarily in the 1973 image (and, perforce, in the change image), are white. Black lines mark the borders of the Boundary Waters Canoe Area, which lies in two sections, one extending from the upper edge of the image and the other extending from the center of the image down. The area between the black lines is part of the Superior National Forest, where logging is permitted.