Eighty years of change: vegetation in the montane ecoregion of Jasper National Park, Alberta, Canada

Jeanine M. Rhemtulla, Ronald J. Hall, Eric S. Higgs, and S. Ellen Macdonald

Abstract: Repeat ground photographs (taken in 1915 and 1997) from a series of topographical survey stations and repeat aerial photographs (flown in 1949 and 1991) were analysed to assess changes in vegetation composition and distribution in the montane ecoregion of Jasper National Park, in the Rocky Mountains of Alberta, Canada. A quantitative approach for assessing relative vegetation change in repeat ground photographs was developed and tested. The results indicated a shift towards late-successional vegetation types and an increase in crown closure in coniferous stands. Grasslands, shrub, juvenile forest, and open forests decreased in extent, and closed-canopy forests became more prevalent. The majority of forest stands succeeded to dominance by coniferous species. Changes in vegetation patterns were likely largely attributable to shifts in the fire regime over the last century, although climatic conditions and human activity may also have been contributing factors. Implications of observed changes include decreased habitat diversity, increased possibility of insect outbreaks, and potential for future high-intensity fire events. Results of the study increase knowledge of historical reference conditions and may help to establish restoration goals for the montane ecoregion of the park.

Résumé : Les mêmes photographies prises au sol en 1915 et 1997 qui provenaient d'une série de stations d'inventaire topographique ainsi que les mêmes photographies aériennes prises en 1949 et 1991 ont été analysées pour évaluer les changements dans la distribution et la composition de la végétation dans la région écologique subalpine du parc national de Jasper, situé dans les Montagnes Rocheuses en Alberta, au Canada. Une approche quantitative pour évaluer les changements relatifs dans la végétation à partir de photographies prises au sol à différents moments a été développée et testée. Les résultats montrent une évolution vers des types de végétation de fin de succession et une plus grande fermeture du couvert dans les peuplements de conifères. La prairie, les arbustes, la jeune forêt et les forêts ouvertes ont diminué en étendue et la forêt avec un couvert fermé est devenue plus abondante. La majorité des peuplements forestiers ont évolué vers une dominance d'espèces résineuses. Les changements dans la configuration de la végétation sont probablement en grande partie attribuables aux modifications survenues dans le régime des feux au cours du siècle dernier quoique les conditions climatiques et l'activité humaine puissent également y avoir contribué. Ces changements ont comme conséquence une moins grande diversité d'habitats, des risques plus élevés d'épidémies d'insectes et la possibilité que surviennent éventuellement des feux de forte intensité. Les résultats de cette étude améliorent notre connaissance des conditions qui ont prévalu dans le passé et peuvent contribuer à établir des objectifs pour la restauration de la région écologique subalpine du parc.

[Traduit par la Rédaction]

Introduction

The importance of acquiring data on historical ecosystem states to guide future land-management practices has been receiving increasing recognition (Parsons et al. 1999). While knowledge of changes in historical conditions (e.g., climate) and disturbance processes (e.g., fire regime) can be used to infer general changes in vegetation pattern and structure, detailed reconstruction of the latter is often lacking. In particular, there are often insufficient data with adequate temporal depth on the historical composition and distribution of vegetation types across the landscape (Landres et al. 1999).

Repeat aerial photographs have often been used to reconstruct temporal variation in land cover (Green et al. 1993; Swetnam et al. 1999). Although the development and use of aerial photography was greatly accelerated during World Wars I and II (Colwell 1997), its use in natural resource assessments was in its infancy during the 1930s and 1940s (Losee 1942). Repeat photography of older ground-based historical photographs can increase temporal depth of reconstructions (Rogers et al. 1984), but because of the geometry of photographs taken at ground level (i.e., they are oblique

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J.M. Rhemtulla, R.J. Hall,[1] and S.E. Macdonald.[2] Department of Renewable Resources, 4-42 Earth Sciences Building, University of Alberta, Edmonton, AB T6G 2E3, Canada.
E.S. Higgs. Department of Anthropology, 13-15 H.M. Tory Building, University of Alberta, Edmonton, AB T6G 2H4, Canada.

[1]Present address: Northern Forestry Centre, Canadian Forest Service, Natural Resources Canada, 5320 - 122 Street, Edmonton, AB T6H 3S5, Canada.
[2]Corresponding author (e-mail: ellen.macdonald@ualberta.ca).

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photographs in which the scale varies throughout the photograph), analysis of these is usually limited to qualitative observation. The few studies that have attempted quantitative analysis usually calculate relative or proportional, rather than absolute, measures of change in repeat ground photographs (Sinclair 1995; Webb 1996).

In 1915, M.P. Bridgland, a Dominion Lands Surveyor, took a series of survey photographs in Jasper National Park (JNP), in the Rocky Mountains of Alberta, Canada. Used to construct the first topographic maps of JNP, the photographs were systematically taken and comprehensive in coverage, thus providing a complete and unbiased view of the landscape (Bridgland 1924). Because the Bridgland photographs were explicitly taken for analytical purposes (i.e., to create topographic maps), we hypothesized that they could be effectively used to quantitatively analyse relative vegetation change over time. By combining analysis of repeat ground photographs with repeat aerial photographs, it was possible to assess successional trends throughout the past century.

The analysis was focused on the montane ecoregion of JNP. Located primarily along the bottom of the main river valley, the montane ecoregion makes up only 6.9% of the total park area, but provides critical reproductive and winter habitat for many species of wildlife and serves as a travel corridor for large carnivores and ungulates (Holland and Coen 1982*a*). Easy accessibility has also resulted in the proliferation of human infrastructure within the montane ecoregion; as such, the ecological integrity of the montane ecoregion is at higher risk than the subalpine or alpine ecoregions that constitute the majority of the park.

Fire-history studies suggest that fire frequency and extent have decreased markedly in the montane ecoregion over the past century (Tande 1977), a pattern common throughout the Rocky Mountains (Hawkes 1979; White 1985; Masters 1990; Van Wagner 1995; Barrett 1996). Corresponding shifts in vegetation from early to later successional species have also been reported (Gruell 1983; Achuff et al. 1996; Barrett 1996). However, knowledge of vegetation history in JNP is limited to basic fire-history data; little if any direct reconstruction of past ecological states has been undertaken.

The objective of this study was to analyse vegetation composition, structure, and successional trends at and between 1915, 1949, and 1997 through the quantitative analysis of both repeat ground photographs and aerial photographs.

Study area

Jasper National Park (52°N, 118°W), located within the Canadian Rocky Mountains in Alberta, Canada, occupies a total area of 10 880 km^2 (Holland and Coen 1982*a*). Three ecoregions are represented within the park; the montane ecoregion occurs at the lowest elevations (1000–1350 m a.s.l.), the alpine ecoregion lies at the highest elevations above tree line, and the subalpine ecoregion occupies the area in between. The study was conducted within the montane ecoregion along the Athabasca River valley in the central region of JNP (Fig. 1). Peaks in this region are underlain by Late Palaeozoic limestone and valleys by Mesozoic shale (Gadd 1986). Surface material in the Athabasca River valley is primarily till and glaciofluvial deposits composed of sandstones and quartzites with some slate and limestone (Stringer and LaRoi 1970). The study area occupied a total of 64 km^2 or 8.5% of the total montane ecoregion within the park.

The climate of the montane ecoregion is generally the warmest and driest in the park (Holland and Coen 1982*a*). Mean daily temperatures vary from 15.1°C in July to –10.7°C in January, the hottest and coldest months, respectively (Environment Canada 1988). The mean annual precipitation is 393.7 mm, two-thirds of which falls as rain with June, July, and August being the wettest months (Environment Canada 1988).

Although the montane ecoregion is dominated by lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), it is characterized by the occurrence of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white spruce (*Picea glauca* (Moench) Voss), and trembling aspen (*Populus tremuloides* Michx.) interspersed with grasslands (Holland and Coen 1982*b*). Fire is generally regarded to be the major disturbance on the landscape, although wind and insect outbreaks are also important. Lodgepole pine establishes rapidly following stand-initiating fire events, and the persistence of open stands of Douglas-fir and grasslands may have been maintained historically by frequent ground fires (Stringer 1973; Tande 1977). Human infrastructure within the study area was minimal in 1915 and included several Métis homesteads and two recently constructed railroad lines.

Methods

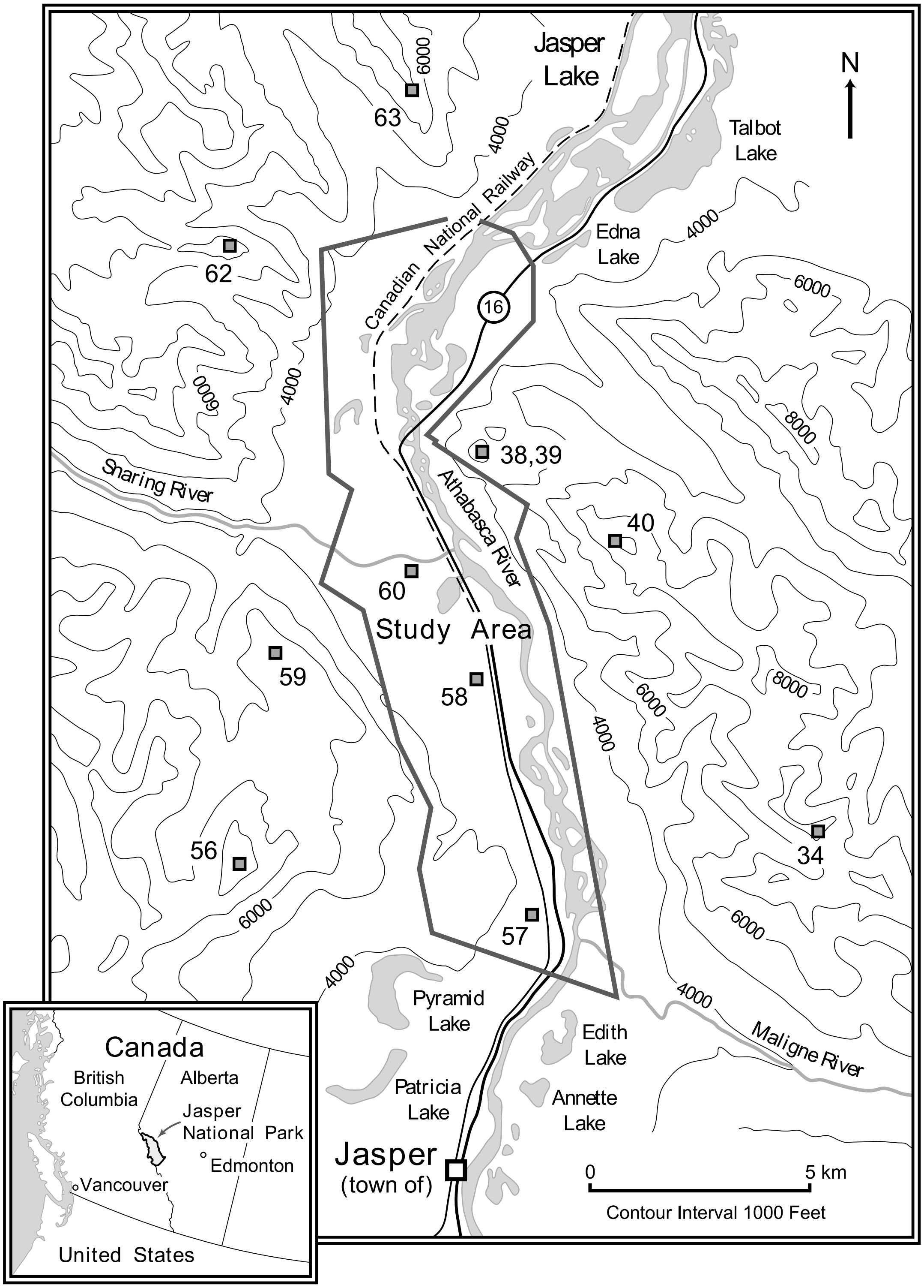
Historical vegetation patterns were reconstructed using repeat ground photographs (1915 and 1997) and repeat aerial photographs (1949 and 1991). A method for quantitative analysis of relative vegetation change in ground-based photographs was developed and tested by comparing relative measures of vegetation composition in the 1997 ground photographs with absolute measures of vegetation composition as interpreted from the 1991 aerial photographs.

Repeat ground photography

The 1915 Bridgland topographical survey team took 735 photographs from 92 survey stations. These survey stations were located primarily on mountain peaks and high ridges, although 10 stations were located in the valley bottom along the newly constructed railroad right-of-way. At each survey station, 8–12 photographs were taken so as to create a 360° panoramic view. The photographs, together with theodolite measurements, were later crafted into a topographic map covering 2300 km^2 in the central part of JNP.

Fifty-three of the Bridgland photographs, showing views that fell partially or completely within the study area, were retaken in the summer of 1997. These photographs were taken from 11 survey stations; three were in the valley bottom, and eight were at higher elevations on mountain peaks or ridges (Fig. 1). The location of each survey station was obtained from the original topographic maps. Precise camera locations were determined in the field by lining up foreground objects (e.g., large boulders) visible in the original photographs with features in the background, using the principle of parallax (Rogers et al. 1984). Camera equipment

Fig. 1. The study area within the montane ecoregion of Jasper National Park, Alberta, Canada. Numbers indicate survey stations from which repeat ground photographs were taken: 34, Roche Bonhomme; 38, Morro Peak I; 39, Morro Peak II; 40, Hawk Mountain; 56, Pyramid Mountain; 57, Power House Cliff; 58, Henry House Flats; 59, The Palisade; 60, Snaring River; 62, Esplanade Mountain; and 63, Mount Greenock.



used included a Linhof Technika 4 × 5 in. (1 in. = 2.54 cm) large-format camera, 90 mm Schneider-Kreuznach Angulon 1:6.8 lens, No. 85C (pale orange) Wratten filter, and Kodak T-max 100 black and white film. This equipment was chosen to approximate as closely as possible that used by the original survey team. It was not possible to repeat the exact day and time of the 1915 photographs, because the original field journals could not be located. The photographs were taken, however, during the summer when the vegetation was nominally at the same phenological stage. Thus, the tonal grey level response on the black and white films was expected to be similar between the two dates.

Analysis of repeat ground photographs

Qualitative analysis was based on visual inspection of all 53 pairs of photographs. Quantitative assessments were conducted on 20 pairs of photographs. Views taken at valley-bottom survey stations that portrayed only local vegetation, or at the highest elevation mountain peaks, for which detailed identification of cover types was difficult, were not included in the quantitative analysis. Where portions of the study area were represented in more than one pair of photographs, the clearest pair was chosen for analysis. Every effort was made to edge match the photographs so that the entire study area was covered. Only the portion of any given photograph that fell within the study area was interpreted; vegetation in the immediate foreground of the photographs was not interpreted.

Areas of homogeneous cover (compositionally and structurally) were delineated and interpreted (see classification system below) in a manner similar to standard aerial photographic interpretation. Photographic prints were approximately 11 × 15 cm. Minimum polygon size was approximately 0.5 cm^2. Polygons on each photograph were digitized using GRASS geographic information system (GIS) software (Shapiro et al. 1993) and analysed (as raster data) in IDRISI (Eastman 1997).

To facilitate overlay of the repeat pairs, 8–12 point features that could be accurately identified on both photographs and that were well distributed throughout the photograph, were selected as control points for each pair. A grid was then established for each pair of photographs with (0,0) at the lower left-hand corner. Coordinates for the control points were measured from the 1997 photographs. A first-order affine transformation was computed to register the photographs to the grid based on the selected control points. An indicator of how well the photographs were registered was obtained by the root mean square error values between the 1997 and 1915 coordinates. RMSE was 0.233 mm for 1997 photographs and 0.500 mm for 1915 photographs (units represent actual photograph measurements).

A spatial cross tabulation of vegetation composition for 1915 and 1997 was created by comparing cover types in corresponding pixels between paired photographs. Results for each pair of photographs were summed to create a summary cross tabulation for the entire study area. This approach assumed that a pixel unit was comparable both within and among photographs. In fact, because the scale of the photographs varied not only within a given photograph, but among photographs, adding photograph pixels in this way biased the summarized data in favour of foreground pixels, and larger scale photographs. A review of the photographs suggested no systematic bias that would favour one vegetation type over another; thus, it was assumed that summarizing data in this way would provide an adequate representation of the relative vegetation trends in the study area.

A transition matrix summarizing directions and amounts of change between pairwise combinations of all the different classification categories between 1915 and 1997 was created from the summarized cross-tabulation data. The extent of overall change in vegetation composition between 1915 and 1997 was estimated by summing the pixels in individual photographs by cover type at the two dates. The validity of this approach is subject to the same assumptions outlined above.

Repeat aerial photography

Two sets of aerial photographs, each covering the entire study area, were selected: the first set flown in the park in 1949 (1 : 40 000 scale, Kodak Super XX black and white film, rolls AS 143–145, flown September 15) and the most recent medium-scale series available, flown in 1991 (1 : 20 000 scale, Kodak Double-X Aerographic black and white film, roll AS4212, flown September 25). Working copies of the 1949 photographs were enlarged to a scale of 1 : 20 000, so that the minimum mapping unit (smallest polygon size) would be equivalent for both sets of aerial photographs. Areas of homogenous vegetation cover (compositionally and structurally) were delineated (see classification system below). The minimum mapping unit was approximately 0.5 cm^2 (2 ha). Ground truthing to check the accuracy of the interpretation was conducted on a subset of the polygons (Rhemtulla 1999). Polygons were transferred to an orthophotographic base map (1 : 20 000), which was subsequently digitized, edited, and labelled using the GIS software Arc/Info. Vector files were transformed to raster coverages with a cell resolution of 10 m. Analysis of the coverages was completed using the GIS software IDRISI (Eastman 1997).

Descriptive statistics were calculated by cover type for the entire study area and by species composition for forested stands. Coniferous forest stands, which dominated the forested area, were also analysed by crown closure. The spatial analysis program, FRAGSTATS (McGarigal and Marks 1995), was used to calculate patch number, mean patch size, and their respective standard errors for forested areas by canopy composition and crown closure. Standard statistical analysis was not undertaken for most of the data, because there were only two time points and no biological rationale for subdividing the study area into independent samples. Only patch size data were amenable to statistical analysis. These were log transformed to ensure normality and simple factorial analysis of variance was used to test for the effect of time period and either forest canopy composition or crown closure class on mean patch size (Zar 1974). Following significant effects in the ANOVA, comparisons were made between years for each crown closure class using Student's t tests and a corrected alpha value of 0.01 (0.05/5 t tests) (Zar 1974; Sokal and Rohlf 1981). Photograph cross tabulation between 1949 and 1991 was executed by cover type and crown closure within the GIS software IDRISI (Eastman 1997). Absolute measures of vegetation composition derived from the 1991 maps were compared with relative measures of vegetation from the 1997 ground photographs to assess whether the quantitative analysis of ground-based photographs provided an accurate estimate of relative vegetation cover. It was assumed that ecological differences in stand composition, structure, and distribution were minor between 1991 and 1997.

Classification system

A hierarchical land-cover classification system was developed based on the Alberta Vegetation Inventory widely in use in the province of Alberta (Nesby 1997), and the ecological land classification used in JNP (Holland and Coen 1982*a*). For both the repeat ground photographs and aerial photographs, each polygon was classified by physiognomic class as follows: forest (>16% crown closure), open forest (6–15% crown closure), juvenile forest (sapling stage), shrub, forb–grassland, wetland, water, sand–gravel, rock, and anthropogenic. Forest polygons were further classified by crown closure: (A) 16–30% cover, (B) 31–50%, (C) 51–70%, and (D) 71–100%. For the aerial photographs only, forest polygons were also classified by overstorey species composition: C (>80% coniferous), CD (60–80% coniferous, 20–40% deciduous), M (40–60% coniferous, 40–60% deciduous), DC (60–80% deciduous, 20–40% coniferous), and D (>80% deciduous).

Results

Analysis of repeat ground photographs

To determine if the results from the repeat ground and repeat aerial photography could be compared, it was necessary to evaluate the method used to quantify relative vegetation change in the repeat ground photographs. By comparing the relative proportions of cover types in 1997, as determined from the ground photographs, with the absolute values as determined from the 1991 aerial photographs, it was possible to assess the accuracy of the quantitative analysis of the ground photographs.

The 1991 and 1997 results for 11 of the 14 cover types were within 2% of one another (Table 1). The other three types (open forest, forest A, anthropogenic) differed by 3–6%. Although further testing of this approach to quantifying vegetation change using ground-based photographs is required, these preliminary results were promising. Since the method provided a reasonable estimate of the absolute vegetation cover in the present, we assumed that the relative vegetation cover values calculated for the 1915 landscape provided a reasonable estimate of absolute values for that time period. Thus, the ground photographs and aerial photographs were directly comparable, and the quantitative results obtained from the two sources could be used to assess changes in relative vegetation cover from 1915 to 1997.

Vegetation change

The greatest vegetation change over the last 80 years was the increase in forest cover and crown closure throughout the study area (Table 1, Figs. 2 and 3). A greater amount of change in vegetation cover on the landscape occurred from 1915 to 1949 than from 1949 to the present (Table 1). Total relative wetland, water, and sand–gravel cover appeared to remain constant over the entire period. Both qualitative analysis of the repeat ground photographs and quantification using the aerial photographs suggested that deciduous stands declined in extent over this time (Fig. 2, Table 2).

Qualitative analysis of the repeat ground photographs suggested that vegetation cover has become more homogeneous over the last 80 years (Fig. 2), although there was little statistical support for a decrease in patch number or increase in patch size (Tables 2 and 3). Overall, the 1915 landscape consisted of patchy vegetation – open coniferous forest stands, large grasslands, juvenile forest stands, and the occasional stand dominated by deciduous species (Fig. 2). By contrast, current vegetation appeared more homogeneous and was dominated by closed-canopy coniferous forests (Figs. 2 and 3).

Table 1. Vegetation cover in 1915, 1949, 1991, and 1997 in the study area in the montane ecoregion of Jasper National Park.

	Year and photograph type			
	1915 oblique	1949 air	1991 air	1997 oblique
Total forest	35	58	66	65
Open forest	16	2	2	5
Forest A	15	4	10	4
Forest B	16	13	9	10
Forest C	3	27	24	23
Forest D	0	13	21	23
Juvenile forest	7	4	0	0
Shrub	13	4	6	4
Forb–grassland	11	9	4	6
Wetland	2	4	3	2
Water	12	13	12	13
Sand–gravel	2	2	1	1
Rock	2	4	3	2
Anthropogenic	1	2	4	8

Note: The 1915 and 1997 data are relative photograph areas (%), as calculated from oblique ground photographs. The 1949 and 1991 data are percent land area as calculated through vertical aerial photographs. By comparing the 1991 and 1997 data, it is possible to assess the accuracy of the technique for quantitative analysis of ground photographs. Forest crown closure classes are as follows: A, 15–30%; B, 31–50%; C, 51–70%; D, 71–100%.

Successional trends

From 1915 and 1949 to the present there was widespread transition of many vegetation types to forest cover (Tables 4 and 5). In particular, former grassland, shrubland, and juvenile forest were replaced by forest (Fig. 2, Tables 4 and 5). Tree cover on discontinuous rocky outcroppings on steeper slopes also increased. Sand–gravel polygons were highly transitory, succeeding either to forb–grassland and forest (Table 4) or being reclaimed by water (Table 5). Wetlands, water, rock, and anthropogenic sites were the most stable of the nonforested cover types (Tables 4 and 5).

Within forested stands, there was a trend toward increased crown closure (Tables 6 and 7). The vast majority of the area covered by open forest or low crown closure forest (<50%, classes A and B) in 1915 had changed to forest with crown closure above 51% (classes C and D) by 1997. The pace of change in the landscape seemed to be relatively constant. The proportional transition from 1949 to 1991 was slightly more than half that from 1915 to 1997: open forest to forest C or D, 30 vs. 70%; forest A to forest C or D 44 vs. 62%; forest B to forest C or D 60 vs. 89% (Tables 6 and 7).

Changes in canopy composition were also prevalent for most forest types. Only conifer stands showed a strong tendency to maintain the same composition from 1949 to 1991 (Table 8). Most conifer-dominated mixedwoods converted to pure conifer (75% by area); mixedwood stands also changed primarily to pure conifer (82% by area). Deciduous-dominated mixedwoods showed multiple trends: 38% main-

Fig. 2. Athabasca River valley, 1915 (top) and 1997 (bottom). Photographs are a mosaic of four photographs taken from survey station No. 57 (photograph Nos. 459–462).

M.P. Bridgland 1915

J.Rhemtulla and E. Higgs 1998

tained the same composition, 17% changed to deciduous-dominated stands, and 32% changed to pure coniferous composition. Pure deciduous stands mostly showed an increase in conifer content either changing to deciduous-dominated mixedwoods, mixedwoods, or pure conifer stands (38, 12, and 18%, respectively).

Discussion

Quantitative methods

The method developed to analyse the repeat ground photographs provided a reasonable estimate of relative vegetation cover within the study area. It did not, however, compensate for the variation in scale within repeat ground photographs. The discrepancy in the estimate of anthropogenic cover between the 1997 ground and 1991 aerial photographs was likely due, in part, to this limitation. A number of the repeat ground photographs showcased human infrastructure prominently in the midground of the photograph, thus biasing the apparent incidence of this cover type upwards. The discrepancy in the estimates of open forest and forest A cover may have resulted from inconsistent classification of forest types resulting from the difficulty in assessing crown closure on repeat ground photographs. If the two categories are combined, there is good concordance between the estimates of cover in 1991 and 1997.

The systematic and comprehensive coverage provided by the repeat ground photographs is key to their effectiveness in this type of analysis. It is possible that biases among vegetation categories due to varying scales were essentially “averaged”. Further testing and development of the technique is currently being undertaken to incorporate a more complex algorithm that will account for the variation in scale and to explore methods to automate the conversion of the repeat ground photographs into planar views, thus making standard analyses possible.

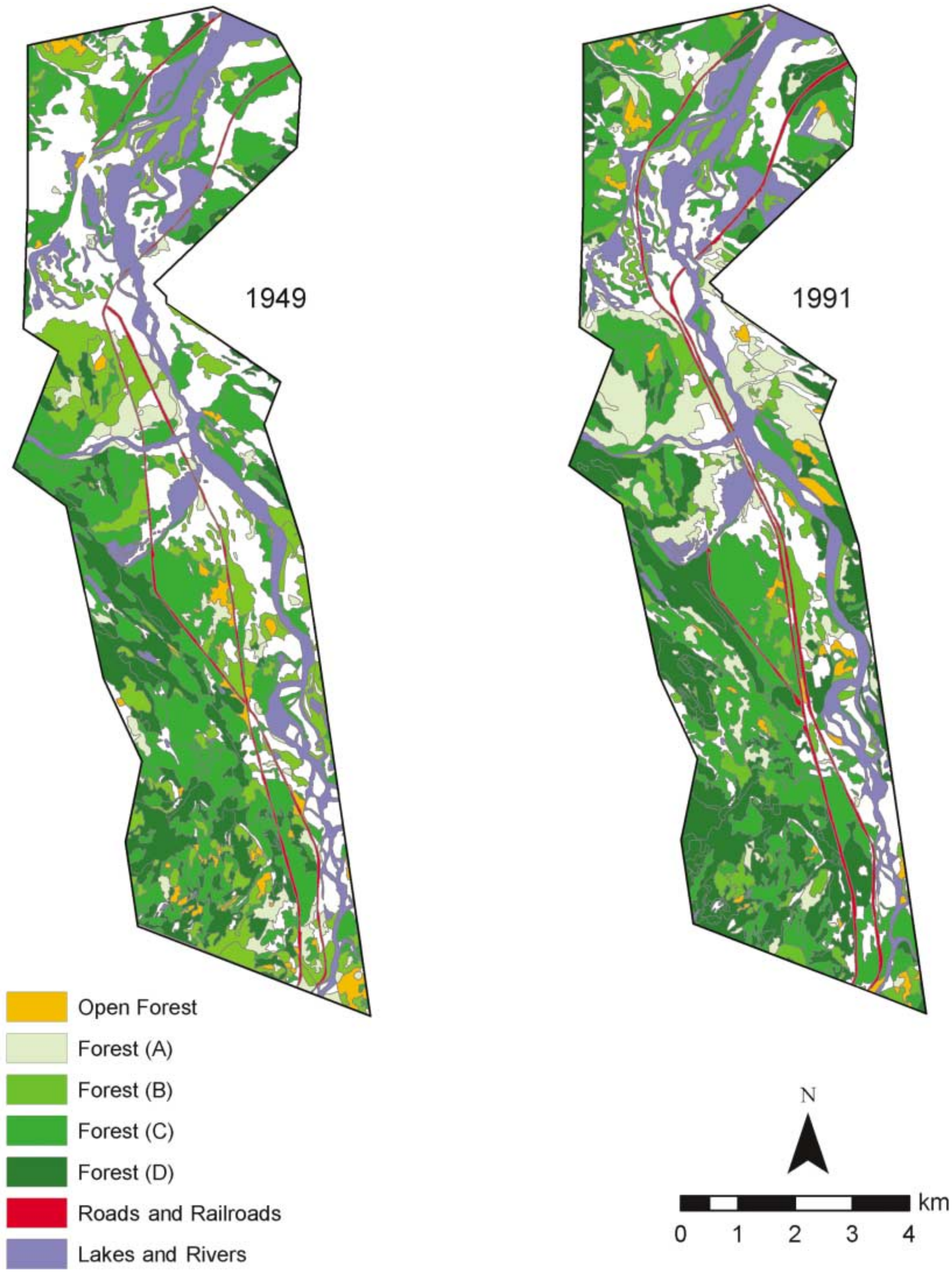
The 1915 survey conducted in JNP was part of a larger effort on the part of the Canadian Dominion Land Survey to map the mountainous regions of western Canada. Similar photo-topographical surveys were conducted throughout the Alberta Rocky Mountains and adjacent foothills as well as in several mountain ranges in British Columbia. The techniques used in this study to analyse relative vegetation change could be applied in a similar manner to these other collections of photographs. Moreover, changes in other landscape features, such as glacier movements or historical human activity could also be analysed this way.

Vegetation change and successional trends

Fire-history records for JNP indicate widespread fire events in the summer of 1889, less extensive fire in 1905, and little fire thereafter (Tande 1979). The vegetation changes evident within the study area were consistent with a landscape recovering from the effects of a major disturbance event early in the century. Successional trends described over this 80-year period were similar to those reported elsewhere in the Rocky Mountains, including dendrochronological research in the Colorado Front Ranges (Mast et al. 1997), qualitative repeat photography in Montana (Gruell 1983; Arno and Gruell 1986), fire-history studies in Waterton Lakes National Parks (Barrett 1996), and modelling in Banff National Park (Achuff et al. 1996). Our results provide the first confirmation from direct observation of vegetation.

Forest encroachment onto grasslands is of particular concern in many jurisdictions (Arno and Gruell 1986; Achuff et al. 1996; Mast et al. 1997). Although total grassland cover diminished by almost 50% over the period studied, core grasslands persisted in the area despite the absence of peri-

Fig. 3. Crown closure for coniferous forest in 1949 and 1991 for the study area within the montane ecoregion of Jasper National Park.



odic low-intensity ground fire. This may be attributable to moisture limitations on specific sites (Stringer 1973). It was also interesting to note that many core persistent grasslands coincided with areas under active cultivation at the turn of the century (Higgs et al. 1999).

Increases in forest crown closure over the past century, have been observed throughout Banff National Park (Achuff et al. 1996), the Colorado Front Ranges (Veblen and Lorenz 1991), and eastern Oregon and Washington (Lehmkuhl et al. 1994). Crown closure typically increases with stand age until the canopy starts to break up as overstorey trees mature. Field observation suggested that in most cases, stand breakup has not yet begun to occur, especially in the case of lodgepole pine stands dating to the 1889 fire. Others have reported a high occurrence of stands with two age-classes of lodgepole pine in the montane ecoregion, with older trees having survived the fire that gave rise to the younger cohort (Tande 1977; LaRoi and Hnatiuk 1980). It is possible that the maturation of the understorey cohort contributed to the canopy closure we observed. The small increase in forest A and open forest stands post-1949 was likely due to the introduction of prescribed burns in the park, several large

Table 2. Total patch number, mean patch size (ha) with standard error, and total area (ha) of forest overstorey species composition classes in study area in 1949 and 1999.

Species composition	No. of patches		Mean patch size (ha)		Total area (ha)	
	1949	1991	1949	1991	1949	1991
C	107	79	32.65±15.24	48.51±21.76	3493.55	3832.29
CD	8	16	8.10±2.82	4.71±1.12	64.80	75.36
M	10	22	3.30±1.31	3.02±0.73	33.00	66.44
DC	6	24	2.29±0.35	4.75±2.23	13.74	114.00
D	19	24	5.86±1.96	3.42±0.88	111.34	82.08
Total	150	165	24.77±10.91	25.28±10.53	3716	4171

Note: There was a significant effect of canopy composition but not of year or the interaction of year and canopy composition on mean patch size (ANOVA, $p > 0.05$). C, coniferous; CD, coniferous dominant with deciduous component; M, mixed coniferous–deciduous; DC, deciduous dominant with coniferous component; D, deciduous.

Table 3. Total patch number, mean patch size (ha) with standard error, and total area (ha) of crown closure classes within coniferous forest in study area.

Crown closure	No. of patches		Mean patch size (ha)		Total area (ha)	
	1949	1991	1949	1991	1949	1991
Open forest	40	35	3.11±0.67	3.00±0.46	124.40	105.00
Forest A	58	55	4.53±0.82	11.61±3.18*	262.74	638.55
Forest B	112	90	7.19±1.42	5.77±0.65	805.28	519.30
Forest C	99	77	16.41±3.95	18.24±4.14	1624.59	1404.48
Forest D	53	49	15.09±5.60	25.92±9.67	799.77	1270.08
Total	362	306	9.99±1.45	12.87±2.00	3617	3938

Note: There were significant effects of the year and crown closure, but not their interaction, on patch size (ANOVA, $p < 0.05$). Open forest, 6–15% cover; forest A, 16–30%; forest B, 31–50%; forest C, 51–70%; forest D, 71–100%.
*Significantly different from 1949 (t test, $p < 0.01$).

Table 4. Transition matrix showing vegetation changes from 1915 to 1997 (%).

1915	1997 Forest	Open forest	Juvenile forest	Shrub	Herb	Wetland	Water	Sand–gravel	Rock	Anthropogenic
Forest	80.37*	2.20	—	3.06	0.94	0.77	1.86	0.06	0.13	10.61
Open forest	64.45	11.10*	—	2.90	4.69	0.12	5.14	—	—	11.59
Juvenile forest	85.91	4.44	—*	3.17	1.51	0.37	1.42	—	0.18	3.02
Shrub	56.18	7.39	0.23	14.09*	2.72	2.46	10.56	2.46	0.35	3.58
Herb	56.60	4.05	0.13	3.81	25.29*	0.53	2.38	—	0.02	7.18
Wetland	15.47	1.18	—	2.39	1.66	62.53*	16.77	—	0.01	—
Water	8.44	1.61	—	2.85	3.73	1.91	78.46*	2.33	0.10	0.59
Sand–gravel	24.52	8.14	—	2.02	51.06	—	13.79	0.47*	—	—
Rock	4.08	1.08	—	0.23	—	—	—	2.26	92.35*	—
Anthropogenic	34.81	0.24	—	—	11.74	—	—	—	—	53.21*

Note: Cross tabulations for individual photograph pairs were first summed (in pixel units). For each 1915 vegetation type, percentage of that vegetation type changing to other types was calculated. Thus, rows sum to 100% (e.g., of the total area that was forest in 1915, 80.37% remained forest in 1997, 2.20% moved to open forest, 0% moved to juvenile forest, etc.).
*Areas that had the same cover type at the two dates.

windthrow events, and the encroachment of new open forest onto formerly unforested areas.

The majority of the forested areas followed expected successional trends, either remaining conifer dominated or changing from mixed composition to dominance by coniferous species between 1949 and 1991 (Stringer and LaRoi 1970; LaRoi and Hnatiuk 1980). A significant proportion (but small total area) of deciduous and mixed stands, however, exhibited unexpected trends by remaining as or succeeding to dominance by deciduous species. Since aspen may dominate a stand for 80 or more years following disturbance (Peterson and Peterson 1992), the results suggested that one-third or more of the area dominated by aspen was less than 40 years old in 1949. Further, the results suggested that this proportion of aspen forest either had no coniferous understorey or hosted a severely suppressed coniferous

Table 5. Transition matrix showing vegetation changes from 1949 to 1991 (%).

1949	1991 Forest	Open forest	Juvenile forest	Shrub	Herb	Wetland	Water	Sand–gravel	Rock	Anthropogenic	Total area (ha)
Forest	91.94*	0.37	—	1.37	0.44	0.51	1.64	0.32	0.78	2.63	3716.15
Open forest	64.38	23.61*	—	1.46	4.91	—	0.67	0.42	0.35	4.21	124.52
Juvenile forest	89.45	4.44	—*	1.89	0.97	0.17	2.30	0.43	0.20	0.14	283.90
Shrub	40.66	2.04	—	40.18*	0.58	8.37	5.53	0.65	0.24	1.76	226.21
Herb	40.07	17.13	—	54.26	62.67*	4.98	11.00	1.03	0.05	8.81	572.57
Wetland	20.42	0.69	—	15.06	1.02	46.97*	12.93	0.75	0.02	2.13	228.02
Water	5.53	0.30	—	3.77	3.02	5.43	76.66*	4.36	—	0.92	815.92
Sand–gravel	12.29	0.36	—	7.04	16.68	13.48	25.91	22.76*	0.04	1.44	110.73
Rock	33.97	2.66	—	—	0.97	—	2.48	—	59.80*	0.12	228.38
Anthropogenic	17.39	0.53	—	4.10	4.33	0.59	1.86	1.15	—	70.05*	144.19
Total area (ha)	4170.53	124.72	—	358.26	283.77	217.40	798.92	81.94	167.30	247.75	6450.59

Note: Cells show percentage of the 1949 cover type changing to 1991 types (see Table 4). Also given is the total area for each cover type in 1949 (last column) and 1991 (bottom row).
*Areas that had the same cover type at the two dates.

understorey, which could not be detected in aerial photographs even in relatively old stands

Although qualitative assessment of the repeat photography suggested a decrease in overall landscape heterogeneity, this finding was not confirmed by statistical analysis of the aerial photographs. It is possible that much of the homogenization occurred from 1915 to 1949 and, thus, was not detected in the aerial photograph analysis. It is also possible that the sample size for forest patches was insufficient to detect any significant change.

Finally, certain unexpected transitions in cover type may have been due, in part, to error including minor inconsistencies in classification and imperfect overlay of data from different time points. For example, the transition from water in 1915 to rock or forest cover in 1997 (Table 4) may be explained in this way, although the result may also have been due to shifts in the main channel of the Athabasca River over this time period. Overall, the magnitude of such changes was small.

Drivers of change

Factors cited as contributing to vegetation changes of this type in other regions include a decrease in fire frequency (Veblen and Lorenz 1991; Lehmkuhl et al. 1994; Achuff et al. 1996; Moore et al. 1999; Radeloff et al. 1999), changes in climatic conditions (e.g., Mast et al. 1997), and an increase in direct human activity on the landscape (Ostlund et al. 1997; Higgs et al. 1999; Jackson et al. 2000).

It is generally accepted that the extent, frequency, and intensity of fire has played a major role in shaping the vegetation patterns in JNP. Over the past 100 years, there has been a shift in the fire regime for many areas in the Rocky Mountain region (Tande 1977; Van Wagner 1995). Historically, the area experienced both frequent low intensity fires and less frequent high intensity fires; burns ranging in size from one-fifth to one-third of the park area occurred once or twice a century between 1600 and 1889 (Van Wagner 1995). Fire has been negligible within JNP and other Canadian Rocky Mountain parks over the past 70 years (Hawkes 1979; Tande 1979; White 1985; Masters 1990; Van Wagner 1995; Barrett 1996). The decrease in fire activity may be due to the implementation of fire suppression, as well as the expulsion of First Nations peoples from JNP at the turn of the century and, consequently, their use of fire as a management tool (Lewis 1980; Pyne 1997; MacLaren 1999, but see Barrett 1981; Johnson and Larsen 1991; Kay and White 1995). Although changes in fire regime corresponding to climatic change during the Little Ice Age have been reported elsewhere in the Canadian Rockies (Johnson et al. 1990; Masters 1990; Johnson and Larsen 1991), no such correlation is apparent in JNP (Van Wagner 1995).

Implications of change

The main ecological effect of decreased disturbance on the landscape is a decline in diversity at multiple scales. In Banff National Park (directly south of JNP), park managers predict that if the current fire regime persists into the future, fully one-third of vegetation types may be lost entirely from the landscape (Achuff et al. 1996). Aspen stands, in particular, are at high risk, as are open Douglas-fir stands and grasslands (Achuff et al. 1996). Declines in vegetation diver-

Table 6. Transition matrix showing changes in forest crown closure from 1915 to 1997 (%).

	1997				
1915	Open forest (6–15%)	Forest A (16–30%)	Forest B (31–50%)	Forest C (51–70%)	Forest D (71–100%)
Open forest	14.69*	3.57	11.51	26.71	43.53
Forest A	5.66	11.65*	20.05	41.01	21.63
Forest B	0.33	1.31	9.96*	41.81	46.60
Forest C	0.11	—	0.59	16.78*	82.53
Forest D	—	—	—	—	—*

Note: Only areas that were forested at both dates are included. (See the caption of Table 4 for more details.)

*Areas that had the same cover type at the two dates.

Table 7. Transition matrix showing changes in coniferous forest crown closure from 1949 to 1991 (%).

	1991					
1949	Open forest (6–15%)	Forest A (16–30%)	Forest B (31–50%)	Forest C (51–70%)	Forest D (71–100%)	Total area (ha)
Open forest	27.73*	13.57	28.92	24.18	5.59	106.02
Forest A	1.49	37.27*	17.23	32.44	11.57	209.65
Forest B	0.64	16.06	24.50*	41.86	16.93	727.42
Forest C	0.30	14.71	6.92	44.89*	33.18	1406.74
Forest D	0.20	2.66	2.25	18.86	76.02*	753.98
Total area (ha)	42.85	436.45	359.37	1171.87	1193.27	3203.81

Note: Only areas that were coniferous-dominated forest at both dates are included. (See the caption of Table 4 for more details.)

*Areas that had the same cover type at the two dates.

Table 8. Transition matrix showing changes in forest overstorey species composition from 1949 to 1991.

	1991					
1949	C	CD	M	DC	D	Total area (ha)
C	95.96*	1.59	0.93	0.72	0.80	3214.24
CD	75.06	7.82*	6.03	5.04	6.05	62.51
M	82.83	6.64	1.87*	8.66	0.00	32.67
DC	31.91	5.82	8.08	37.56*	16.64	12.38
D	17.84	0.47	11.98	37.69	32.02*	94.89
Total area (ha)	3179.20	59.33	46.74	69.63	61.79	3416.69

Note: Only areas that were forested at both dates are included. Also given is the total area for each composition type in 1949 (last column) and 1991 (bottom row). C, coniferous; CD, coniferous dominant with deciduous component; M, mixed coniferous–deciduous; DC, deciduous dominant with coniferous component; D, deciduous. (See the caption of Table 4 for more details.)

*Areas that had the same cover type at the two dates.

sity at both the stand and landscape levels over the past century have also been reported in other ecosystem types (Ostlund et al. 1997; Radeloff et al. 1999; Jackson et al. 2000).

Decreased fire occurrence and associated fuel accumulation may also be sufficient to alter the fire regime in the park from a historic regime of frequent low-intensity fires to one characterized by less frequent higher intensity burns (Barrett 1996).

Finally, the increase in homogeneity of forest stands may facilitate the spread of insect disturbance. The mountain pine beetle (*Dendroctonus ponderosae* Hopk.) is the most serious insect enemy of mature lodgepole pine in western Canada (Safranyik et al. 1981). Stands greater than 80 years of age are considered highly susceptible (Shore and Safranyik 1992), and large, pure mature and overmature stands would sustain an outbreak more so than relatively younger, more vigorous stands, especially in mixed compositions.

Reference conditions

The concept of reference conditions has been proposed as a useful framework to guide the work of park management and ecological restoration (Aronson et al. 1995). Quantifying reference conditions (the range of historic variability in the ecological structures and processes of a system) can provide both a measure of the current state of an ecosystem, as well as goals for restoration treatments (Aronson et al. 1995; Fule et al. 1997; White and Walker 1997).

Park managers and ecologists are worried that the current state of the montane ecoregion of JNP is outside the historical range of variability for the area (Achuff et al. 1996). Many of the changes documented in this study represent expected successional trends in the absence of disturbance, but whether this lack of disturbance is natural or desired continues to be debated.

Concern over the issue has prompted the introduction of restorative practices onto the landscape, such as prescribed fire. Clear restoration goals have proved elusive so far.

Although it might be tempting to view vegetation conditions at the turn of the century as benchmarks for restoration, the range in variability over a longer period may have been even greater. A recent paleoecological study of macrocharcoal and pollen from lake cores in the montane ecoregion of JNP suggested that the fire regime 1000 years ago may in fact have been characterized by very infrequent high-intensity fire (C. Zutter and D.W. Schindler, unpublished data). Some grassland sites in the montane ecoregion of JNP are underlain by forest soils (Eutric Brunisols) suggesting that the current forest dominance may have been even more widespread in the past (Holland and Coen 1982*b*).

Although further research is needed to extend our knowledge of structure and composition of this landscape further back into the past and to determine the appropriate time frame for defining the extent of historical variability, the implementation of restorative practices in JNP will require the blending of historical knowledge with societal values to set goals for the future of the montane ecoregion.

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