J. Range Manage.
57: 66-75 January 2004

Landscape-level dynamics of grassland-forest transitions in British Columbia

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Abstract

Grasslands in the interior British Columbia of Canada are adjacent to forests and are susceptible to tree encroachment. Grazing, fire suppression, and climate variability are among factors affecting vegetation dynamics in the ecotone between grassland and forest, but topographic factors such as slope aspect, slope degree and elevation may interact with these factors and result in uneven changes in vegetation among landscape elements. Nine sites with a total of approximately 50,000 ha of grasslands and forests in the Cariboo/Chilcotin forest region of British Columbia were selected to study the effect of slope aspect, slope degree and elevation on vegetation distribution, dynamics and forest expansion from the 1960's to 1990's. Vegetation maps of the 1960's and 1990's were generated using aerial photos and overlaid with GIS layers including aspect, slope and elevation. The classification of open grassland, treed grassland, open forest and closed forest was based on the percent coverage of coniferous species, ranging from 0–5%, 5–15%, 15–35%, and ≥ 35%, respectively. A probability index (P-value) was developed to test the effect of aspect, slope, and elevation on vegetation distribution, dynamics, and forest expansion based on the distribution and changed areas. Results show that open grasslands occurred on southerly aspects and the shift to treed grassland occurred mostly on these aspects. The probability of vegetation shift from open to treed grasslands decreased with increasing slope degree, probably due to the less favorable moisture regime on steep slopes. Treed grassland also shifted to open forest on south facing slopes and more level sites. In contrast, closed forest most often occurred on northerly facing slopes and the shift from open to closed forests was most likely to occur there. The greatest changes in vegetation cover types occurred at mid-elevations between 700 and 1,000 m. Management plans aimed at the control of tree encroachment and forest ingrowth should take these topographic factors into consideration.

Key Words: Geographic Information Systems, slope, aspect, elevation, digital elevation model, forest

Resumen

Los pastizales en el interior de Columbia Británica en Canadá están adyacentes a los bosques y son susceptibles a la invasión por árboles. El apacentamiento, la supresión del fuego y la variabilidad climática están entre los factores que afectan la dinámica de la vegetación en el ecotono entre el pastizal y el bosque, pero los factores topográficos, tales como la exposición de la pendiente, el grado de pendiente y la elevación pueden interactuar con estos factores y resultar en cambios no uniformes de vegetación entre los elementos del paisaje. Se seleccionaron nueve sitios en la región boscosa de Cariboo/Chilcotin de Columbia Británica, con un total aproximado de 50,000 ha de pastizal y bosque, para estudiar los efectos de la exposición de la pendiente, grado de pendiente y elevación en la distribución de la vegetación, dinámica y expansión del bosque de la década de 1960 a la de 1990. Mapas de las décadas de 1960 y 1990 fueron generados usando fotografías aéreas y sobreponiendolas con capas de GIS que incluían la exposición, la pendiente y la elevación. La clasificación del pastizal abierto, pastizal arbolado, bosque abierto y bosque cerrado se basó en el porcentaje de cobertura de especies de coníferas variando de 0–5%, 5–15%, 15–35% y $35%, respectivamente. Se desarrolló un índice de probabilidad (valor-P) para evaluar los efectos de la exposición, pendiente y elevación en la distribución de la vegetación, dinámica y expansión del bosque basado en la distribución y áreas cambiadas. Los resultados muestran que el pastizal abierto ocurrió en la exposición sur y el cambio hacia pastizal arbolado ocurrió principalmente en estas exposiciones, la probabilidad de un cambio de vegetación de pastizal abierto a pastizal arbolado disminuye con el aumento del grado de pendiente, probablemente debido al régimen de humedad menos favorable en las pendientes pronunciadas. Los pastizales arbolados también cambiaron a bosque abierto en las pendientes con exposición sur y sitios más planos. En contraste, el bosque cerrado ocurrió más frecuentemente en las pendiente con exposición norte y el cambio de bosque abierto a bosque cerrado es más probable a que ocurra aquí. Los mayores cambios en la cobertura de tipos de vegetación ocurrió en elevaciones medias entre 700 y 1,000 m. Los planes de manejo enfocados al control de la expansión de los arboles y la contracción de los bosques debe tomar en consideración estos factores topográficos

The increases in density, biomass, and stature of trees and shrubs in the arid and semiarid ecosystems have been reported around the world (Branson 1985, Grover and Musick 1990, Bahre 1991, Archer 1994). The encroachment of woody plants is a major threat to range resources, reducing grassland area and car-

Funding was provided by Grazing Enhancement Fund (Cariboo/Chilcotin), Beef-Cattle Industry Development Fund, and AAFC Matching Investment Initiative. The authors wish to thank the following persons for providing information and technical assistance: Chris Armes, Peter Fofonoff, Kevin Franck, Ross Fredell, Dave Hill, Peter Holub, Michael Howard, Fred Knezovich, Dave Michel, Pierre Rainville, Bruce Roddan, Martin Sills, Ordell Steen, and Brian Wilson.
Manuscript accepted 17 Apr. 2003.

rying capacity, and inhibiting livestock movement (Burkhardt and Tisdale 1976, Strang and Parminter 1980, Gruell 1983, MacDonald and Wissel 1991, Richardson and Bond 1991). Similar impact on wildlife habitats has also been reported (Kazmaier et al. 2001). Woody plant encroachment into grasslands also has broader ecological implications, for example, modifications on soil carbon sink (Gill and Burke, 1999, Jackson et al. 2002). Fire suppression, human disturbance, climatic variation, livestock grazing, and interactions of these factors in the last 100 to 200 years have led to woody species expansion (Tisdale 1950, Parminter 1978, Strang and Parminter 1980, Madany and West 1983, Bahre 1991, Arno and Gruell 1986, Mast et al. 1998). Tree encroachment/forest ingrowth is a very complicated issue and the cause-effect is often a source of disagreement among researchers and varies among geographic regions.

In addition to the above general biotic and abiotic factors, topographic factors such as slope, aspect, and elevation, may also affect vegetation dynamics (Titshall et al. 2000). This is particularly true in the interior of British Columbia (B.C.), where elevation controls vegetation distribution. Aspect, slope and elevation in many respects determine the microclimate (Geiger 1966). Elevation determines the altitudinal zonality of soil and vegetation, slope degree controls the velocity of wind, and slope aspect determines the insulation, evaporation, snow retention and melting, land drainage, and therefore soil moisture. The ecotone between grassland and forest in B.C. provides a good opportunity for testing hypothesis related to the distribution and dynamics of grasslands and forests as affected by topographic factors.

In the southern interior of B.C., tree encroachment and forest ingrowth were first reported about 80 years ago (Whitford and Craig 1918). The loss of rangelands due to tree encroachment and forest ingrowth in recent years was more than 30% over a 30-year period in selected areas of the Cariboo/Chilcotin and the Kamloops forest regions (Ross 1997, 2000, Bai et al. 2000b). There have been many speculations regarding the relationship between tree encroachment/ingrowth and elevation, aspect, and slope. For example, tree encroachment and forest ingrowth are believed to be more prevalent on the north-facing slopes (Tim Ross, personal observation). However, further scientific analysis and investigation are necessary to verify this. Recent developments in the science and technology of Geographic Information Systems (GIS) and spatial analysis make such analysis possible. Specific objectives of this study were to determine 1) whether the distribution area of grassland and forest has changed from 1960's to 1990's and if so, whether it is related to aspect, slope and elevation, and 2) how forest expansion from forest edges from 1960's to 1990's is affected by aspect, slope and elevation. The analysis was based on the vegetation maps of the 1960's and 1990's of 9 sites in the Cariboo/Chilcotin forest region, a product of 2 Cariboo/Chilcotin Grazing Enhancement Fund projects (Ross 1997, 2000).

Materials and Methods

Site description:

The study area is located in the Interior Douglas-fir and Bunchgrass biogeoclimatic zones in the Cariboo/Chilcotin region, B.C., Canada (Steen and Coupe 1997). Major tree species include interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), trembling aspen (*Populus tremuloides* Michx.), and white spruce (*Picea glauca* (Moench) Voss). Dominant grasses are bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), Richardson's needle grass (*Stipa richardsonii* Link), sheep fescue (*Festuca ovina* L.), Kentucky bluegrass (*Poa pratensis* L.) and pine grass (*Calamagrostis rubescens* Buckl.) (Ross 1997, 2000). Nine sites within the study area, including Bald Mountain, Becher Prairie, Canoe Creek, Dog Creek, Lone Cabin Creek, the Junction, Meadow Lake, Two Lakes, and Word Creek, were selected with a total area of approximately 50,000 ha (Fig. 1). Word Creek and Dog Creek are geographically connected and were treated as 1 site in the analysis.

Data acquisition and conversion

Vegetation maps of these sites in 1961–75 and 1993–97 were created using visual interpretation and manual delineation of 1:15,000 aerial photographs combined with field surveys. Eleven vegetation types were identified: open grassland, treed grassland, open forest, closed forest, aspen forest, forest that has been recently logged, wetland, shrubland, riparian area, riparian-saline area, and water body. The classification of open grassland, treed grassland, open forest and closed forest was based on the percent coverage of coniferous species, ranging from 0–5%,

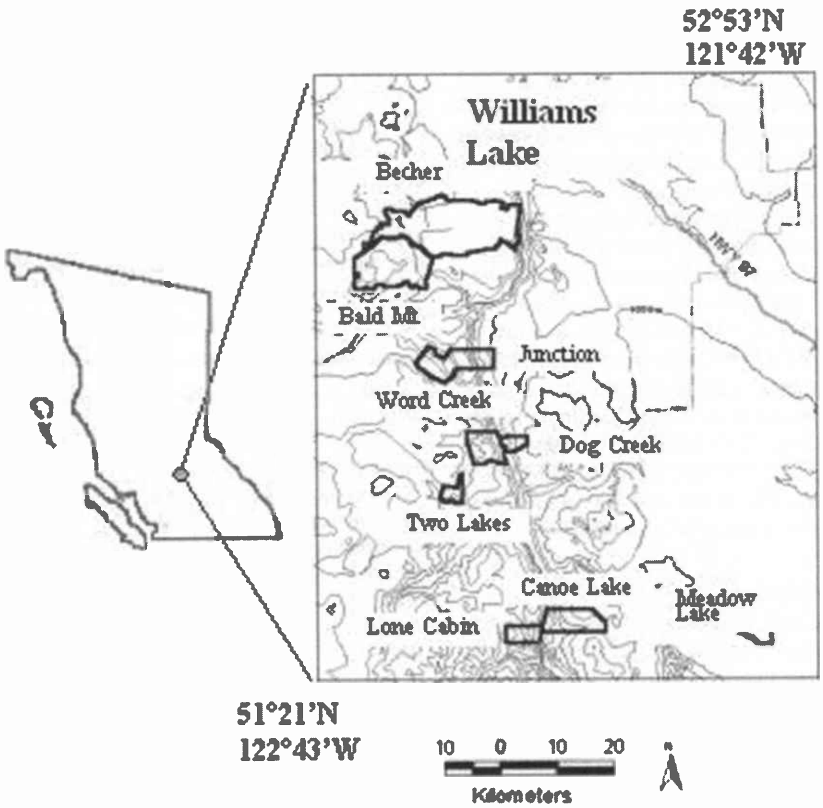

Fig. 1. Locations of the 9 study sites in the Cariboo/Chilcotin region, British Columbia.

5–15%, 15–35%, and ≥ 35%, respectively. The first sets of photographs were from 1961 to 1965 except for Meadow Lake where the photographs were from 1975, but are referred to as 1960's in this paper. The second sets were from 1993 to 1997 and are referred to as 1990's. Polygons of all vegetation types were digitized, converted to raster format with a 10 m resolution, and imported to IDRISI32 (IDRISI Project, Clark University, Worcester, Mass.) for further analysis.

Generating Digital Elevation Model and aspect and slope images

Sixteen, 1:20,000 Terrain Resource Information Mapping (TRIM) sheets in Arc/Info coverage format were obtained from BC Ministry of Environment, Land and Parks, Canada. The average distance between elevation points was about 100 m in the TRIM. The projection of TRIM was changed from B.C. Albers to Universal Transverse Mercator (UTM) and only the point elevation data were used in the analysis. The TRIM point coverage was saved as an Arc/View shape file and imported into IDRISI. The Digital Elevation Model (DEM) was generated separately for each coverage sheet and then pasted together according to study sites. A triangulated irregular network (TIN) model was first created using TRIM vector points, followed by TIN Interpolation which generates a raster surface image from the TIN model and the vector point coverage that defines the vertices of the TIN. The pixel resolution of DEM was 10 m, corresponding to the raster vegetation maps.

The aspect and slope images for each site were created in IDRISI using DEM. The aspect image was reclassified into 45° groups: north (N), northeast (NE), east (E), southeast (SE), south (S), southwest (SW), west (W), and northwest (NW). Aspects with a slope degree less than 5° were classified as flat. The slope image was reclassified into 1) flat (0–5°), 2) 5–10°, 3) 10–20° and 4) ≥ 20°. The DEM image was classified into 100 m elevation (meter above sea level) groups.

GIS analysis

Three null hypothesises were tested in GIS analysis: 1). each vegetation type was distributed evenly among different levels of aspect, slope and elevation in both the 1960's and 1990's, 2). the increased and decreased area of each vegetation type between the 1960's and 1990's occurred equally among different levels of aspect, slope and elevation, and 3). forest expansion from the forest edge was not affected by aspect, slope or elevation.

Vegetation types within each of the 8 sites in the 1960's and 1990's were separated and saved as individual GIS layers. Aspect, slope and elevation were used to categorize vegetation classes among the 8 sites for both dates. The increased and decreased areas of each vegetation type between the 1960's and 1990's were then determined by image calculation. A 500-m buffer zone was created along edges of: 1) treed grassland, open forest and closed forest, 2) open forest and closed forest, and 3) closed forest to determine the effect of vegetation edge on the increase of treed grassland, open forest, and closed forest. This was done by first identifying the contact zone (forest edge) between related vegetation types, then calculating the distance from the edge and reclassifying the image to keep pixels within 500 m from the edge. Isolated vegetation layers, including each vegetation type in the 1960's and 1990's, the increased area, the decreased area, and the increased area within the 500-m buffer zone, were overlaid with images of aspect, slope and elevation. The total area of each vegetation type within each level of the 3 factors was calculated by counting pixels (10 x 10 m) for each site and converting them into hectares.

A probability index (P-value) was developed to test the effect of aspect, slope, and elevation on vegetation distribution, dynamics, and forest expansion. The P-value was calculated as the ratio between the distribution area or changed area and the total available area for each vegetation type within each level of aspect, slope or elevation for each site. It is a relative measure with the value of 1 representing average probability. For example, the total area of Bald Mountain was 10,071 ha and 490 ha of which (or 4.9%) had south facing aspect. There were 2844.4 ha of open grasslands in Bald Mountain and 251.8 ha of which (or 8.9%) was distributed on south facing aspect. On average, only 4.9% of open grassland would be expected on south facing aspect if it is equally distributed on all aspects (P = 1). In fact, a greater percentage of open grassland was found on the south facing aspect than the average and the actual probability of distribution of open grassland on the south facing aspect would be 8.9%/4.9% = 1.82.

Statistical analysis

Because of the limitation of original data resolution, small polygons were ignored in the analysis by removing vegetation types with less than 25 ha in total area and with a base area smaller than 100 ha per site. P-values ≥ 5 were treated as missing data because they were mostly caused by small areas and can result in misinterpretation of the analysis. Aspen, wetland, water, shrubland, riparian land and riparian-saline land were not analyzed because of their small areas. The distribution of open grassland, treed grassland, open forest and closed forest in the 1960's and 1990's and the area change during this period were analyzed. Forest expansion from forest edges during the same period was based on the analysis of the increased area of treed grassland, open forest and closed forest. Because logging has disturbed the "natural" vegetation pattern and the probability of vegetation change, the logged area immediately prior to 1960's and 1990's was assumed to be closed forest for each period. The probability data

Table 1. Vegetation distribution (ha) at all sites in 1960's and 1990's according to aspect.

	Vegetation type				
Year/aspect	OG	TG	OF	CF	LG
	(ha)				
1960's					
N (including NE)	1510	359	310	3458	870
E (including SE)	2442	496	326	2608	290
S (including SW)	2745	381	455	1182	154
W (including NW)	1693	239	184	1404	371
Flat	9855	773	535	10211	922
Total	18245	2249	1809	18863	2607
1990's					
N (including NE)	1023	275	183	4348	602
E (including SE)	1740	643	317	3068	381
S (including SW)	1984	587	515	1483	315
W (including NW)	1300	249	258	1788	327
Flat	6598	1388	647	8525	4948
Total	12646	3141	1920	19213	6573

OG = open grassland; TG = treed grassland; OF = open forest; CF = closed forest; LG = recently logged.

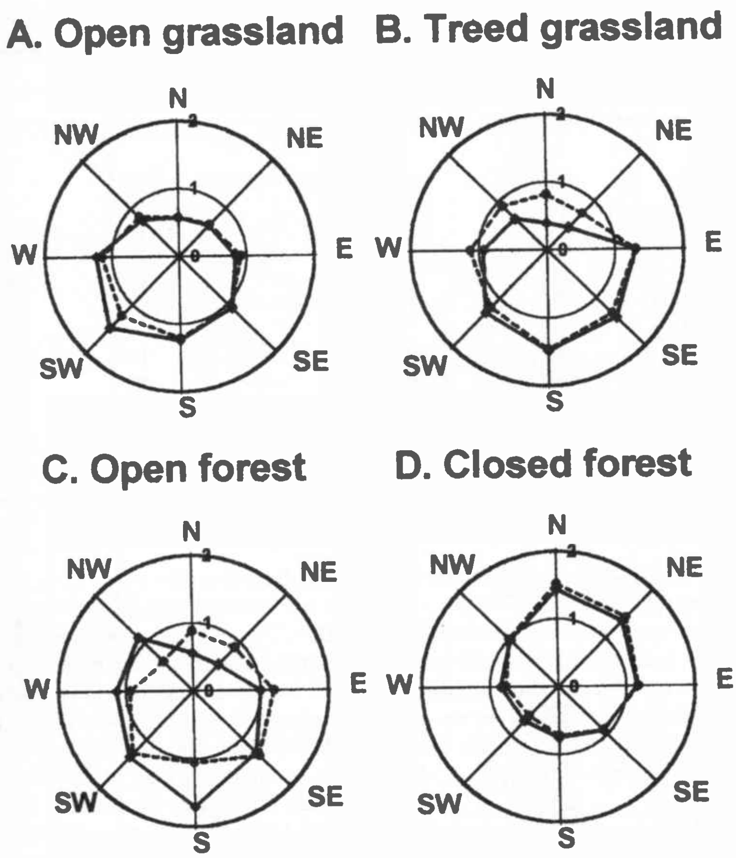

Fig. 2. The probability of vegetation distribution in 1960's (dashed line) and 1990's (solid line) according to aspect for open grassland, treed grassland, open forest, and closed forest. The numbers indicate probability values of distribution among aspects.

were first tested for normal distribution using Proc UNIVARIATE in SAS (Version 8.02, SAS Institute Inc., Cary, N.C., USA) in the context of General Linear Model (GLM) or regression analysis. Data points with standardized residuals greater than 3 were considered outliers and treated as missing data. Data were then analyzed with GLM using 8 sites as replications and means were separated using the least significant difference (LSD). Significant effect ($P \leq 0.05$) for elevation-related data was further analyzed with regression analysis and the best-fit regression equations were selected.

Results

Vegetation distribution by aspect

In both the 1960's and 1990's, over 50% of open grasslands were on flat terrain (Table 1). Open grassland, treed grassland and open forest tended to occur more on east to west aspects than other aspects. Closed forest occurred more on north, northeast and east aspects than other aspects for both periods. There was less closed forest on the flat in the 1990's than in 1960's. The area of both treed grassland and open forest increased on flat from 1960's to 1990's, occupying more east-facing aspects. Logging before 1960's was concentrated on north, northeast and northwest aspects but shifted mostly to flat areas by the 1990's. Total logged area immediately prior to the 1990s was 3-times that of the 1960's. Open grassland had higher probability of distribution on southeast, south, southwest, west aspects and flat terrain than northwest, north, northeast and east aspects in both 1960's and 1990's ($P < 0.001$, Fig. 2A). On the other hand, closed forest was more likely to be distributed on the north, northeast and east aspects than others including flat terrain ($P < 0.001$, Fig. 2D). The optimal aspects for treed grassland and open forest ranged clockwise from east to southwest in 1990's ($P < 0.001$, Fig. 2D, 2C) but aspect did not affect their distribution in 1960's ($P > 0.05$).

Vegetation distribution by slope

More than 50% of open grassland and 40% of closed forest occurred on the flat terrain and their distribution decreased with increasing slope degree in both the 1960's and 1990's (Table 2). Over 30% of treed grassland and open forest were on the flat terrain and were relatively evenly distributed among slopes, except for treed grassland in the 1990's. The distribution probability of grassland decreased with increasing slope in both 1960's and 1990's ($P < 0.001$, Fig. 3). Conversely, the distribution probability of treed grassland increased with increasing slope degree in 1960's ($P < 0.001$), but was not affected by slope in 1990's ($P > 0.05$). Open forest had higher probability on slopes $\geq 10°$ than those $< 10°$ in 1960's ($P = 0.003$), and was not affected by slope in 1990's ($P > 0.05$). Closed forest had higher probability of distribution on slopes between 5 and 20°than flat terrain or slopes $\geq 20°$ in 1960's and 1990's ($P = 0.047$ and < 0.001, respectively).

Table 2. Vegetation distribution at all sites in 1960's and 1990's according to slope.

Year/aspect	OG	TG	OF	CF	LG
	Vegetation type				
	(ha)				
1960's					
N (including NE)	1510	359	310	3458	870
0–5° (flat)	9855	773	535	10211	922
5–10°	4569	531	322	4659	1249
10–20°	2517	471	491	2799	409
≥ 20°	1303	473	460	1194	26
Total	18245	2249	1809	18863	2607
1990's					
0–5° (flat)	6598	1388	647	8525	494
5–10°	3143	828	451	5714	1164
10–20°	1862	526	451	3448	379
≥ 20°	1043	398	371	1526	81
Total	12646	3141	1920	19213	6573

OG = open grassland; TG = treed grassland; OF = open forest; CF = closed forest; LG = recently logged.

Vegetation distribution by elevation

The elevation of the study area is between 300 and 1,600 m and the majority of vegetation distributed between 800 and 1,200 m (data not shown). The distribution probabilities of open grassland and open forest were not correlated with elevation in either the 1960's or the 1990's possibly due to variations among sites, even though they seem to be higher at mid-elevation than at lower or higher elevation. Treed grassland had optimal distribution range between 700 and 1,000 m ($P = 0.008$ and 0.037 for 1960's and 1990's, respectively), whereas the distribution probability of closed forest increased linearly with increasing elevation ($P = 0.002$ and <0.001 for 1960's and 1990's, respectively).

Table 3. Vegetation change at all sites between 1960's and 1990's according to slope aspect.

Change/aspect	Vegetation type				
	OG	TG	OF	CF	LG
	(ha)				
Increased					
N (including NE)	153	213	149	1560	563
E (including SE)	246	477	257	998	373
S (including SW)	220	503	357	681	315
W (including NW)	171	222	205	791	317
Flat	550	1318	610	3015	4873
Total	1340	2733	1578	7044	6441
Decreased					
N (including NE)	641	296	276	670	830
E (including SE)	948	331	266	538	282
S (including SW)	980	298	298	380	154
W (including NW)	563	212	130	407	361
Flat	3807	702	499	4701	847
Total	6939	1840	1468	6694	2475

OG = open grassland; TG = treed grassland; OF = open forest; CF = closed forest; LG = recently logged.

Vegetation change by aspect

Vegetation change from1960's to 1990's was observed in all 4 vegetation types (Table 3). There was a net loss (31%) in open grassland area, with the decreased area being 5-fold greater than the increased area. The gain in treed grassland, open forest and closed forest exceeded the loss by approximately 13%. Over 70% of decrease in closed forest occurred on the flat terrain. Logging is the major cause for the decrease in closed forest area.

The probability of area increase from 1960's to 1990's was significantly affected by aspect in treed grassland, open forest, and closed forest ($P < 0.001$), but not in open grassland ($P > 0.05$, Fig. 4). The probability for open grassland to increase was not significantly affected by aspect, possibly due to large variations among sites. East, southeast, south, southwest aspects had higher probability for treed grassland to increase than northwest, north and northeast aspects, with west aspect and flat being intermediate. Southeast, south, southwest, and west aspects had higher probability for open forest to increase than northwest, north and northeast aspects and flat terrains, with east aspect being intermediate. Northwest, north, and northeast aspects had higher probability for closed forest to increase than east, southeast, south, southwest and west aspects, with flat terrains being intermediate.

The probability of area decrease was significantly affected by aspect in open grassland ($P < 0.001$), treed grassland ($P = 0.043$) and closed forest ($P = 0.013$), but not in open forest ($P > 0.05$). For open grassland reduction, aspects from east to southwest and flat had higher probability than north and northeast aspects; west and northwest aspects were intermediate. Treed grassland decreased more on southeast and south aspects than northwest, north, northeast aspects and flat, with east, southwest and west aspects being intermediate. Closed forest decreased more on northeast, north and northeast aspects than east through west aspects and flat.

Vegetation change by slope

Area changes in all vegetation types were concentrated on flat or near flat slopes (< 10°) (Table 4). The increased area of grassland was relatively even among slopes with various steepness, but the decreased area was far more prevalent on the less steep slopes. Increased area of treed grassland occurred more on flat or near flat slopes (< 10°). Decreased area of closed forest was most common on flat and near flat slopes.

Increases in open grassland were not related to slope steepness ($P > 0.05$), but the probability for open grassland to decrease lessened with increasing slope ($P < 0.001$, Fig. 5). The probability for treed grassland to increase decreased as slope degree increased ($P = 0.015$) whereas the opposite trend was observed for open forest ($P < 0.001$). The probability for closed forest to increase was higher on slopes between 0 and 10° than that ≥ 10° ($P = 0.014$). Decreases in closed forest were not significantly affected by slope ($P > 0.05$), but the probability of decreases in treed grassland and open forest was higher on slopes ≥ 10° than those between 0 and 10° ($P < 0.001$ and $= 0.044$, respectively).

Table 4. Vegetation change at all sites between 1960's and 1990's according to slope.

Change/aspect	Vegetation type				
	OG	TG	OF	CF	LG
	(ha)				
Increased					
0–5° (flat)	550	1318	610	3015	4873
5–10°	322	757	400	2324	1117
10–20°	266	427	331	1153	371
≥ 20°	201	231	237	553	80
Total	1340	2733	1578	7044	6441
Decreased					
0–5° (flat)	3807	702	499	4701	847
5–10°	1749	460	272	1268	1201
10–20°	921	372	371	504	401
≥ 20°	462	306	327	222	25
Total	6939	1840	1468	6694	2475

OG = open grassland; TG = treed grassland; OF = open forest; CF = closed forest; LG = recently logged.

Vegetation change by elevation

Most changes (both increased and decreased areas) were found at mid-elevation between 800 and 1,200 m for all vegetation types (data not shown), corresponding to the distribution patterns of vegetation. The decreased area was not

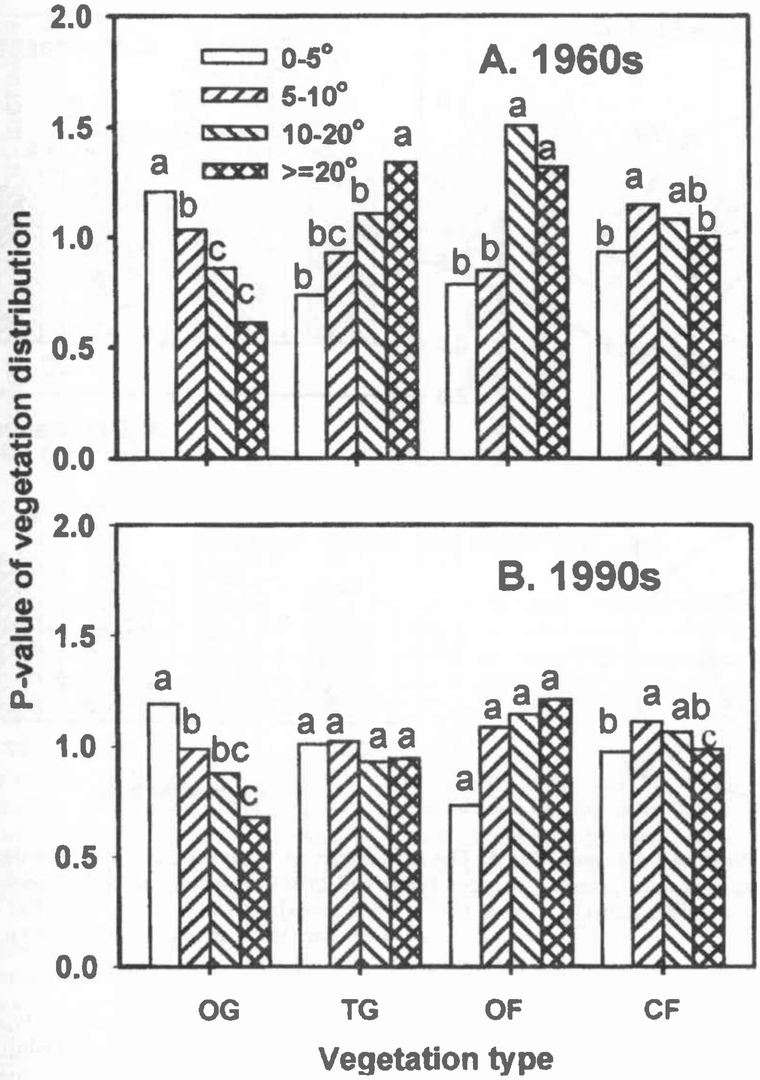

Fig. 3. The probability of vegetation distribution in 1960's and 1990's according to slope for open grassland (OG), treed grassland (TG), open forest (OF), and closed forest (CF). Bars with the same letters within a group are not significantly different at P ≤ 0.05.

significantly affected by elevation in any vegetation types. Increases in vegetation were not affected by elevation for treed grassland and closed forest. Elevation only affected the probability of increases in open grassland (P = 0.013) and open forest (P = 0.030, Fig. 6). Increases in open grassland were less likely with increasing elevation, while increases in open forest were highest at mid-elevation between 700 and 1,000 m.

Probability of tree expansion by aspect within the buffer zone

Tree expansion from the edge, either as the result of encroachment or ingrowth, occurred more on flat terrain than on all aspects (Table 5). Treed grassland and open forest expanded more on aspects from east to southwest than others, while closed forest expanded more on aspects from northeast to south. The probability of tree expansion from the forest edge, however, was only significantly affected by aspect for closed forest (P = 0.002, Fig. 7). For closed forest, the probability of expansion from the forest edge was higher on northwest, north and northeast aspects than aspects from southeast to northwest including flat with east aspect being intermediate.

Probability of tree expansion by slope within the buffer zone

Areas of tree expansion from the edge decreased with increasing slope, but the buffer area also decreased with increasing slope (Table 6). The probability for treed grassland to expand from the edge of treed grassland, open forest and closed forest within the buffer zone was higher at slopes between 0 and 20° than > 20° (P = 0.011, Fig. 8). The expansion of open forest was highest at slopes ≥ 10°, lowest at slopes between 0 and 5°, and intermediate at slopes between 5 and 10° (P = 0.001). Closed forest expansion was not significantly affected by slope (P > 0.05).

Probability of tree expansion by elevation within the buffer zone

Areas for tree expansion from its edge were found mostly at mid-elevation between 800 and 1,200 m, the range at which most of the buffer areas were found (data not shown). The probability for forest expansion from its edge increased linearly with increasing elevation for closed forest (Fig. 9) but was no correlation was found between other vegetation types and elevation.

Discussion

Fire suppression has been practiced as a management tool in B.C. forests for over 60 years (Gayton 1996). It is the main cause for tree encroachment and forest

Table 5. Forest expansion at all sites from 1960's to 1990's within a 500 m buffer zone from the forest edge according to aspect.

	Vegetation type					
	TG		OF		CF	
Aspect	Buffer	Increased	Buffer	Increased	Buffer	Increased
	(ha)					
N (including NE)	1644	162	1851	105	1987	694
E (including SE)	2455	380	2665	180	2842	740
S (including SW)	2682	399	2853	274	3120	649
W (including NW)	1642	162	1746	146	1798	482
Flat	9170	1070	9720	403	10105	3054
Total	17594	2173	18835	1111	19852	5619

TG = treed grassland; OF = open forest; CF = closed forest.

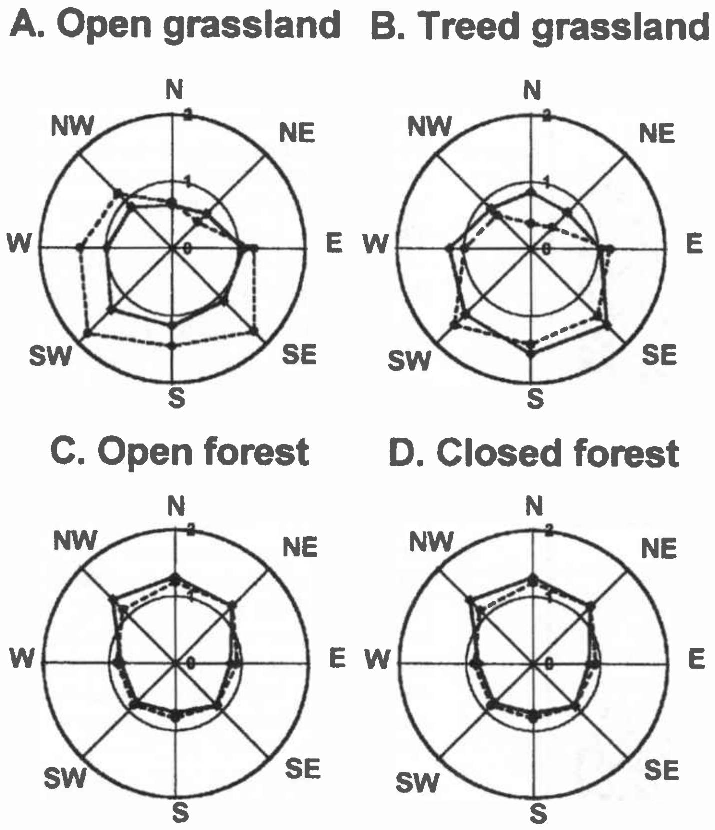

Fig. 4. The probability of vegetation increase (dashed line) and decrease (solid line) between 1960's and 1990's according to aspect for open grassland, treed grassland, open forest, and closed forest. The numbers indicate probability values of vegetation change among aspects.

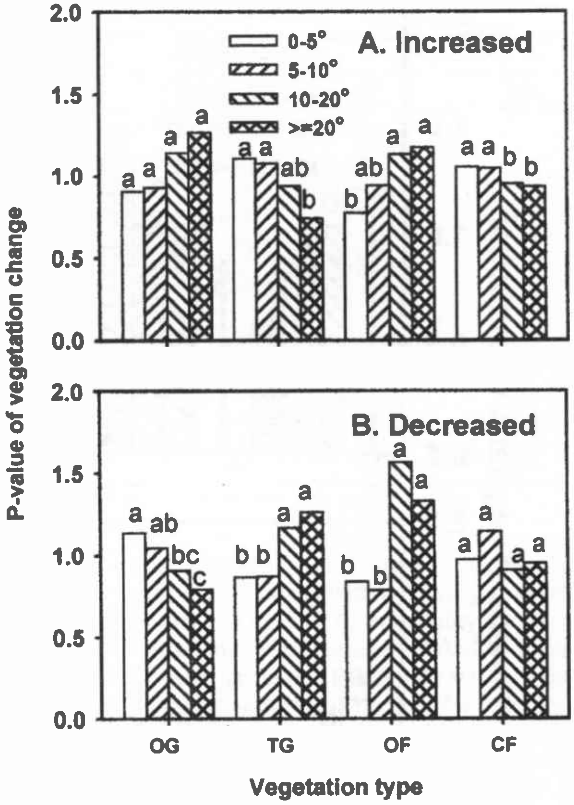

Fig. 5. The probability of vegetation increase and decrease between 1960's and 1990's according to slope for open grassland (OG), treed grassland (TG), open forest (OF), and closed forest (CF). Bars with the same letters within a group are not significantly different at P ≤ 0.05.

ingrowth in the grassland-forest ecotone (Tisdale 1950, Parminter 1978, Strang and Parminter 1980) and may have modified the realized niche of tree species such as Douglas-fir, ponderosa pine (*Pinus ponderosa* Dougl.) and lodgepole pine. This change is demonstrated by the different vegetation distribution patterns in 1960's and 1990's. Both aspect and slope modify the solar energy received and water balance whereas elevation controls air temperature and moisture, thus creating micro-environments and affecting vegetation distribution (Raven et al. 1981). Results from the current study indicate that among these topographic factors, aspect is the main determining factor for vegetation distribution in the study area. Open grassland had the highest probability of occupying drier and warmer south to west aspects, while closed forest had the highest probability of occupying north to east aspects. It is generally agreed that water balance is the primary determinant of terrestrial vegetation distribution (Woodward 1987, Eamus and Jarvis 1989, Stephenson 1990, Neilson et al. 1992) and the moisture limitation on the south to west facing aspect favors grassland more than forest. It has been reported that tree seedling survival varies among aspects, for example, higher mortality of Garry oaks (*Quercus garryana* Dougl. ex Hook.) on south-facing slopes of British Columbia has been reported (Fuchs et al. 2000).

Vegetation changes, both as increases and decreases in area, were observed for all vegetation types. Interestingly, aspects that are correlated with high probability for increase in certain vegetation types are also correlated with high probability for decrease in the same vegetation types. For example, closed forest exhibited greater changes on moist, cool aspects than dry, warm aspects. The aspect-specific increases of woody species has been previously reported in African sour grasslands after the exclusion of fires, reflecting water availability (Titshall 2000) and in the tallgrass prairie (Bragg and Hulbert 1976). In the tall prairie, woody plants increased more than 40% on deeper and more per-

Table 6. Forest expansion at all sites from 1960's to 1990's within a 500 m buffer zone from the forest edge according to slope.

	Vegetation type					
	TG		OF		CF	
Aspect	Buffer	Increased	Buffer	Increased	Buffer	Increased
	(ha)					
0–5° (flat)	9170	1070	9720	403	10105	3054
5–10°	4279	631	4551	297	4716	1308
10–20°	2535	329	2750	249	3069	795
> = 20°	1611	143	1814	161	1963	462
Total	17594	2173	18835	1111	19852	5619

TG = treed grassland; OF = open forest; CF = closed forest.

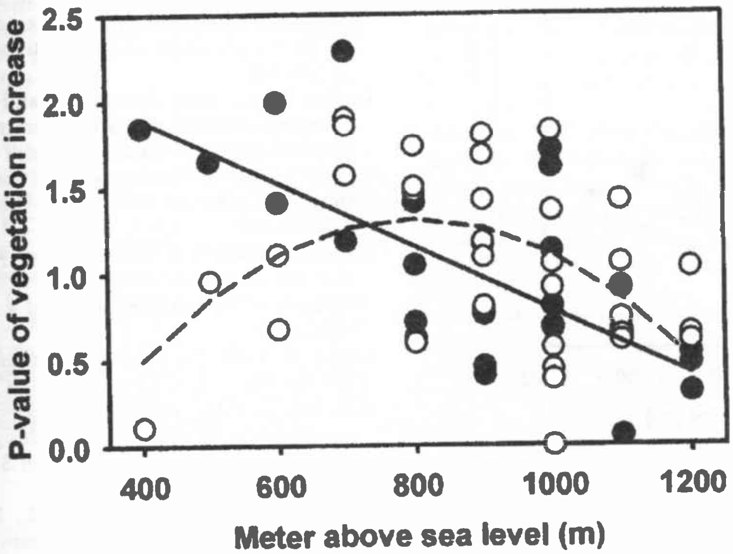

Fig. 6. The probability of vegetation increase between 1960's and 1990's according to elevation for open grassland (solid circle and line) and open forest (empty circle and dashed line). Regression lines represent the best-fit equations for vegetation types with significant elevation effect in GLM: Open grassland: $Y = 2.6339-0.001849X$, $R^2_{adj} = 42.5\%$, $P < 0.001$; Open forest: $Y = -1.9364 + 0.0081X-0.000005X^2$, $R^2_{adj} = 19.4\%$, $P = 0.015$.

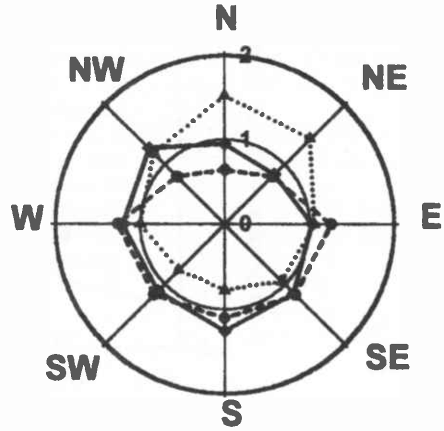

Fig. 7. The probability of tree expansion from 1960's to 1990's according to aspect within a 500 m buffer zone from the edge of treed grassland (dashed line), open forest (solid line) and closed forest (dotted line). The numbers indicate probability values of tree expansion among aspects.

meable middle- and lower-slope soils, but only slightly on shallow, droughty clay loam soils located on level uplands, ridgetops and upper slopes from 1937 to 1969 (Bragg and Hulbert 1976). As for the effect of slope, our results indicate that open grassland on less steep slopes is more susceptible to tree encroachment than those on steeper slopes. Treed grassland had higher probability to expand on less steep slopes than more steep slopes, but open forest had higher probability to expand on steeper slopes. The probability for closed forest to expand decreased with increasing elevation.

Douglas-fir and lodgepole pine, the 2 main tree species in the study areas, rely on seeds for regeneration. The successful invasion of forest into grasslands depends first on good years for seed crops because few seeds of these species survived more than a year in the field (Bai, Thompson and Broersma, unpublished data). It also depends on seed dispersal from parent trees, which is a distance-related process (Kondo and Tsuyuzaki 1999, Endress and Chinea 2001) and seedbeds that favor seed germination and seedling establishment (Bai et al. 2000a). Different expansion patterns of forest reported in the current study indicate that the availability of favorable conditions for the successful invasion of trees into the grasslands vary according to topographic factors. For examples, the probability for closed forest to expand from its edge was higher on the northwest, north, and northeast aspects than others. On the other hand, in treed grassland and open forest, tree expansion from their edges were not significantly affected by aspect, indicating that other factors such as random trees other than the edge had an overwhelming influence.

If environmental or management conditions change in ways favoring one of the adjacent ecosystems in the ecotone, its patch size is likely to increase in this system and it is likely to invade habitats previously unsuitable in the adjacent system (Risser 1995). Management practices, such as timber harvesting and fire suppression, are considered important for the grassland and forest dynamics in the study area, but climatic variability between 1960's and 1990's was not addressed. However, weather records from a nearby station at Big Creek (1893-1978, recorded by Environment Canada) indicate that there were 8 periods with 2 or more consequent years of above average precipitation. These wetter then average years interspersed with drier periods tend to correlate with successful establishment of tree

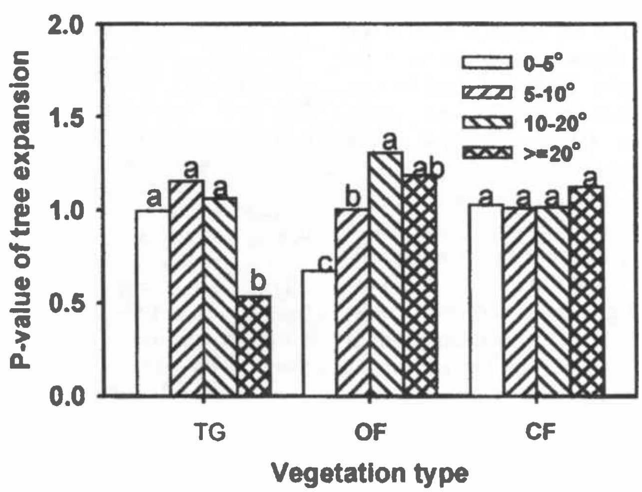

Fig. 8. The probability of tree expansion from 1960's to 1990's according to slope within a 500 m buffer zone from the edge of treed grassland (TG), open forest (OF), and closed forest (CF). Bars with the same letters within a group are not significantly different at $P \leq 0.05$.

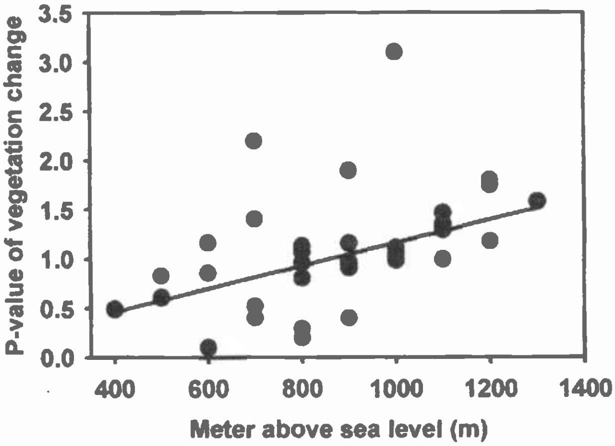

Fig. 9. The probability of tree expansion at all sites from 1960's to 1990's according to elevation within a 500 m buffer zone from the edge of closed forest. Regression line represents the best-fit equation: Y=-0.0093-0.00117X, R^2_{adj} = 44.1%, P < 0.001.

seedlings (Arno and Gruell 1983). Increasing temperature and evapotranspiration under the global change scenario may result in grasslands eventually replace the adjacent forests in the interior of B.C.

Summary and Conclusions

The transitional zone between vegetation types, or ecotone, is where most changes in forest cover have occurred. Aspect is the most important topographic factor for vegetation distribution and changes. Open grasslands were most probable on drier and warmer south to west aspects while closed forests were most common on cooler and moister north and east aspects. The distribution of open grasslands was equally probable along the elevation gradient on suitable aspects but that of closed forests was more likely at higher elevations. Different distribution patterns between the 1960's and 1990's were observed. Changes in tree cover classes were related to their distribution range with the greatest change occurring at mid-elevations. Closed forest had a probability of expansion that was significantly greater for northwest to northeast aspects. Treed grassland and open forest were more likely to expand on gradual than on steep slopes. The probability of forest expansion increased with increasing elevation. Therefore, management plans aiming at the control of tree encroachment and forest ingrowth can take these topographic factors into consideration by focusing on areas with topographic features favoring tree encroachment.

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