

5238

Reprinted from

Forest Ecology and Management

Forest Ecology and Management 121 (1999) 215–225

Dendroecological studies of tree growth, climate and spruce beetle outbreaks in Central British Columbia, Canada

Qibin Zhang^{a,*}, René I. Alfaro^b, Richard J. Hebda^c

^a*School of Earth and Ocean Sciences, University of Victoria, Victoria B.C., V8W 3P6, Canada and Royal British Columbia Museum, Victoria, B.C., V8W 9W2, Canada*

^b*Canadian Forest Service, Pacific Forestry Center, Victoria B.C., V8Z 1M5, Canada*

^c*Royal British Columbia Museum, Victoria, B.C., Canada V8W 9W2, and Biology and School of Earth and Ocean Sciences, University of Victoria, Victoria B.C., V8W 3P6, Canada*

Received 10 January 1998; accepted 14 December 1998



Forest Ecology and Management

Aims and scope. *Forest Ecology and Management* publishes scientific articles concerned with forest management and conservation, and in particular the application of biological, ecological and social knowledge to the management of man-made and natural forests. The scope of the journal includes all forest ecosystems of the world. A refereeing process ensures the quality and international interest of the manuscripts accepted for publication. The journal aims to encourage communication between scientists in disparate fields who share a common interest in ecology and natural-resource management, and to bridge the gap between research workers and forest managers in the field to the benefit of both. The journal should be of interest to research workers, managers and policy makers in forestry, natural resources, ecological conservation and related fields.

FOUNDING EDITOR

Laurence L. Roche, Murroe, Ireland

EDITORS-IN-CHIEF

For the Americas, Australia, New Zealand and the Pacific:

R.F. Fisher

Department of Forest Science

Texas A&M University

College Station, TX 77843-2135, USA

For the rest of the world:

G.M.J. Mohren

Forest Production Ecology Group

Department of Vegetation Ecology

DLO-Institute for Forestry and Nature Research

P.O. Box 23

6700 AA Wageningen, The Netherlands

BOOK REVIEWS EDITOR

Margaret R. Gale

School of Forestry and Wood Products

Michigan Technological University

1400 Townsend Drive

Houghton, MI 49931, USA

EDITORIAL ADVISORY BOARD

G. Abrahamsen, Agricultural University of Norway, Ås, Norway

R. Alfaro, Canadian Forestry Service, Victoria, B.C., Canada

F. Andersson, Swedish University of Agricultural Sciences, Uppsala, Sweden

P.M.S. Ashton, Yale University, New Haven, USA

P. Attiwill, University of Melbourne, Parkville, Vic., Australia

J. Boyle, Oregon State University, Corvallis, USA

S. Brown, US Environmental Protection Agency, Corvallis, USA

J.C. Calvo, Institute of Technology, Cartago, Costa Rica

R.-J. Chen, University of Hong Kong, Pokfulan Road, Hong Kong

J.D. Deans, Institute of Terrestrial Ecology, Penicuik, Midlothian, UK

R.M. DeGraaf, USDA Forest Service, University of Massachusetts, Amherst, MA, USA

S. Diamandis, Forest Research Institute, Thessaloniki, Greece

D.P. Dykstra, President, World Forestry Centre, 4033 SW Canyon Road, Portland, OR 97221 USA

E.P. Farrell, University College Dublin, Dublin, Ireland

P.M. Fearnside, Instituto Nacional de Pesquisas da Amazonia-INPA, Manaus-Amazonas, Brazil

P.H. Freer-Smith, Forestry Commission, Farnham, UK

S.T. Friedman, Vegetation Management and Protection Research, Washington DC, USA

O. Garcia, ENGREF, Nancy, France

D.W. Gilmore, University of Minnesota, North Central Experiment Station, 1861 Highway 169 East, Grand Rapids, MN 55744, USA

R.A. Goyer, Louisiana State University, Baton Rouge, LA, USA

J.B. Hall, University College of North Wales, Bangor, UK

F. Houllier, Campus International de Baillarguet, Laboratoire

Associe de Modelisation des Plantes (AMAP), Montpellier, France

B.M. Kumar, Kerala Agricultural University, Kerala, India

J.P. Lassoie, Cornell University, Ithaca, NY, USA

J.N. Long, Utah State University, Logan, UT, USA

A.E. Lugo, International Institute of Tropical Forestry, Rio Piedras, PR, USA

J.A. Maghembe, SADCC/ICRAF Agroforestry Project, Zomba, Malawi

F. Makeschin, Institut für Bodenkunde und Standortslehre, Tharandt, Germany

D.C. Malcolm, University of Edinburgh, Edingburgh, UK

E. Mälikönen, Finnish Forest Research Institute, Vantaa, Finland

M.A.R. Nahuz, Instituto de Pesquisas Tecnológicas,

São Paulo, SP, Brazil

R. Päivinen, European Forestry Institute, Joensuu, Finland

S.G. Pallardy, University of Missouri, Columbia, MO, USA

R.F. Powers, Pacific Southwest Research Station, Redding, CA, USA

T. Pukkala, University of Joensuu, Joensuu, Finland

F.E. Putz, University of Florida, Gainesville, FL, USA

L. Rasmussen, RISØ, Roskilde, Denmark

D.D. Reed, Michigan Technological University, Houghton, MI, USA

R. Sands, University of Canterbury, Christchurch, NZ

J.A. Stanturf, Stoneville, MS, USA

J.R. Toliver, USDA Forest Service, Washington, DC, USA

K. von Weissenberg, University of Helsinki, Helsinki, Finland

D. Whitehead, Manaaki Whenua Landcare Research, Lincoln, New Zealand

Publication information: *Forest Ecology and Management* (ISSN 0378-1127). For 1999 volume(s) 111-122 are scheduled for publication. Subscription prices are available upon request from the Publisher or from the Regional Sales Office nearest you or from this journal's website (<http://www.elsevier.nl/locate/foreco>). Further information is available on this journal and other Elsevier Science products through Elsevier's website: (<http://www.elsevier.nl>). Subscriptions are accepted on a prepaid basis only and are entered on a calendar year basis. Issues are sent by standard mail (surface within Europe, air delivery outside Europe). Priority rates are available upon request. Claims for missing issues should be made within six months of the date of dispatch.

Orders, claims, and product enquiries: please contact the Customer Support Department at the Regional Sales Office nearest you:

New York: Elsevier Science, PO Box 945, New York, NY 10159-0945, USA; Tel. (+1) (212) 633 3730, [toll free number for North American customers: 1-888-4ES-INFO (437-4636)]; fax: (+1) (212) 633 3680; e-mail usinfo-f@elsevier.com

Amsterdam: Elsevier Science, PO Box 211, 1000 AE Amsterdam, The Netherlands; Tel.: (+31) 20 485-3757; fax: (+31) 20 485 3432; e-mail nlinfo-f@elsevier.nl

Tokyo: Elsevier Science, 9-15, Higashi-Azabu 1-chome, Minato-ku, Tokyo 106-0044, Japan; Tel. (+81) (3) 5561 5033; fax (+81) (3) 5561 5047; e-mail: info@elsevier.co.jp

Singapore: Elsevier Science, No. 1 Temasek Avenue, #17-01 Millenia Tower, Singapore 039192; Tel. (+65) 434 3727; fax: (+65) 337 2230; e-mail: asiainfo@elsevier.com.sg

Rio de Janeiro: Elsevier Science, Rua Sete de Setembro 111/16 Andar, 20050-002 Centro, Rio de Janeiro - RJ, Brazil; phone: (+55) (21) 509 5340; fax: (+55) (21) 507 1991; e-mail: elsevier@campus.com.br [Note (Latin America): for orders, claims and help desk information, please contact the Regional Sales Office in New York as listed above]



ELSEVIER

Forest Ecology and Management 121 (1999) 215–225

Forest Ecology
and
Management

Dendroecological studies of tree growth, climate and spruce beetle outbreaks in Central British Columbia, Canada

Qibin Zhang^{a,*}, René I. Alfaro^b, Richard J. Hebda^c

^a*School of Earth and Ocean Sciences, University of Victoria, Victoria B.C., V8W 3P6, Canada and Royal British Columbia Museum, Victoria, B.C., V8W 9W2, Canada*

^b*Canadian Forest Service, Pacific Forestry Center, Victoria B.C., V8Z 1M5, Canada*

^c*Royal British Columbia Museum, Victoria, B.C., Canada V8W 9W2, and Biology and School of Earth and Ocean Sciences, University of Victoria, Victoria B.C., V8W 3P6, Canada*

Received 10 January 1998; accepted 14 December 1998

Abstract

Dendroecological techniques were used in this study to compare the radial growth patterns of different conifer species and to identify regional climatic anomalies and spruce beetle (*Dendroctonus rufipennis* Kirby) outbreaks for the past four centuries in the McGregor Model Forest, central British Columbia, Canada. Tree-ring chronologies of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and interior spruce (*Picea engelmannii* Parry × *P. glauca* (Moench) Voss) were developed for the Model Forest. Response function analysis showed that (1) Douglas-fir is the most climate sensitive species, and its radial growth is mainly controlled by spring precipitation and early summer temperature, and (2) the ring growth of subalpine fir and spruce is negatively affected by high summer temperature. Comparisons of the tree-ring chronologies among the three species revealed dynamics of growth releases and suppressions which reflected climate variations and forest disturbance patterns in the past several centuries. The climate during the late 1750s–1800s was characterized by slightly moist springs and probably moderate summers. During the late 1860s and early 1870s, the region experienced dry springs, hot summers, and probably cold late falls. This study identified three intervals of major disturbances attributable to severe spruce beetle outbreaks: the late 1720s, 1810s–1820s, and 1960s–early 1980s. These coincided with periods of above average growth in Douglas-fir. The association suggested a possible moist spring-outbreak pattern. The multicentury tree-ring records of climate anomalies and spruce beetle outbreaks could provide insight into the dynamics of forest growth and its response to environmental changes. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Dendroecology; Forest disturbance; Spruce beetle outbreak; Climate change

1. Introduction

The growth dynamics of forest ecosystems is affected by a complex of environmental factors which

include climate, insect infestations, fire, competition among trees, soil characteristics, and others. Trees respond to these influences with corresponding changes in their annual growth rings. Therefore, a record of past influences on growth is retained in tree-rings and can be unraveled through dendroecological techniques (Fritts and Swetnam, 1989).

*Corresponding author. Tel.: +1-250-360-1874; fax: +1-250-721-6200; e-mail: qzhang1@uvic.ca

The radial growth responses of trees to climate have been extensively studied for climate sensitive species in North America. The ring growth of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) on southern Vancouver Island of British Columbia is sensitive to spring and early summer precipitation (Zhang, 1996). Dendrochronological studies of white spruce (*Picea glauca* (Moench) Voss), Engelmann spruce (*P. engelmannii* Parry), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in boreal forests of northwestern Canada and in Canadian Rockies show that the growth rings of these species are affected by summer temperature (D'Arrigo et al., 1992; Szeicz and MacDonald, 1995; Luckman et al., 1997). Insect infestations play a key role in modifying forest structure, and severe outbreaks can cause tree mortality, reduction of growth rates, reduced lumber quality, and proliferation of the understory (Veblen et al., 1991b; Alfaro and Maclauchlan, 1992). Major infestations and their effects on tree growth can be inferred by comparing tree-ring chronologies from host and non-host species (Swetnam et al., 1985; Heath and Alfaro, 1990; Alfaro and Shepherd, 1991; Veblen et al., 1991b; Weber and Schweingruber, 1995). A relationship between insect infestation and increased spring precipitation has been reported from long-term reconstruction of outbreaks and climate in northern New Mexico (Swetnam and Lynch, 1993).

Forest ecosystems of central British Columbia are sensitive to climate variations, yet there is insufficient historical and modern climate and species response data to assess the nature of forest adjustments to climatic changes (Hebda, 1997). The spruce beetle (*Dendroctonus rufipennis* Kirby) is a severe disturbance factor in these forest ecosystems, causing widespread mortality in mature spruce stands. Three outbreaks occurred in the Prince George Forest Region between 1962 and 1982 during which spruce beetles killed an estimated $18 \times 10^6 \text{ m}^3$ of spruce in the region (Humphreys and Safranyik, 1993). Understanding long-term pattern of outbreaks is important for resource management. However, historical records of spruce beetle outbreaks in the region are scarce.

In this study we developed ring-width chronologies of interior spruce (*Picea engelmannii* Parry \times *P. glauca* (Moench) Voss), interior Douglas-fir (*Pseu-*

dotsuga menziesii var. *glauca* (Beissn.) Franco), and subalpine fir for the McGregor Model Forest, located in central British Columbia. Instrumental climate data were used to identify climate–growth relationships. Tree growth dynamics for the past several centuries were examined, and major climate anomalies and spruce beetle outbreaks were reconstructed and discussed.

2. Area description

This study was conducted within the McGregor Model Forest, a component of Canada's Model Forest Network, encompassing Northwood Pulp and Timber's Tree Farm License 30, northeast of the city of Prince George, in the central interior of British Columbia (Fig. 1). It occupies $\approx 165\,000$ ha of forests mostly within the Sub-Boreal Spruce (SBS) biogeoclimatic zone (Meidinger and Pojar, 1991).

The climate of the SBS zone is continental, characterized by long, cold winters and relatively short, warm and moist summers (Fig. 2). According to long-term climatic data (A.D. 1895–1992) from Fort St. James, ca. 100 km northwest of Prince George, mean annual temperature ranges from 0.4° to 4.9°C , with mean January temperature of -12.5°C and mean July temperature of 14.3°C . Mean annual precipitation ranges from 336.7 to 739.2 mm, with April receiving the lowest amount of precipitation.

The forest is dominated by interior spruce and subalpine fir, which are climate-perpetuated climax tree species for the SBS zone. Subalpine fir regenerates more readily than spruce under the canopy; however, it has shorter longevity due to its susceptibility to pathogenic fungi (Lindgren and Lewis, 1997). Douglas-fir is a shade intolerant and long-lived seral species in the SBS zone, occurring mainly on relatively dry and warm sites. Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), also a seral species in the SBS, pioneers extensive seral stands and is common in mature forests in the drier parts of the zone (Meidinger and Pojar, 1991).

Fire, insect attack, windthrow, and harvesting practices are the general disturbance regimes that affect forest renewal, structure, and composition. Wildfire is the dominant stand-replacing process in the SBS zone, creating a complex landscape spatial pattern with a

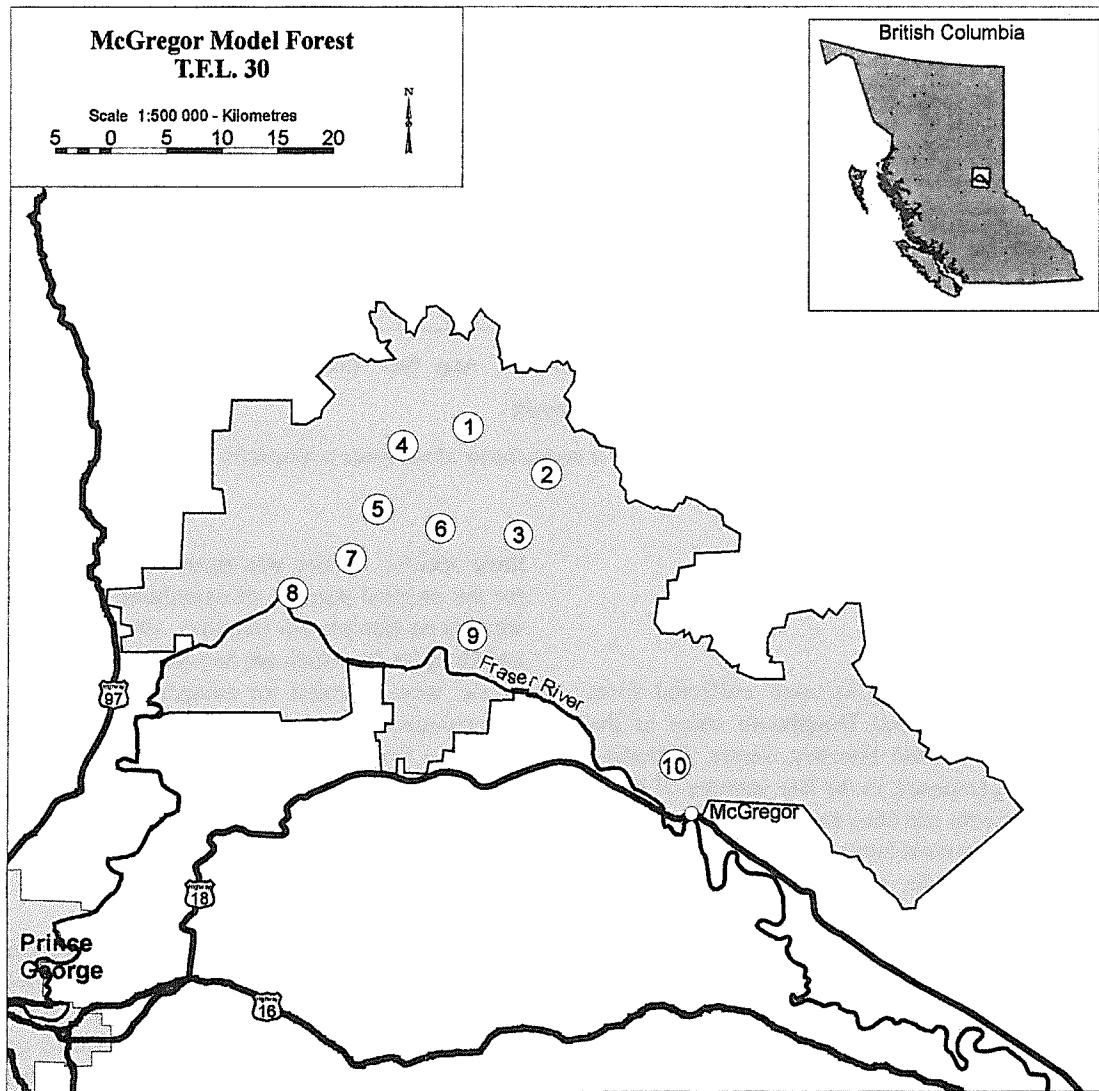


Fig. 1. Tree-ring sampling sites at the McGregor Model Forest, British Columbia.

large range in patch size and irregular disturbance boundaries (DeLong and Tanner, 1996). The average fire size for the zone ranges from 50 to 500 ha (Parminter, 1992), and the time required for fire to cycle through the zone is estimated to range from 200 to 700 years (B. Hawks, personal communication, Pacific Forestry Centre, Victoria, BC, Canada). Widespread disturbance by forest insect outbreaks is frequent and severe. The spruce beetle is the most damaging insect in the area, and can kill many mature

spruce during outbreaks (Erickson and Loranger, 1983). Other insects developing outbreaks in this region include tree defoliators, e.g. eastern spruce budworm (*Choristoneura fumiferana* Clements), and the white pine weevil (*Pissodes strobi* Peck) which destroys the apical shoots of young spruce. Spruce trees have shallow root systems, and are susceptible to windthrow (Coates et al., 1994). The area has sustained selective harvesting and clearcutting since the early 1900s (Erickson and Loranger, 1983).

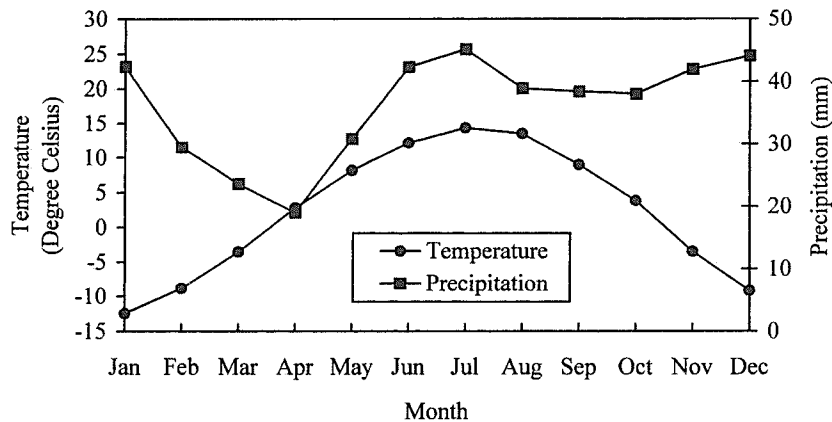


Fig. 2. Representative diagram of the climate for the SBS zone of the McGregor Model Forest (averaged for A.D. 1895–1992 using records from the weather station at Fort St. James, BC).

3. Methods

3.1. Field sampling

Increment cores and disks were collected from spruce, subalpine fir, and Douglas-fir trees in the Model Forest by Pacific Forestry Centre, Canadian Forest Service personnel, in the late summer of 1995. The cores (one core per tree) were extracted at breast height with an increment borer. The disks, 20 of spruce and two of Douglas-fir, were cut in 5 cm thickness from felled trees (at breast height) or stumps (at 50 cm above ground surface) in sites 4 to 8 and 10 (Fig. 1; Table 1). The two Douglas-fir disks, made available to us from a separate study at site 10, contained the oldest rings and were used in this study to maximize the length of tree-ring chronology. The sample stands were selected in areas that had not sustained logging, and were chosen to provide a reasonable representation of the Model Forest. The selected stands were dominated by spruce and contained a mixture of the

three species. Spruce was most extensively sampled for the original purpose of examining the impacts of weevils on tree growth (Kimoto, 1996). Subalpine fir and Douglas-fir, which are non-host species for spruce beetle, were sampled for comparison of the growth patterns among species. A total of 240 spruce trees, 26 subalpine fir, and 16 Douglas-fir trees from 10 sites were sampled and these were used in the tree-ring analysis (Fig. 1; Table 1).

3.2. Tree-ring chronology development

The core and disk samples were prepared and surfaced to enhance ring boundaries before measurement. Cores were mounted on grooved wooden boards and sanded by hand with a series of sandpaper grits up to 600. Disks were prepared using a sharp 17-mm wide carving gouge. Ring-width measurement was carried out using a Measu-Chron incremental measuring system (Micro-Measurement Technology, Bangor, Maine, USA) in the Tree-Ring Laboratory of the

Table 1

Number of increment core samples and disk samples (in brackets) collected at each site in the McGregor Model Forest, British Columbia during the late summer of 1995

Species	Site number										Total
	1	2	3	4	5	6	7	8	9	10	
Douglas-fir			2	1		7	2	1	1	(2)	16
Subalpine fir	5	4	2	7	1	1	1	5			26
Interior spruce	42	39	19	34	19(7)	17(7)	17(3)	13(3)	20		240

Pacific Forestry Centre. The precision of measurement was 0.01 mm.

The measured ring-sequences were plotted and the patterns of wide and narrow rings were cross-dated among trees. The cross-dating was aided by the presence of distinctive narrow rings and the quality of cross-dating was examined by the program COFECHA (Holmes, 1983). The age-related growth trend within each ring-sequence was removed using the program ARSTAN (Grissino-Mayer et al., 1993) in which the detrending curve selected was a negative exponential curve, horizontal line, or a straight line with negative slope. Deviations from this curve were standardized to produce a set of annual growth indices for each sample. Ring-width chronology for each species was derived by averaging the growth indices for each year among different trees (Fritts, 1976). The chronology of spruce for the Model Forest was obtained by averaging nine site (sites 1 to 9) chronologies of spruce to emphasize the common features of the chronologies.

3.3. Dendroecological analysis

Relationships between climate and tree growth were detected using a computer program PRECON (Fritts, 1994) which calculates the principal components of climate data to identify the factors influencing tree growth and represents these as response functions. The climate data consisted of 98 years (A.D. 1895–1992) of monthly mean temperature and monthly total precipitation from Fort St. James, which is located within the Sub-Boreal Spruce (SBS) biogeoclimatic zone. The correlation coefficient of these climate variables between Fort St. James and Prince George, over the common period A.D. 1943–1992, averaged 0.60 for monthly total precipitation and 0.92 for monthly mean temperature (both significant at the $p \leq 0.001$ level). In addition, the climate record from Fort St. James provided the longest series in the region; therefore, it was considered as the best representation of the regional climate for this study. The tree-ring data of Douglas-fir, subalpine fir, and spruce used in the response function analysis were residual chronologies in which the autocorrelation of ring-widths had been removed by fitting a first-order autoregressive model to each ring-series so as to

emphasize the effects of climate on tree growth (Grissino-Mayer et al., 1993).

The history of forest disturbances was reconstructed by examining and comparing the differences in ring-width indices of different species. The analysis of climate–growth relationships in this study provided information on the effects of climate on tree growth. Short-term (<5 years) growth increases were attributed to transient, above normal, positive environmental effects on growth. Veblen et al. (1991b) indicated that growth rates of released spruce and subalpine fir trees after beetle attack remained high for >40 years. Therefore, sustained (>5 years) growth increases in surviving spruce and subalpine fir were attributed to spruce beetle removal of competing spruce. Growth suppressions in these species might be caused by climate factors or might be the consequence of insect defoliators. However, except for the western hemlock looper, *Lambdina fiscelloria lugubrosa* (Hulst), little defoliator activity has been documented in the area in the last 50 years.

4. Results

4.1. Ring-width chronologies

The ring-width chronologies of Douglas-fir, spruce, and subalpine fir for the McGregor Model Forest and the statistics describing the three chronologies were presented in Fig. 3 and Table 2. Douglas-fir had the longest chronology due to its longevity and its resistance to moderate surface fires as a result of its thick bark. Spruce, which became established primarily after stand-replacing fires, had an age ca. 200 years younger than the oldest Douglas-fir. Subalpine fir is susceptible to pathogenic and decay fungi infection (Lindgren and Lewis, 1997); therefore, it had the shortest chronology length. Spruce exhibited the highest mean ring width and standard deviation, reflecting its fast growth relative to the other species and the variable influences of environmental factors. Subalpine fir had the highest mean sensitivity, indicating that it had high interannual variability in ring-widths and was sensitive to yearly environmental changes (Fritts, 1976). All the three species exhibited high first-order autocorrelation, suggesting the existence of low frequency variation in the chronologies caused by

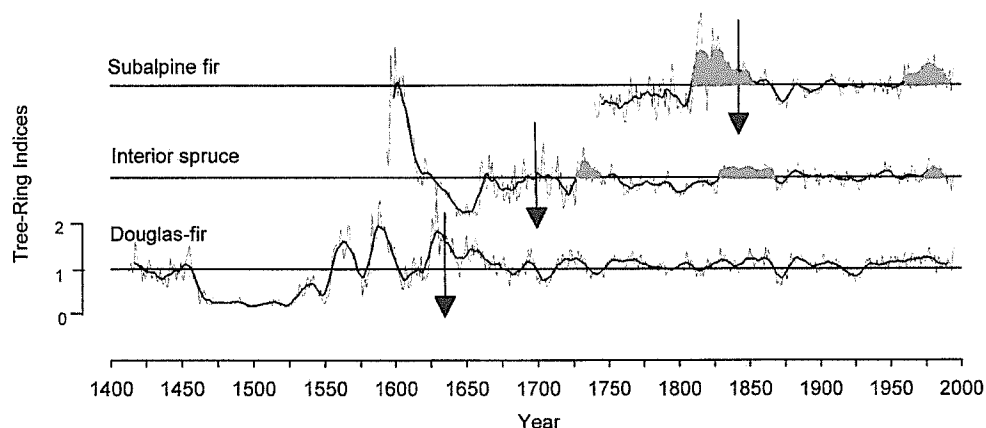


Fig. 3. Ring-width indices of subalpine fir, interior spruce, and Douglas-fir at the McGregor Model Forest, British Columbia. Superimposed on the ring indices are smoothing lines derived from a centered 10-year moving average. The vertical arrows indicate the earliest year with five sample replications. The shaded intervals in subalpine fir and spruce represent growth release attributable to major disturbances, e.g., spruce beetle outbreaks. The Douglas-fir chronology is indicative of climate variations (see text).

propagation of climatic effects from one year into following years or by long-term effects of insect infestations (Swetnam and Lynch, 1993).

4.2. Climate–tree growth relations

The response functions of Douglas-fir, subalpine fir, and spruce ring-width chronologies with monthly mean temperature and monthly total precipitation, for interval A.D. 1895–1992, were presented in Fig. 4. Radial growth of Douglas-fir was positively correlated with precipitation in May of the growth year, with precipitation and temperature in the previous November, and was negatively correlated with temperature in June, July, and the previous July. Ring growth of subalpine fir was negatively correlated with temperature in June and precipitation in July. Ring

growth of spruce was negatively correlated with temperature in July and the previous August.

All three species showed negative correlations between growth and high summer temperatures. This suggested that increased evapotranspiration and water loss induced by high temperatures reduced the radial growth of these species. The positive effect of spring precipitation on ring-width growth of Douglas-fir suggested that water availability during the growing season is one limiting factor for radial growth of Douglas-fir, an observation consistent with information from other regions (Zhang, 1996). The positive effect of high late fall temperature and precipitation on ring-width growth of Douglas-fir suggested that warm and moist days in late fall favour active photosynthesis and continuous food storage, leading to large ring-width in the following year (Fritts, 1976; Waring and

Table 2
Statistics for tree-ring chronologies of Douglas-fir, subalpine fir, and interior spruce in the McGregor Model Forest, British Columbia

Species	Douglas-fir	Subalpine fir	Interior spruce
Entire chronology length	A.D. 1414–1995	A.D. 1740–1995	A.D. 1594–1995
Length with minimum 10 trees	A.D. 1767–1995	A.D. 1878–1995	A.D. 1742–1995
Length with minimum five trees	A.D. 1634–1995	A.D. 1838–1995	A.D. 1698–1995
Mean ring width (mm)	1.31	1.46	1.66
Standard deviation	0.657	0.737	0.805
Mean sensitivity	0.185	0.245	0.206
First-order autocorrelation	0.858	0.799	0.832

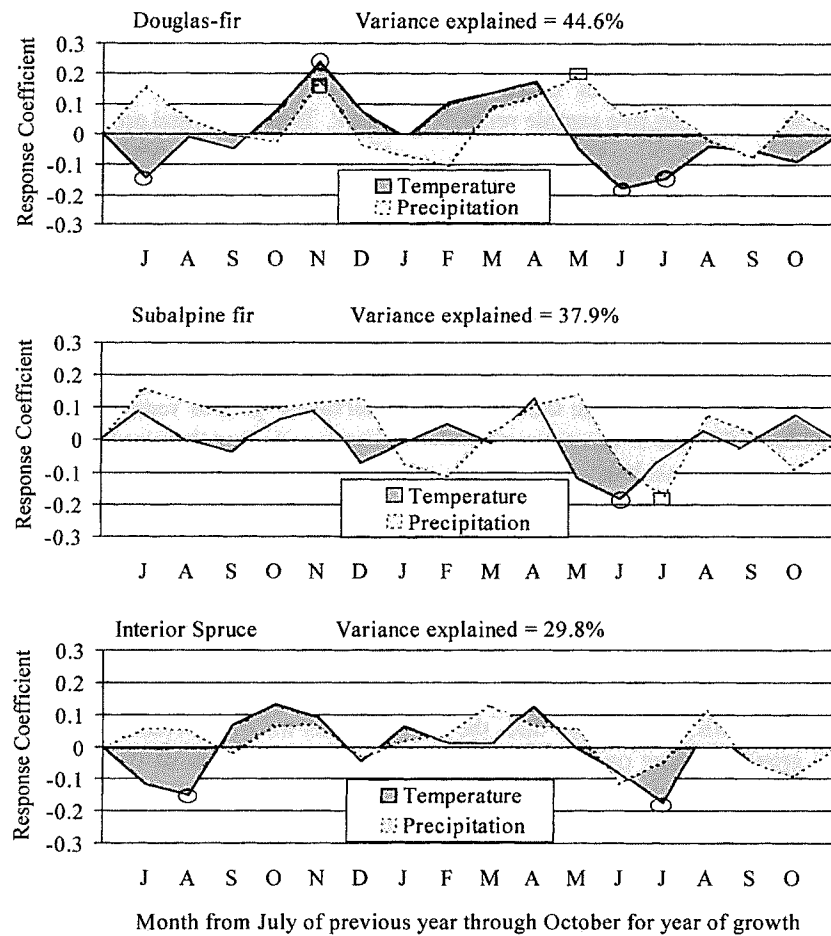


Fig. 4. Response functions of the McGregor Model Forest tree-ring chronologies. Monthly climate variables for the interval A.D. 1895–1992 are used to explain the variance in tree-rings. The labeled points represent a significant (95% level) effect of either temperature or precipitation on growth.

Franklin, 1979). The inverse association of ring-width growth of subalpine fir with July precipitation was contrary to expectation, and might be related to collinearity among predictor variables of growth or to the limitation of the autoregressive models used (Fritts and Dean, 1992). No significant coefficients were found between the growth of spruce and precipitation, which suggested that the radial growth of this species might not be sensitive to the range of variation in precipitation in the study area. It should be noted that non-climatic factors, e.g. insect infestation and competition among trees, may degrade the climate–growth relationships. Therefore, the response functions presented here gave a conservative estimate of the

climate–growth relations. The proportion of variance in tree-rings explained by climate was 44.6% for Douglas-fir, 37.9% for subalpine fir, and 29.8% for spruce, i.e., tree-rings of Douglas-fir contained the highest amount of climate information, followed by subalpine-fir, whereas spruce provided the least climate information.

4.3. History of forest growth anomalies

Comparisons of the tree-ring chronologies of Douglas-fir, subalpine fir, and spruce and their relationships with the environmental factors provided useful clues for the history of forest disturbances in the

McGregor Model Forest. All chronologies had smaller sample sizes in the early years. Therefore, less confidence should be placed on inferences based on chronology intervals with less than five sample replications.

The chronology of Douglas-fir was the oldest, dating back to A.D. 1414 (Fig. 3). It showed that there was a century-long period of low radial growth during the late 1450s to the late 1550s. Although there was only one sample for this interval, it was interesting to note that this century-long suppressed growth also occurred in the ring-width chronology of Douglas-fir on southern Vancouver Island (≈ 630 km southwest from the McGregor Model Forest) in the same interval, where it was interpreted as a result of a long period of dry springs (Zhang, 1996). The agreement between these distant chronologies suggested that the growth of Douglas-fir during the late 1450s to the late 1550s was influenced by a large-scale climatic phenomenon of dry springs and probably cold late falls which might have affected much of British Columbia.

Extremely high values of growth indices of spruce occurred in the early 1600s, indicating that the sampled trees were growing under open conditions probably created by stand-replacing fires or some other disturbances such as severe spruce beetle outbreaks (Heath and Alfaro, 1990; Veblen et al., 1991a). The following extreme low growth during the 1630s to 1650s indicated that the sampled trees might have been suppressed by increased competition among trees or by disturbances such as defoliation by insects, possibly eastern spruce budworm which presently defoliates spruce in the northern forest of B.C. (Erickson and Loranger, 1983). The growth indices of non-host Douglas-fir during this period were above average, suggesting moist springs and warm late falls.

A rapid decrease and sustained low radial growth of spruce occurred in the late 1710s to late 1720s which was followed by a period of above-average growth lasting until the mid-1740s. The climate during the late 1710s to late 1720s was characterized by moist springs, warm late falls and probably cool summers as suggested by the above average growth of Douglas-fir. Therefore, this decade of severe growth suppression of spruce was not caused by climate factors, but by either insect outbreaks such as spruce defoliator infestations or by other factors such as windstorms which could cause damage to trees' root systems. Coates et al.

(1994) indicated that strong windstorms promote the build-up of spruce beetle populations and create stressed trees that may be more susceptible to beetle attack. Thus, the radial growth pattern of spruce in the 1710s to 1740s suggested a possible spruce beetle outbreak in the late 1720s, after which the growth release for the surviving trees was a result of reduced competition among trees.

The long period of growth reduction in spruce during the late 1750s to late 1820s suggested a state of increased tree to tree competition as recruitment increased overall tree density in the area sampled. This interval of growth reduction was followed by four decades of growth release which might have been caused, again, by spruce beetle infestations which thinned this overstocked forest. Lindgren and Lewis (1997) presented a chronology for this area based on samples collected from site 3. They reported a description of dying forests and desolate landscapes found in a fur trader's diary in 1836, and also hypothesized a major spruce beetle outbreak in the 1820s. By comparison of the ring growths in spruce, subalpine fir, and Douglas-fir, we provided additional evidence supporting the hypothesis of spruce beetle outbreak in the 1820s. The subalpine fir, which is sensitive to canopy disturbance (Veblen et al., 1991b), showed prolonged slow growth in the 1740s to 1800s, but then exhibited an abrupt and significant release in the 1810s–1820s. The former suggested closed canopy structure and intense competition among trees, and the latter suggested large removal of overstory spruce, possibly by spruce beetle infestation (Veblen et al., 1991a). The growth of Douglas-fir, a climate sensitive species, during the late 1750s to 1820s was slightly above average, suggesting that no severe climate anomalies occurred in the period to either suppress or release tree growth in the area. The delayed growth release in spruce compared to the release in subalpine fir might be caused by the lag in response of spruce to beetle disturbance, or it might simply be an anomaly caused by the small number of samples ($n = 2$) in subalpine fir for this period. In summary, the tree-ring growth features of these three species suggested a dense canopy structure and moderate climate during the late 1750s–1800s, and a large scale spruce beetle outbreak in the 1810s–1820s.

The chronologies of Douglas-fir, spruce, and subalpine fir (non-host for spruce beetles) showed syn-

chronous growth reductions during the late 1860s and early 1870s. This suggested that the reduced growth might have been caused by large-scale climate anomalies. Based on the response functions of the three species to climate factors (Fig. 4), the climate in the late 1860s to early 1870s might have been characterized by severe dry springs, hot summers, and probably cold late falls. Such dry springs and hot summers in the years around 1870 were also reported from several tree-ring studies of climate in the Pacific Northwest region (Graumlich, 1987; Wiles et al., 1996; Zhang, 1996).

The growth release of subalpine fir since the 1960s indicated reduced competition from overstory spruce. The canopy disturbance agent during this period was three confirmed spruce beetle outbreaks as recorded in 1963–1965, 1969–1970, and 1979–1983 (Erickson and Loranger, 1983). The effect of these outbreaks was also reflected in the ring-width indices of surviving spruce which showed increased radial growth in the 1970s. The chronology of Douglas-fir showed above average growth since the 1930s, suggesting a favorable climate for growth through the period.

5. Discussion

The radial growth rates of Douglas-fir, subalpine fir, and spruce exhibited different response characteristics to environmental factors; therefore, comparisons of growth anomalies among these three species could provide useful information on past major climate events and forest disturbances such as insect outbreaks. The reliability of the inferences was mainly dependent on the sensitivity of tree-rings to these different factors and on the degree to which the sampled tree-rings represent the regional forest. Of the three species studied in this project, Douglas-fir was the most climate sensitive species. Nearly half of the ring-width variation in Douglas-fir could be explained by climate variables, whereas the remainder was attributed to local factors such as microclimate, local soil conditions, and competition among trees. Subalpine fir and spruce were sensitive to forest disturbances such as severe insect outbreaks. In this study, only major climate events and moderate to severe insect infestations were reconstructed from tree-ring chronologies of the three species. The con-

fidence of these reconstructions was limited in the earlier periods when the sample sizes declined below five trees.

Tree-ring data in non-host and climate sensitive species and in host species are especially useful in studying long-term climate-insect infestation patterns because they provide replicated observations of past outbreaks and climatic fluctuations (Swetnam and Lynch, 1993). Our study showed that the occurrence of spruce beetle outbreaks in the 1960s to early 1980s and the suspected occurrences in the 1810s–1820s and the late 1720s happened in periods of moist springs as deduced from the Douglas-fir chronology. The same positive relationship between spring precipitation and outbreak was also found in a study of western spruce budworm (*Choristoneura occidentalis* Freeman) outbreaks in northern New Mexico, USA (Swetnam and Lynch, 1993). However, a negative relationship between precipitation and western spruce budworm outbreaks was reported in British Columbia (Thomson et al., 1984). Thus, the exact mechanisms of weather-outbreak association are not clearly understood.

This study also supported the finding of Kimoto (1996) that the severe insect infestations in this study area during the late 20th century are not primarily a consequence of present day forest management practices. Such severe spruce beetle outbreaks occurred several times during the 17th–19th centuries. Severe disturbance by spruce beetle played a role in shaping the forest structure, composition, and renewal by causing mortality of infested spruce, reducing competition among trees, and accelerating the growth rates of survivors and understory tree species. Mature spruce forest with dense canopies and moist weather were favorable to spruce beetle activity and dispersal, thus were more suitable to the development of outbreaks. More extensive sampling of old growth host and non-host species is required to provide long-term and reliable records of outbreaks and climate variations. These records can improve our understanding of the patterns of outbreaks as well as their relationships with climate.

6. Conclusions

Our study demonstrated that tree-ring chronologies of Douglas-fir, subalpine fir, and spruce can provide

useful information on past forest growth dynamics, climate variations, and spruce beetle outbreaks. Douglas-fir was the most climate sensitive species, followed by subalpine fir. The climate during the late 1750s–1800s was characterized by slightly moist springs and probably moderate summers. The synchrony of suppressed growths of all three species during the late 1860s and early 1870s suggested dry springs, hot summers, and probably cold late falls. The spruce forest was probably infested by spruce defoliators during the 1630s–1650s, and was infested by spruce beetle in the late 1720s, 1810s–1820s, and 1960s–early 1980s as inferred by comparisons of the growth anomalies among the three species. The spruce beetle outbreaks occurred during period of above average spring precipitation, suggesting a possible weather–outbreak relationship. Further investigation of long tree-ring records will improve our knowledge of forest growth dynamics and their relationships with the environmental factors.

Acknowledgements

We thank Drs. Brad Hawkes, Staffan Lindgren, and Kathy Lewis for providing some of the tree-ring samples; Emil Wegwitz and George Brown for providing technical support and conducting the field work; and the McGregor Model Forest Association for funding this research.

References

- Alfaro, R.I., Shepherd, R.F., 1991. Tree-ring growth of interior Douglas-fir after one year's defoliation by Douglas-fir Tussock Moth. *For. Sci.* 37, 959–964.
- Alfaro, R.I., Maclauchlan, L.E., 1992. A method to calculate the losses caused by western spruce budworm in uneven-aged Douglas-fir forests of British Columbia. *For. Ecol. Manage.* 55, 295–313.
- Coates, K.D., Haeussler, S., Lindeburgh, S., Pojar, R., Stock, A.J., 1994. Ecology and silviculture of interior spruce in British Columbia. FRDA report 220. Forestry Canada and Ministry of Forests, Victoria, B.C., pp. 126.
- D'Arrigo, R.D., Jacoby, G.C., Free, R.M., 1992. Tree-ring width and maximum latewood density at the North American Tree line: parameters of climatic change. *Can. J. For. Res.* 22, 1290–1296.
- DeLong, S.C., Tanner, D., 1996. Managing the pattern of forest harvest: lesson from wildfire. *Biodiversity and Conservation* 5, 1191–1205.
- Erickson, R.D., Loranger, J.F., 1983. History of population fluctuations and infestations of important forest insects in the Prince George Forest Region 1942–1982. Canadian Forestry Service, Forest Insect and Disease Survey. Pacific Forestry Centre, Victoria, B.C., pp. 37.
- Fritts, H.C., 1976. *Tree Rings and Climate*. Academic Press, London, pp. 567.
- Fritts, H.C., 1994. Quick help for PRECON now called PRECONK Version 4.0. Dendrochronological Modelling. Tucson, Arizona, pp. 26.
- Fritts, H.C., Swetnam, T.W., 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Adv. Ecol. Res.* 19, 111–188.
- Fritts, H.C., Dean, J.S., 1992. Dendrochronological modelling of the effects of climatic change on tree-ring width chronologies from the Chaco Canyon area, Southwestern United States. *Tree-Ring Bull.* 52, 31–56.
- Graumlich, L.J., 1987. Precipitation variation in the Pacific Northwest (1675–1975) as reconstructed from tree rings. *Annals of the Association of American Geographers* 77, 19–29.
- Grissino-Mayer, H., Holmes, R., Fritts, H.C., 1993. International Tree-Ring Data Bank Program Library User's Manual. Laboratory of Tree-Ring Research, University of Arizona, pp. 76.
- Heath, R., Alfaro, R.I., 1990. Growth response in a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle. *J. Entomol. Soc. Brit. Columbia* 87, 16–21.
- Hebda, R., 1997. Impact of climate change on biogeoclimatic zones of British Columbia and Yukon. In: Taylor, E., Taylor, B. (Eds.), *Responding to Global Climate Change in British Columbia and Yukon*. Ministry of Environment, Lands and Parks, Victoria, B.C., Chap. 13, pp. 1–15.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–75.
- Humphreys, N., Safranyik, L., 1993. Spruce beetle. Natural Resources Canada, Forest Pest Leaflet 13. Pacific Forestry Centre, Victoria, B.C., pp. 7.
- Kimoto, T.T.M., 1996. Past infestations by the white pine weevil (*Pissodes strobi* Peck) within naturally regenerated stands of the McGregor Model Forest, Prince George, B.C. M.S. Thesis, Simon Fraser University, Vancouver, pp. 49.
- Lindgren, B.S., Lewis, K.G., 1997. The natural role of spruce beetle and root pathogens in a sub-boreal spruce forest in central British Columbia: a retrospective study. In: Gregoire, J.C., Liebholt, A.M., Stephen, F.M., Day, K.R., Salom, S.M. (Eds.), *Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests*, USDA For. Serv. Gen. Tech. Rep. NE-236, pp. 122–130.
- Luckman, B.H., Briffa, K.R., Jones, P.D., Schweingruber, F.H., 1997. Tree-ring based reconstruction of summer temperatures at the Columbia Icefield, Alberta, Canada, AD 1073–1983. *The Holocene* 7, 375–389.
- Meidinger, D., Pojar, J., 1991. *Ecosystems of British Columbia*. Research Branch, B.C. Ministry of Forests, Victoria, B.C., pp. 330.

- Parminter, J., 1992. Typical historic patterns of wildfire disturbance by biogeoclimatic zone. Table adapted from: Old-growth forest: Problem analysis. Research Branch, B.C. Ministry of Forests. Victoria, B.C., pp. 104.
- Swetnam, T.W., Lynch, A.M., 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecol. Monog.* 63, 399–424.
- Swetnam, T.W., Thompson, M.A., Sutherland, E.K., 1985. Using dendrochronology to measure radial growth of defoliated trees. USDA For. Serv. Agric. Handb. No. 639, pp. 39.
- Szeicz, J.M., MacDonald, G.M., 1995. Dendroclimatic reconstruction of summer temperatures in northwestern Canada since A.D. 1638 based on age-dependent modeling. *Quat. Res.* 44, 256–266.
- Thomson, A.J., Shepherd, R.F., Harris, J.W.E., Silversides, R.H., 1984. Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (*Lepidoptera: Tortricidae*), in British Columbia. *Can. Entomol.* 116, 375–381.
- Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991a. Methods of detecting spruce beetle outbreaks in Rocky Mountain subalpine forests. *Can. J. For. Res.*, 21, pp. 242–254.
- Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991b. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology*, 72, pp. 213–231.
- Waring, R.H., Franklin, J.F., 1979. Evergreen coniferous forests of the Pacific Northwest. *Science* 204, 1380–1386.
- Weber, U.M., Schweingruber, F.H., 1995. A dendroecological reconstruction of western spruce budworm outbreaks (*Choristoneura occidentalis*) in the Front Range, Colorado, from 1720 to 1986. *Trees* 9, 204–213.
- Wiles, G.C., D'Arrigo, R.D., Jacoby, G.C., 1996. Temperature changes along the Gulf of Alaska and the Pacific Northwest coast modelled from coastal tree rings. *Can. J. For. Res.* 26, 474–481.
- Zhang, Q., 1996. A 2122-year tree-ring chronology of Douglas-fir and spring precipitation reconstruction at Heal Lake, southern Vancouver Island, British Columbia. M.S. Thesis, University of Victoria, Victoria, pp. 88.

Forest Ecology and Management

Submission of manuscripts.

Manuscripts should be submitted in triplicate. Authors from the Americas, Australia, New Zealand and the Pacific are requested to send their manuscripts to *Forest Ecology and Management*, Dr. Richard F. Fisher, Department of Forest Science, Texas A&M University, College Station, TX77843-2135, USA; all other authors are requested to send their manuscripts to the Editorial Office, *Forest Ecology and Management*, P.O. Box 181, 1000 AD Amsterdam, The Netherlands.

Authors in Japan please note: Upon request, Elsevier Science Japan will provide authors with a list of people who can check and improve the English of their paper (*before submission*). Please contact our Tokyo office: Elsevier Science Japan, 1-9-15 Higashi-Azabu, Minato-ku, Tokyo 106-0044, Japan; tel. (+81)-3-5561-5033; fax (+81)-3-5561-5047.

Electronic manuscripts: Electronic manuscripts have the advantage that there is no need for the rekeying of text, thereby avoiding the possibility of introducing errors and resulting in reliable and fast delivery of proofs.

For the initial submission of manuscripts for consideration, hardcopies are sufficient. For the processing of *accepted papers*, electronic versions are preferred. After *final acceptance*, your disk plus two, final and exactly matching printed versions should be submitted together. Double density (DD) or high density (HD) diskettes (3.5 or 5.25 inch) are acceptable. It is important that the file saved is in the native format of the wordprocessor program used. Label the disk with the name of the computer and wordprocessing package used, your name, and the name of the file on the disk. Further information may be obtained from the Publisher.

Enquiries concerning manuscripts and proofs: questions arising after acceptance of the manuscript, especially those relating to proofs, should be directed to Elsevier Science Ireland Ltd., Elsevier House, Brookvale Plaza, East Park, Shannon, Co. Clare, Ireland; Tel. (+353-61) 709600; Fax: (+353-61) 709100.

Advertising information: Advertising orders and enquiries can be sent to: **USA, Canada and South America:** Mr Tino de Carlo, The Advertising Department, Elsevier Science Inc., 655 Avenue of the Americas, New York, NY 10010-5107, USA; phone: (+1) (212) 633 3815; fax: (+1) (212) 633 3820; e-mail: t.decarlo@elsevier.com **Japan:** The Advertising Department, Elsevier Science K.K., 9-15 Higashi-Azabu 1-chome, Minato-ku, Tokyo 106, Japan; phone: (+81) (3) 5561 5033; fax: (+81) (3) 5561 5047. **Europe and ROW:** Rachel Gresle-Farthing, The Advertising Department, Elsevier Science Ltd., The Boulevard, Langford Lane, Kidlington, Oxford OX5 1GB, UK; phone: (+44) (1865) 843565; fax: (+44) (1865) 843976; e-mail: r.gresle-farthing@elsevier.co.uk

Orders, claims, and product enquiries: please contact the Customer Support Department at the Regional Sales Office nearest you:

New York: Elsevier Science, PO Box 945, New York, NY 10159-0945, USA; Tel.: (+1) (212) 633 3730 [toll free number for North American customers: 1-888-4ES-INFO (437-4636)]; Fax: (+1) (212) 633 3680; E-mail: usinfo-f@elsevier.com

Amsterdam: Elsevier Science, PO Box 211, 1000 AE Amsterdam, The Netherlands; Tel.: (+31) 20 4853757; Fax: (+31) 20 4853432; E-mail: nlinfo-f@elsevier.nl

Tokyo: Elsevier Science, 9-15, Higashi-Azabu 1-chome, Minato-ku, Tokyo 106-0044, Japan; Tel.: (+81) (3) 5561 5033; Fax: (+81) (3) 5561 5047; E-mail: info@elsevier.co.jp

Singapore: Elsevier Science, No. 1 Temasek Avenue, #17-01 Millenia Tower, Singapore 039192; Tel.: (+65) 434 3727; Fax: (+65) 337 2230; E-mail: asiainfo@elsevier.com.sg

Rio de Janeiro: Elsevier Science, Rua Sete de Setembro 111/16 Andar, 20050-002 Centro, Rio de Janeiro – RJ, Brazil; Tel.: (+55) (21) 509 5340; Fax: (+55) (21) 507 1991; E-mail: elsevier@campus.com.br [Note (Latin America): for orders, claims and help desk information, please contact the Regional Sales Office in New York as listed above]

US mailing info: *Forest Ecology and Management* (0378-1121) is published monthly by Elsevier Science B.V. (Molenwerf 1, Postbus 211, 1000 AE Amsterdam). Annual subscription price in the USA is US\$ 2307.00 (valid in North, Central and South America), including air speed delivery. Second class postage rate is paid at Jamaica, NY 11431.

USA POSTMASTERS: Send address changes to *Forest Ecology and Management* Publications Expediting, Inc., 200 Meacham Avenue, Elmont, NY 11003.

AIRFREIGHT AND MAILING in the USA by Publications Expediting Inc., 200 Meacham Avenue, Elmont, NY 11003.

***Forest Ecology and Management* has no page charges**

For a full and complete Guide for Authors, please refer to *Forest Ecology and Management*, Vol. 115, No. 1, pp. 93–96. The instructions can also be found on the World Wide Web: access under <http://www.elsevier.nl> or <http://www.elsevier.com>

⊗ The paper used in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Printed in The Netherlands

LANDSCAPE AND URBAN PLANNING

An International Journal of Landscape Ecology,
Landscape Planning and Landscape design

Editor-in-Chief:

J.E. Rodiek, *College of Architecture, Texas A & M University, College Station, TX 77843-3137, USA*

AIMS AND SCOPE

A journal concerned with conceptual, scientific and design approaches to land use. By emphasizing ecological understanding and a multi-disciplinary approach to analysis and planning and design, it attempts to draw attention to the interrelated nature of problems posed by nature and human use of land. In addition, papers dealing with ecological processes and interactions within urban areas, and between these areas and the surrounding natural systems which support them, will be considered. Papers in which specific problems are examined are welcome. Topics might include but are not limited to landscape ecology, landscape planning and landscape design. Landscape ecology examines how heterogeneous combinations of ecosystems are structured, how they function and how they change. Landscape planning examines the various ways humans structure their land use changes. Landscape design involves the physical strategies and forms by which land use change is actually directed. *Landscape and Urban Planning* is based on

the premise that research linked to practice will ultimately improve the human made landscape.

Editorial Advisory Board:

I.D. Bishop, *Parkville, Vic., Australia*,
E.G. Bolen, *Wilmington, NC, USA*,
I.D. Bruns, *Schorndorf, Germany*,
J.B. Byrom, *Edinburgh, UK*,
T.C. Daniel, *Tucson, AZ, USA*,
R.M. DeGraaf, *Amherst, MA, USA*,
J.G. Fabos, *Amherst, MA, USA*,
S. Gonzalez Alonso, *Madrid, Spain*,
M. Hough, *Etobicoke, ON, Canada*,
P. Jacobs, *Montreal, PQ, Canada*,
D.S. Jones, *Melbourne, Vic., Australia*,
H. Lavery, *Milton, Qld., Australia*,
W.M. Marsh, *Flint, MI, USA*,
D.L. Mitchell, *Dallas, TX, USA*,
D.G. Morrison, *Athens, GA, USA*,
J.I. Nassauer, *St. Paul, MN, USA*,
M. Nelischer, *Guelph, ON, Canada*,
D.D. Paterson, *Vancouver, BC, Canada*,
A. Ramos, *Madrid, Spain*,
P. Shepard, *Claremont, CA, USA*,
O.R. Skage, *Alnarp, Sweden*,
R.C. Smardon, *Syracuse, NY, USA*,
G. Sorte, *Alnarp, Sweden*,
F. Stearns, *Rhineland, WI, USA*,

R.C. Szaro, *Washington, DC, USA*,
J.W. Thomas, *La Grande, OR, USA*,
P.J. Trowbridge, *Ithaca, NY, USA*,
T.H.D. Turner, *London, UK*,
M.J. Vroom, *Wageningen, The Netherlands*,
W.V. Wendler, *College Station, TX, USA*,
B.-E. Yang, *Seoul, Korea*,
E.H. Zube, *Tucson, AZ, USA*

ABSTRACTED/INDEXED IN

Applied Ecology Abstracts,
Biological Abstracts,
Current Contents B & S,
Environmental Periodicals
Bibliography, Geobase,
Geographical Abstracts,
LandSearch.

1994 SUBSCRIPTION DATA

Volumes 28-30 (in 9 issues)
Subscription price:
Dfl. 1080.00 (US \$ 584.00)
incl. Postage
ISSN 0169-2046



ELSEVIER
SCIENCE PUBLISHERS

Elsevier Science Publishers,
P.O. Box 211, 1000 AE Amsterdam,
The Netherlands
Fax: (020) 5803-203

Customers in the USA and Canada:
Elsevier Science Publishers
P.O. Box 945, Madison Square Station,
New York, NY 10160-0757, USA
Fax: (212) 633-3680

The Dutch Guilder price quoted applies worldwide, except in the Americas (North, Central and South America). The US Dollar price quoted applies in the Americas only. Non VAT registered customers in the European Community should add the appropriate VAT rate applicable in their country to the price.