# Old-growth, disturbance, and ecosystem management

## E.A. Johnson, K. Miyanishi, and J.M.H. Weir

Abstract: The forested landscape consists of a mosaic of patches of different times since the last disturbance (i.e., different stand ages). Therefore, we can form a distribution of forest ages for the entire landscape (landscape age distribution). Studies of disturbance by fire in boreal and subalpine conifer forests have shown that the cumulative age distribution (landscape survivorship distribution) is best fit by a negative exponential model for which the parameter, the disturbance cycle, gives the time required to disturb an area equal in size to the study area. This distribution describes the rate at which parts of the landscape will survive disturbance, and consequently it tells us the percentage of the landscape that will survive to be old-growth forest. Empirical studies show that old forests make up a small proportion of the boreal and subalpine landscape. We introduce the concept of characteristic oldest age, which is a function of disturbance cycle and size of the study area. This landscape approach to old growth allows one to estimate the minimum area required to ensure the continued existence of some user-defined old-growth forest for any given disturbance cycle.

Key words: old growth, disturbance cycle, ecosystem management, landscape age distribution, boreal forest, landscape ecology.

**Résumé**: Le paysage forestier est constitué d'une mosaïque de surfaces dont le moment de la dernière perturbation varie (i.e., stations d'âges différents). Par conséquent, il est possible de présenter une distribution des âges des forêts pour l'ensemble du paysage (distribution des âges dans le paysage). Les études des perturbations par le feu dans les forêts conifériennes boréales et subalpines montrent que la distribution cumulative des âges (distribution de la survie dans le paysage) concorde le mieux avec un modèle exponentiel négatif pour lequel le paramètre, le cycle de perturbation, donne le temps requis pour perturber une surface égale en dimensions à la région étudiée. Cette distribution décrit le taux avec lequel les parties du paysage survivront aux perturbations et conséquemment, elle nous renseigne sur le pourcentage du paysage qui survivra pour devenir une forêt surannée. Les études empiriques montrent que les forêts surannées constituent une petite proportion des paysages boréaux et subalpins. Les auteurs présentent le concept de plus vieil âge caractéristique, lequel est fonction du cycle de perturbation et de la surface étudiée. L'étude des forêts surannées dans une perspective de paysage permet d'évaluer la surface minimale nécessaire pour garantir la persistance d'organismes dont l'habitat est constitué de forêts surannées, pour un cycle de perturbation donné.

*Mots clés* : forêt surannée, cycle de perturbance, aménagement des écosystème, distribution des âges dans le paysage, forêt boréale, écologie du paysage. [Traduit par la rédaction]

## Introduction

The generally accepted concept of old growth is derived from extensive ecological studies of Pacific Northwest forests (Cline et al. 1980; Harmon et al. 1986; Pike et al. 1977; Sollins et al. 1980; Spies and Franklin 1988; Vogt et al.

Guelph, Guelph, ON N1G 2W1, Canada.

Can. J. Bot. 73: 918-926 (1995). Printed in Canada / Imprimé au Canada

1983). The concept is not restricted to the chronological age of a forest but also involves a suite of structural and functional characteristics (Franklin et al. 1981). Structural characteristics include features such as large trees, wide variation in tree sizes and spacing, accumulation of large, dead standing, and fallen trees, broken and deformed tops, bole and root rot, multiple canopy layers, canopy gaps and understory patchiness. Some of the functional characteristics involve cessation in height growth of oldest trees, near zero net productivity, and biochemistry of secondary metabolic products in old trees that may provide high resistance to insects and disease (Kaufmann et al. 1992). All of these characteristics of old-growth forests focus on properties within individual forest stands or ecosystems.

We suggest that the concept of old growth should be based on landscape-level properties as well as on properties within individual stands or ecosystems. First, we present a widely

Received July 15, 1994.

**E.A. Johnson.**<sup>1</sup> Department of Biological Sciences and Kananaskis Field Stations, The University of Calgary, Calgary, AB T2N 1N4, Canada. **K. Miyanishi.** Department of Geography, University of

J.M.H. Weir. Prince Albert National Park, Waskesiu Lake, SK S0J 2Y0, Canada.

<sup>&</sup>lt;sup>1</sup> Author to whom all correspondence should be addressed.

**Fig. 1.** Example of a map of time since last disturbance. Dates give year in which disturbance last occurred.



**Table 1.** Data from a hypothetical map of time since last disturbance for a study area of  $1000 \text{ km}^2$  ( $10^5 \text{ ha}$ ).

Time since

last disturbance			
(years)	Area (ha)	% area	Cumulative %
0	34 076	34.1	100.0
50	22 464	22.5	65.9
100	14 809	14.8	43.4
150	9 763	9.8	28.6
200	6 4 3 6	6.4	18.8
250	4 243	4.2	12.4
300	2 797	2.8	8.2
350	1 844	1.8	5.4
400	1 216	1.2	3.6
450	801	0.8	2.4
500	528	0.5	1.6
550	348	0.3	1.1
600	230	0.3	0.8
650	151	0.2	0.5
700	293	0.3	0.3
Total	100 000	100.0	

Note: Percent area is used to derive the example landscape age distribution (Fig. 2), and cumulative percent is used to derive the survivorship curve (Fig. 3).

used quantitative disturbance frequency model of how the age distribution of stands across the landscape comes about, with examples from published studies on boreal and subalpine forests. Second, from that model we derive a means of defining the proportion of the landscape covered by old-growth forests as well as of calculating the oldest age stand expected and use the previous examples to illustrate this definition of old growth. Finally, we discuss implications of this landscape model of old growth for management.



#### Landscape disturbance frequency model

The landscape disturbance frequency model we present here is, in fact, a widely accepted fire-frequency model (Van Wagner 1978; Johnson 1979; Johnson and Van Wagner 1985; Johnson and Gutsell 1994). The landscape consists of a mosaic of patches of different ages since the last disturbance. In the boreal forest, the disturbance is typically fire or insect outbreaks, both of which usually involve extensive death of the canopy and the understory (Johnson 1992). Each disturbance creates a patch of a given size and date of occurrence. This patch then gets progressively smaller over time as subsequent disturbances overlap it. Eventually these overlapping disturbances result in the disappearance of the patch. Therefore, at any point in time, the landscape mosaic will consist of only the most recent disturbance represented in its entirety and the remaining fragments of earlier disturbances.

The disturbance cycle (b) is defined as the time required to disturb an area equal in size to the study area. This does not require that all parts of the study area be disturbed during this time but only that an area equal to the study area be disturbed. Consequently, some areas may be disturbed more than once. The average frequency (f) of disturbance is defined as the inverse of the disturbance cycle (i.e., f = 1/b). Note that the word cycle is used in a very specific sense here. It is the time required to disturb a given areal size once and is only in this sense a cycle. If the disturbance cycle is very short (i.e., average disturbance frequency is high), the areas of forest dating from the older disturbances will disappear relatively rapidly, whereas, if the disturbance cycle is long, patches



Fig. 3. Empirical landscape age and survivorship distributions for four studies in the boreal forest. Twenty-year age-classes were used in all examples. (A) Boundary Waters Canoe Area, Minn. (Heinselman 1973). (B) Rutledge Lake, N.W.T. (Johnson 1979). (C) Lake St. Joseph, Ont. (Suffling et al. 1982). (D) Porcupine River, Alaska (Yarie 1981).

created by older disturbances will persist for longer periods. Consequently, the amount of old-growth forest remaining at any time will depend to a large degree on the frequency of disturbance. The persistence of patches of different ages (i.e., areas that are not affected by later disturbances) can thus be seen as describing a survivorship curve of the landscape.

To construct this landscape survivorship curve (see Johnson and Gutsell 1994), it is necessary to produce a time since last disturbance map. Figure 1 provides an example of such a map. From a time since last disturbance map we can determine the area covered by each time since disturbance. A hypothetical example is given in Table 1, in which these areas are given in column 2. We can then express this area as a percentage of the entire study area (column 3). Column 3 thus describes the age distribution of the forest since last disturbance (Fig. 2A). Each age-class in this distribution represents the Fig. 4. Empirical landscape age and survivorship distributions for two studies in the subalpine forest in the southern Canadian Rockies. Twenty-year age-classes were used in both examples. (A) Kootenay National Park, B.C. (Masters 1990). (B) Kananaskis, Alta. (Johnson and Larsen 1991).



proportion of the study area that has survived from the time of the last disturbance to the present. Finally, the percentages can be plotted cumulatively (column 4), starting with 100% at the time of the study and decreasing monotonically with time, to produce the survivorship curve for the study area (Fig. 2B). The area under the curve to the right of time *t* represents the proportion of the study area that has not been disturbed (i.e., has survived without further disturbance) since at least time *t*. Thus, for example, at t = 300 years, the area under the curve that is shaded represents the proportion of the landscape that has not been disturbed for at least the last 300 years (i.e., is 300 years or older). It is also obvious that at t = 0, the entire study area (100%) will have survived without a disturbance!

If the survivorship distribution, A(t), is a good fit to a negative exponential function, it will give a straight line on semilog scale and can be defined by the equation

[1] 
$$A(t) = \exp -\left(\frac{t}{b}\right)$$

where t is the time since last disturbance and b is a parameter that defines the steepness of the slope. The parameter b can be interpreted as the disturbance cycle. Other distributions have been used in studying disturbance (see, e.g., Johnson and Gutsell 1994). Only the negative exponential is presented here, since it is the one that best fits the data used below.

Figures 3 and 4 are examples of the age and survivorship

distributions for six published studies from upland boreal (Heinselman 1973; Johnson 1979; Suffling et al. 1982; Yarie 1981) and subalpine forests (Johnson and Larsen 1991; Masters 1990) of North America. All six studies were based on maps of time since last fire or statistically acceptable sampling designs (see Johnson and Gutsell 1994) for large areas. The survivorship distributions are plotted on a semilog scale.

Inspection of the survivorship distributions in Figs. 3 and 4 reveals that in every study there is not one straight line but a series of straight lines. These indicate changes in slope (the parameter b) and hence changes in the disturbance cycle. The studies that extend beyond 300 BP show a change to a longer disturbance (in this case fire) cycle some time in the mid-1700s. This change has often been correlated with the cooler, moister conditions during the Little Ice Age. The studies also show a change in disturbance cycle at the end of the 1800s and early 1900s. This change has again been associated with climatic change because similar changes show up for all study areas from Alaska and the Northwest Territories to southern Alberta, Minnesota, and Ontario, whether there was fire suppression or not (Johnson 1992). The implication of these changes in disturbance cycles is that there are some older stands in these forests that started under one disturbance cycle and that have survived through at least one change in disturbance cycle. A further obvious conclusion from these studies is that there is only a relatively small proportion of the area older than 300 years.

In the context of this model, an equilibrium landscape





(e.g., Shugart 1984; Sprugel 1991) is one in which the disturbance cycle (b) is constant for the time span covered by the distribution. In other words, if the landscape could be sampled at 50-year intervals over a period of 400 years, the time since disturbance distribution for each of these sample periods would be identical if the landscape was in equilibrium. We have seen that for the boreal and subalpine forest, none of the areas studied is in equilibrium, i.e., the disturbance cycle has changed in the past 400 years, apparently because of changes in climate. Note that lack of equilibrium in these landscapes is due not to the study area being too small but to the large scale of the landscape process and to changes in the rate of that process, i.e., the disturbance frequency is being controlled by a large-scale climatic process.

#### Landscape model of old growth

The survivorship distributions derived from the landscape age mosaic provide an empirical and theoretical basis for defining old growth in terms of the dynamics of the landscape. The empirical basis is provided by the fact that the landscape age distribution is obtained from measurements of the actual area covered by forests of different ages (i.e., times since last disturbance). The theoretical basis is that the parameter of this distribution provides a definition of the landscape ecology process of disturbance cycle. Old growth is, by definition, a discussion of the proportion of the landscape within the tail of either the age distribution or the survivorship distribution. As mentioned previously, an examination of the empirical survivorship curves for the boreal and subalpine forests (Figs. 3 and 4) shows that older forests have generally made up a small proportion of the forested landscape. This is also the case in the Douglas-fir regions of Oregon and Washington (Hemstrom and Franklin 1982; Dunwiddie 1983; Swetnam et al. 1983; Sprugel 1991).

Therefore, these older forests are, by their nature, rare, and the probability of encountering them is a function of the size of the study area. To obtain a reliable estimate of the oldest age forests in the landscape, we require a definition of old growth that incorporates both the survivorship nature of the landscape mosaic (i.e., the disturbance cycle) and the effect of study area size. Taking these factors into account, we can define the characteristic oldest age in the landscape by the following equation (Gumbel 1958):

[2] 
$$n A(U_n) = 1$$

where *n* is the size of the study area,  $U_n$  is the characteristic oldest age, and  $A(U_n)$  is the survivorship function.

To explain the derivation of this equation, we have to clarify the definition of study area size (n). If the smallest unit of the landscape we are considering is 1 ha, then n would be the total number of hectares in the study area. However, if the smallest unit of the landscape is 10 or 100 ha, then n would be equal to the number of these 10- or 100-ha units in the study area. The actual dimensions of the landscape unit would be determined by (i) the resolution of the field methods and (ii) the minimum area considered viable for old-growth forest. By setting the value of the above expression equal to 1, we are attempting to find the age (or time) beyond which there is one single oldest unit of the landscape.

We have shown in the previous section that the survivorship function for these forests is best fit by the negative exponential function  $A(t) = \exp -(t/b)$ . Therefore, substitution of A(t) for  $A(U_n)$  and the oldest age  $(U_n)$  for time t gives

$$[3] \quad n \exp -\left(\frac{U_n}{b}\right) = 1$$

We now have an expression that can give the characteristic oldest age  $(U_n)$  taking into account both the disturbance cycle (b) and the size of the study area (n). By solving this equation for  $U_n$  we can find the characteristic oldest age forest for a landscape of a given size (n) with a constant (homogeneous) disturbance cycle (b).

Figure 5 shows the change in the characteristic oldest age forest with change in the disturbance cycle from 50 to 300 years for different values of n from 10 to 10 000. As the disturbance cycle increases, the rate of disappearance of patches of given ages would decrease, resulting in an increase in the characteristic oldest aged forest. Also, for a given disturbance cycle, the characteristic oldest aged forest increases with increasing size of the study area. The fact that the relationship between disturbance cycle and the characteristic oldest age is defined by a straight line (regardless of the value of n)





indicates that the tail of the age or survivorship distribution simply moves outward (to the right) with increase in mean age of the landscape. However, the slope of the line describing the relationship between disturbance cycle and characteristic oldest age increases as n increases. For example, when n = 10 and the disturbance cycle increases from 100 to 200 years, the characteristic oldest age increases by 231 years from 230 to 461 years. On the other hand, when n = 1000, the same increase in disturbance cycle results in the characteristic oldest age increasing by 691 years from 691 to 1382 years.

To illustrate the application of the concept of characteristic oldest age, we have used the data from the subalpine forest of the Kananaskis watershed in the southern Canadian Rockies (Johnson and Larsen 1991) for which the map of time since last fire was available. The total study area was 1300 km<sup>2</sup> (130 000 ha). The smallest areal unit (determined by the resolution of the methods used to produce the map of time since last disturbance) was 30 ha. Therefore, the value of *n* would be 130 000/30 = 4333. The survivorship distribution produced two values for the disturbance cycle (*b*), 50 years for the period 1600–1730, and 90 years for 1730–1980. Therefore the following equation for a mixed distribution (Johnson and Gutsell 1994) was used:

$$[4] \quad A(t) = p_1 A_1(t) + p_2 A_2(t)$$

where  $p_1$  and  $p_2$  are the proportions of the mixed distribution included in the first period (1600-1730) and second period (1730-1980), respectively. Substituting the negative exponential for each part of the distribution with  $p_1 = 0.156$ ,  $p_2 = 0.844$ ,  $b_1 = 50$ , and  $b_2 = 90$  into [3] gives

[5] 4333 
$$\left[ 0.156 \exp -\left(\frac{U_n}{50}\right) + 0.844 \exp -\left(\frac{U_n}{90}\right) \right] = 1$$

Solving this equation for  $U_n$ , we get 738 years as the characteristic oldest age. To date, the oldest stand found in the Kananaskis watershed is 686 years old.

The fact that the survivorship distributions for the boreal and subalpine forest landscape (Figs. 3 and 4) fit a negative exponential function indicates that the hazard rate does not change with age of the forest. In demographic terminology, hazard is defined as the mortality force or the instantaneous death rate  $(q_x)$ . If we assume that this fire hazard (i.e., the probability of being burned) increases with age of the forest, the survivorship could be a Weibull distribution (Johnson and Van Wagner 1985) as

$$[6] \quad A(t) = \exp -\left(\frac{t}{b}\right)^c$$

where b is the scale parameter and c is the shape parameter. As can be seen from this equation, the negative exponential is a special case of the Weibull when c = 1 and the hazard is constant. When c < 1, the hazard decreases with age, and when c > 1, the hazard increases with age.

We can see the effect of the value of parameter c on the characteristic oldest age by substituting the Weibull function rather than the negative exponential into the equation used to calculate the characteristic oldest age (i.e.,  $n \exp$  $-(U_n/b)^c = 1$ ). Figure 6 shows the change in characteristic oldest age with change in disturbance cycle for varying values of c. This family of curves shows that the relationship between disturbance cycle and characteristic oldest age continues to be linear. However, as with changing values of n, the effect of changing values of c is to alter the slope, which decreases as c increases. Thus, as c increases (i.e., as the effect of aging on disturbance hazard increases), the effect of a given increase in the disturbance cycle has less of an effect on the characteristic oldest age. For example, if c = 1, an increase in the disturbance cycle from 100 to 200 years results in an increase in the characteristic oldest age by 460 years from 461 to 921 years. On the other hand, if c = 2, the same increase in disturbance cycle increases the characteristic oldest age by only 214 years from 215 to 429 years. Consequently, if older stands have an increased chance of being disturbed, it is not surprising that the characteristic oldest age would be lower.

Size of the study area has often been a criterion for

equilibrium; small areas often lack not only the old-age tail of the landscape age distribution but also the very young stands. The distribution for these small areas may also consist of all old-age forest or all very young forest. Equation 2 (Fig. 5) has already shown the relationship between the disturbance cycle, the size of the study area, and the characteristic oldest age. Clearly a similar relationship could be presented that would indicate the effect of varying disturbance cycle and size of the study area on the characteristic youngest age. Young-growth forests are rarely discussed but could equally be missing from the landscape age distribution. However, in managed landscapes, this is an increasingly infrequent problem.

Finally, we suggest one way that stand-level definitions of old growth could be incorporated into this model. Suppose we establish from stand-level characteristics such as those given by Franklin et al. (1981), the minimum age at which a stand develops old-growth characteristics. We could then modify [3] so that we substitute this particular minimum age for  $U_n$ . With given values of n and b, we now solve [3] for the right-hand side of the equation rather than setting this value equal to 1. This value will give the number of units and hence the proportion of the total landscape that is greater than the age at which these forests show the stand-defined ecological characteristics of old growth.

#### Implications for management

Management of ecosystems requires an understanding of processes operating at the landscape level. It also requires that these landscape processes be more than theoretical or intuitive concepts and that they be both measurable and testable. Therefore, for the management of old-growth forests, we have developed a disturbance-frequency model of old growth that not only defines disturbance frequency as the process that allows the survival of stands to old age but also shows how this process can be measured.

Studies of old-growth forest that focus on stand characteristics alone do not recognize the landscape nature of old forests (i.e., they do not generally look at the age distribution of the landscape). The lack of such a landscape perspective may account for the commonly held view (Harris 1984) that the majority of the North American forested landscape was in old growth prior to European settlement (but see Sprugel 1991). Given the estimated fire cycles for the boreal and subalpine forests, it is obvious that regardless of the chronological criterion for old growth, the majority of the landscape would not have been considered very old.

Furthermore, the empirical distributions obtained for the boreal and subalpine forests (Figs. 3 and 4) indicate that there is no single natural disturbance frequency, because the disturbance frequencies seem to change on the time scale of hundreds of years. Thus most forests will have experienced within the lifetime of the oldest trees one or more changes in disturbance frequency associated with changes in the large-scale processes that control the disturbance frequency. This suggests that the usual search for a natural-disturbance regime may be inappropriate.

It has also been argued, often with little evidence, that disturbance is in some way dependent on the age of the forest (e.g., Romme 1982). Figure 6 illustrates the effect that assumptions of age-dependent disturbance have on the characteristic oldest age. In the situation in which older stands are more subject to disturbance than younger stands (c > 1), an increase in the disturbance cycle (interval between disturbances) does not lead to the same proportionate increase in old-age forests as when every age stand has an equal probability of being disturbed (c = 1). Obviously, the situation in which younger stands have an increased probability of disturbance (c < 1) leads to a greater proportionate increase in old-age forest for a given change in disturbance cycle. It is therefore important to boreal-forest managers that the present empirical evidence suggests a constant hazard of burning for the boreal and subalpine conifer forests (Figs. 3 and 4).

Another point to recognize is that landscape-level processes may be beyond the manipulation or control of managers. A good example is provided by current fire management and fire suppression activities in the boreal and subalpine forests. As shown by the earlier examples (Figs. 3 and 4), the landscape age mosaic (and hence the proportion of the landscape in old growth) is largely determined by the fire cycle, which evidence suggests is controlled by climate (Schroeder et al. 1964; Newark 1975; Street and Birch 1986; Flannigan and Harrington 1988; Swetnam and Betancourt 1990; Johnson and Wowchuk 1993). We know that the majority of the area burned is burned by a few large fires, the general rule being that 95% of the area burned is due to 5% of the fires (Straus et al. 1989). The years in which these large fires occur have been characterized by weather conditions that produce dry fuels and high winds. These weather conditions are associated with large-scale blocking high pressure systems and midtropospheric anomalies (Newark 1975; Street 1985; Flannigan and Harrington 1988; Johnson and Wowchuk 1993) and are thus controlled by large-scale meteorological processes over which managers have little or no control. Therefore, it may be virtually impossible, regardless of fire-suppression policies, to manipulate the fire cycle and hence the age mosaic of the boreal forest landscape.

There are at least two strategies in managing for old-growth forests: (i) to create at least some characteristic oldest age forest stands (e.g., 500-year-old stands) or (ii) to maintain a given proportion of the landscape in forests greater than a certain age. In either case, it is important to keep in mind that the larger the area, the greater the chance of capturing more of the tail of the age distribution (Fig. 6). Consequently, if the area is small (e.g., n = 10), a disturbance cycle of approximately 225 years would be required to obtain some forest greater than 500 years old. However, if the area is large (e.g., n = 1000), we should find some forest greater than 500 years old, even with a disturbance cycle as low as 50 years. Another way to look at it is that, with a given disturbance cycle (e.g., 100 years), the two smaller areas (n =10 or n = 100) will not have any forest greater than 500 years while the two larger areas (n = 1000 or n = 10000) would.

## Conclusions

In conclusion, the ideas of landscape-disturbance equilibrium and old growth seem to have acquired almost metaphysical overtones. The model presented in this paper shows that both concepts can be defined and given empirical content in terms of the rates at which landscape disturbances are operating. As indicated by our examples, the boreal and subalpine forests and probably most natural areas will not be in equilibrium for periods extending over 500 years, particularly if the disturbance cycles are controlled by climate. Age distributions of forested landscapes (and the amount of old-age forests) are controlled by large landscape-scale processes and not by smallscale processes involved in forest management. Although there has been some shift towards more of a landscape perspective on management, there is still some problem with understanding and appreciating that these landscape level natural processes may be beyond any kind of management control. For example, we are interested in understanding the relationship between weather and fire behaviour and in forecasting weather, not because in doing so we will be able to control either the weather or the resulting fires but because such information can warn us of problems. This forewarning can allow us to manage people such that the impacts of these disturbances (e.g., lives and property lost) are lessened.

## Acknowledgements

We thank M. Kellman, C. Clark, S. Gutsell, and C. Nash for thoughtful comments on the manuscript. We also thank M. Puddister for producing the figures. This research was supported by the Natural Sciences and Engineering Research Council of Canada and Parks Canada.

### References

- Cline, S.P., Berg, A.B., and Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44: 773-786.
- Dunwiddie, P.W. 1983. Comment on "Fire and other disturbances of the forests in Mount Rainier National Park" by M.A. Hemstrom and J.F. Franklin. Quat. Res. 19: 402-403.
- Flannigan, M.D., and Harrington, J.B. 1988. A study of the relation of meteorological variables to monthly provincial area burned by wildfire in Canada (1953-1980). J. Appl. Meteorol. 27: 441-452.
- Franklin, J.F., Cromack, K., Jr., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F., and Juday, G. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. No. PNW-118.
- Gumbel, E.J. 1958. Statistics of extremes. Columbia University Press, New York.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133-302.
- Harris, L.D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. The University of Chicago Press, Chicago, Ill.
- Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res. 3: 329-382.
- Hemstrom, M.A., and Franklin, J.F. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. Quat. Res. 18: 32-51.

- Johnson, E.A. 1979. Fire recurrence in the subarctic and its implications for vegetation composition. Can. J. Bot. 57: 1374-1379.
- Johnson, E.A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge, U.K.
- Johnson, E.A., and Gutsell, S.L. 1994. Fire frequency models, methods and interpretations. Adv. Ecol. Res. 25: 239-287.
- Johnson, E.A., and Larsen, C.P.S. 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. Ecology, **72**: 194–201.
- Johnson, E.A., and Van Wagner, C.E. 1985. The theory and use of two fire history models. Can. J. For. Res. 15: 214-220.
- Johnson, E.A., and Wowchuk, D.R. 1993. Wildfires in the southern Canadian Rocky Mountains and their relationship to mid-tropospheric anomalies. Can. J. For. Res. 23: 1213-1222.
- Kaufmann, M.R., Moir, W.H., and Covington, W.W. 1992. Old-growth forests: what do we know about their ecology and management in the southwest and Rocky Mountain regions? *In* Old-growth forests in the Southwest Rocky Mountain Regions: proceedings of a workshop, USDA For. Serv. Gen. Tech. Rep. No. RM-213. pp. 1-11.
- Masters, A.M. 1990. Changes in forest fire frequency in Kootenay National Park, Canadian Rockies. Can. J. Bot. 68: 1763-1767.
- Newark, M.J. 1975. The relationship between forest fire occurrence and 500 millibar longwave ridging. Atmos. Ocean, 13: 26-33.

Pike, L.H., Rydell, R.A., and Denison, W.C. 1977. A 400-year-old Doulgas-fir tree and its epiphytes: biomass, surface area, and their distributions. Can. J. For. Res. 7: 680-699.

- Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol. Monogr. 52: 199-221.
- Schroeder, M.J., Glovinsky, M., Hendricks, V.H., et al. 1964. Synoptic weather types associated with critical fire weather. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, Calif.
- Shugart, H.H. 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York.
- Sollins, P., Grier, C.C., McCorison, F.M., Cromack, K., Jr., Fogel, R., and Fredriksen, R.L. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon and Washington. Ecol. Monogr. 50: 261-285.
- Spies, T.A., and Franklin, J.F. 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. Nat. Areas J. 8: 190-201.
- Sprugel, D.G. 1991. Disturbance, equilibrium, and environmental variability: what is 'natural' vegetation in a changing environment? Biol. Conserv. 58: 1-18.
- Street, R.B. 1985. Drought and synoptic fire climatology of the boreal forest region of the Canadian prairie provinces. *In* Proceedings of the 8th Conference on Fire and Forest Meteorology, Detroit, Mich., April 29 –

May 2, 1985. Society of American Foresters, Washington, D.C. pp. 108-112.

- Strauss, D., Bednar, L., and Mees, R. 1989. Do one percent of forest fires cause ninety-nine percent of the damage? For. Sci. **35**: 319-328.
- Street, R.B., and Birch, E.C. 1986. Synoptic fire climatology of the Lake Athabasca – Great Slave Lake area, 1977–1982. Climatol. Bull. 20: 3–18.
- Suffling, R., Smith, B., and Dal Molin, J. 1982. Estimating past forest age distributions and disturbance rates in northwestern Ontario: a demographic approach. J. Environ. Manage. 14: 45-56.
- Swetnam, T.W., and Betancourt, J.L. 1990. Fire-Southern Oscillation relations in the southwestern United States. Science (Washington, D.C.), **249**: 1017-1020.

- Swetnam, T.W., Sutherland, E.K., and Thompson, M.A. 1983. Comment on dating forest disturbances. Quat. Res. **19**: 400-401.
- Van Wagner, C.E. 1978. Age-class distribution and the forest fire cycle. Can. J. For. Res. 8: 220-227.
- Vogt, K.A., Grier, C.C., Meier, C.E., and Keyes, M.R. 1983. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington, as affected by fine-root input. Ecol. Monogr. 53: 139-157.
- Yarie, J. 1981. Forest fire cycles and life tables: a case study from interior Alaska. Can. J. For. Res. 11: 554-562.