

Forest Ecology and Management 150 (2001) 259-265

Forest Ecology and Management

www.elsevier.com/locate/foreco

The relative importance of fire and watercourse proximity in determining stand composition in mixed conifer riparian forests

William H. Russell*, Joe R. McBride

Department of Environmental Science, Policy, and Management, Forest Science Division, University of California, Berkeley, CA 94720, USA

Received 15 February 2000; accepted 24 July 2000

Abstract

Factors related to the composition of riparian forest stands on three streams in the northern Sierra Nevada mixed conifer forest type were related to proximity to the water course and years since fire. Using a linear regression analysis 46 variables were correlated to the natural log of distance from the thalweg "ln(distance)" including a highly significant positive correlation to dominance and percent canopy cover of conifers, and a significant negative correlation to the same variables when applied to hardwoods. Twenty six variables were correlated to years since fire "years" including similar correlations to the dominance and cover of hardwood and conifer species. However, the significance of the correlation and the degree of sample variability described by fire age was relatively low in comparison to that found for distance from the thalweg. In addition the relative frequency of fire scars increased in a linear fashion with distance from the watercourse. The results of this study indicate that the importance of fire as a determining influence on forest composition declines in proximity to the riparian zone. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Fire history; Riparian; Species composition

1. Introduction

The composition of forest stands are determined by a variety of biotic and abiotic factors including recruitment sources, disturbance regime, environmental site conditions, and management history. In a particular stand, the importance of any one of these factors is determined by the life history and survival strategy of the species within the stand and by interaction with other factors. In this study, we contrast the relative importance of fire history and riparian influence in the composition of mixed conifer riparian forests.

Fire has is an important factor in determining the structure and composition of mixed conifer forests in the Sierra Nevada (Bock et al., 1978; Conard and Radosevich, 1982; Kercher and Axelrod, 1984; Russell et al., 1998). In fact, the suppression of fire has been shown to significantly affect species composition in a number of forest types (Baker, 1992; Lunan and Habeck, 1973; Murray, 1992; Phillips and Sure, 1990).

Riparian systems differ from their upland counterparts in a number of important ways. As the ecotone

^{*}Corresponding author. Present address: P.O. Box 1690, Mendocino, CA 95460, USA. Tel.: +1-707-937-3139. E-mail address: wrussell@mcn.org (W.H. Russell).

between terrestrial and aquatic ecosystems, they encompass sharp gradients of environmental factors, ecological processes, and plant communities (Gregory et al., 1991). In many cases species composition within riparian zones can be quite different from the forest matrix in which they are embedded. For example, the riparian zones of the Sierra Nevada, mixed-conifer forest type are often dominated by nonconiferous deciduous trees (Holstein, 1984). The reasons for these differences are all in some way connected to the proximity of the water course. The microclimate created by the zone, and the physical action of the water course, in distinct ways shape the adjacent forest community (Leighton and Risser, 1989; Lisle, 1989; McBride and Strahan, 1984). In addition, the conditions within riparian areas can reduce the importance of fire as a disturbance (Weaver, 1960).

The importance of riparian vegetation in relation to aquatic ecosystem function has been noted in the literature (Knight and Bottorf, 1984; Mahoney and Erman, 1984). Significant changes to riparian vegetation can affect water temperature, water quality, and inputs of woody debris and detritus, which in turn can affect populations of fish and aquatic invertebrates (Baltz and Moyle, 1984; Mahoney and Erman, 1984; Meehan et al., 1977). The question addressed by this study is whether fire suppression can alter the species composition of riparian forest stands sufficiently to effect aquatic habitat of adjacent watercourses. Or, in contrast, does riparian influence supersede the effects of fire regime in regard to the composition of riparian communities?

2. Research methods

Data regarding stand structure, species composition, and fire history of riparian forests were collected on three sites within Lassen National Forest, located at 40° latitude where the Sierra Nevada meets the Cascade mountain ranges in north-central California. Results were analyzed using a variety of statistical methods in order to determine the importance of fire in the dynamics of riparian communities in the mixed conifer forest type. Study sites were selected in areas with late seral forest stands, with a minimum of logging history.

2.1. Sampling methods

Transects were randomly located perpendicular to stream channels on three sites within Lassen National Forest including Deer Creek, Mill Creek, and Battle Creek. Study sites were selected to be as geographically and ecologically similar as possible.

Data were collected on a total of 195 circular 40 m² plots located at random distances along each transect. Within each plot the species and diameter of all trees greater than 10 cm dbh, as well as the occurrence of sapling size trees (height > 1 m, dbh < 10 cm), and seedling size trees (height < 1 m), in addition to the occurrence and percent cover of all shrub species, were recorded. At the center of each plot the total canopy cover, and canopy cover of conifers and hardwood species separately, as well as, the slope, aspect, distance from thalweg (the lowest point in the crosssection of the stream channel), and height from the stream channel, were also recorded. Where fire scars were visible on trees within plots or in proximity to transects, fire history was determined using the methods described in Barrett and Arno (1988).

3. Results

Comparison between physical factors with variables related to the composition of riparian stands resulted in a number of interesting correlations. Both years since fire "years" and distance from thalweg "ln(distance)" were found to have significant relationships with the relative dominance of conifer over hardwood species in terms of both canopy cover and basal area.

3.1. Canopy cover

Analysis of the sample variables indicates a significant positive correlation (P = 0.027) between the years since fire "years" and percent canopy cover of conifers (Fig. 1). Though the correlation was significant the slope of increase was modest and the amount of sample variability explained by the model was low ($R^2 = 0.025$).

A much stronger relationship (P < 0.001) was found between the distance in meters from the thalweg "ln(distance)" and the percent canopy cover of

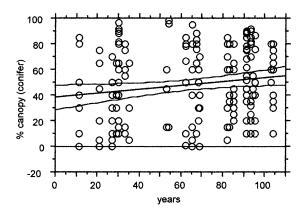


Fig. 1. Regression of years since fire with percent canopy cover of conifers (with 95% confidence intervals for the mean).

conifers (Fig. 2). The slope was significant and the R^2 (0.451) relatively high. A significant linear relationship was also found between % canopy cover and the square of channel width "width²" which may relate to the susceptibility of a section of the stream to flood (P = 0.038). However, the slope of the regression line was small, and the R^2 (0.005) quite low.

Height from the stream channel "ln (height)" and width of the riparian zone "width²" also exhibited a correlation (P < 0.001) with conifer canopy. However, because the model including "ln(distance)" had a greater R^2 value than the model including "ln(height)", and because these two variables exhibited a high degree of covariance, "ln(height)" was removed from the model. The variable "width²" was

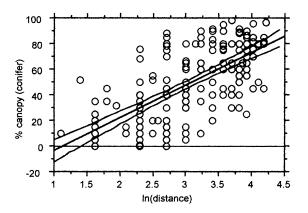


Fig. 2. Regression of ln(distance) with percent canopy cover of conifers. The variable distance was transformed with the natural log function in order to give the data a normal distribution.

also left out of the model due to covariance with "ln(distance)", and because of its limited importance in the proceeding analysis. Considering the variables "ln(distance)" and "years" in a multiple-regression analysis resulted in the following model with an R^2 of 0.473.

% Conifer canopy =
$$22.6 + 1.3 \ln(\text{distance})$$

+ 0.2 years

A similar analysis for the percent canopy cover of hardwood species yielded a highly significant negative correlation (P < 0.001) with "ln(distance)". In contrast no significant correlation (P = 0.611) was found between hardwood canopy and "years".

3.2. Basal area and dominance

The total basal area of all trees found on the sample plots increased in a linear fashion (P = 0.014) as a function of "years". This trend can be generally attributed to an increase in conifer dominance relative to fire age as hardwood dominance exhibited a decline relative to the same variable.

A significant correlation (P = 0.029) was also found between the relative basal area of conifer species and "years" since the last fire (Fig. 3). As was the case with the canopy cover of conifers, the correlation with "years" was significant, but the slope of increase was modest, and the amount of sample variability explained by the model was low ($R^2 = 0.024$). In

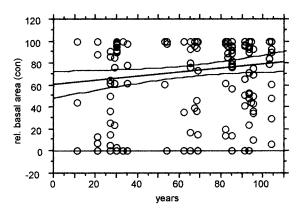


Fig. 3. Regression of years since fire with the relative basal area of conifers.

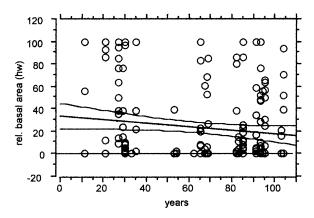


Fig. 4. Regression of years since fire with the relative basal area of hardwood species.

contrast, there was a significant negative correlation (P = 0.050) between the relative basal area of hardwood species and years since the last fire (Fig. 4). The sample variation explained by the model was low $(R^2 = 0.020)$.

In addition, comparing the relative basal areas of conifer and hardwood species to distance from the thalweg yielded highly significant positive correlation (P < 0.001) between the relative basal area of conifers (Fig. 5), and the basal area of hardwoods with "ln(distance)" (Fig. 6).

Combining the variables " $\ln(\text{distance})$ " and "time" in a model with the relative basal area of conifers and hardwood species resulted in an R^2 value

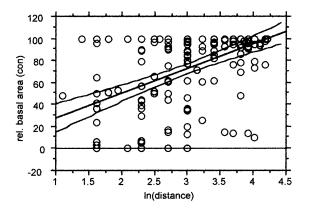


Fig. 5. Regression of the natural log of distance from thalweg with the relative basal area of conifers.

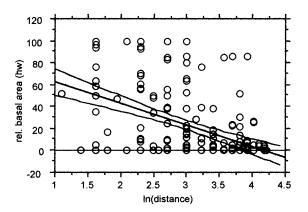


Fig. 6. Regression of the natural log of distance from thalweg with the relative basal area of hardwoods.

of 0.243 and 0.213, respectively.

Relative basal area (conifers)

$$= -6.21 + 2.28 \ln(\text{distance}) + 0.18 \text{ years}$$

Relative basal area (hardwoods)

$$= 91.42 - 19.45 \ln(\text{distance}) - 0.15 \text{ years}$$

3.3. Relative importance of fire

Fire as a factor appeared to be a less important influence than distance on the variables measured on these sites. To demonstrate the relationship between these two factors a linear regression was performed with the relative frequency of fire scars as the independent variable and distance from the thalweg as the dependent resulting in a positive correlation (P = 0.006) with an R^2 value of 0.307.

3.4. Combined model

In order to unify the analysis, the preceding models were combined by calculating a dominance ratio.

Dominance ratio

$$= \frac{\% \operatorname{Canopy} \left(\operatorname{conifer} \right) + \operatorname{basal} \operatorname{area} \left(\operatorname{conifer} \right)}{\% \operatorname{Canopy} \left(\operatorname{total} \right) + \operatorname{basal} \operatorname{area} \left(\operatorname{total} \right)}$$

This ratio was then included in a model with time and distance factors yielding a *P*-value of less than

0.001, and an R^2 of 0.128.

Dominance ratio (conifer)

 $= 0.5 + 0.001 \ln(\text{distance}) \times \text{years}$

3.5. Correlation analysis

In addition to the relationship of "ln(distance)" and "years" to factors related to the dominance of conifers and hardwoods, these factors were also correlated to a number of other sample variables. A total of 26 variables were significantly correlated to "years" using a standardized *z*-test (Table 1).

In comparison, 46 variables were significantly correlated to "ln(distance)" (Table 2). In every general

Table 1 Variables correlated to years since last fire ^a

Correlation with years	z-score	P-value
% Canopy (conifer)	0.16	0.027
% Canopy (total)	0.16	0.024
Mature (hardwood)	No correlation	No correlation
Alnus rhombifolia	-0.19	0.009
Poles (total)	0.16	0.026
Poles (conifer)	0.24	0.001
P. ponderosa	0.19	0.007
Poles (hardwood)	No correlation	No correlation
Populus fremontii	-0.19	0.008
Saplings (conifer)	0.16	0.026
Pinus lambertiana	0.14	0.049
P. ponderosa	0.20	0.005
Pseudotsuga menziesii	0.21	0.003
Saplings (hardwood)	No correlation	No correlation
Salix lutea	-0.15	0.035
Quercus kelloggii	0.16	0.024
Seedlings (conifer)	0.26	< 0.001
Abies concolor	0.27	< 0.001
P. menziesii	0.30	< 0.001
Basal area (total)	0.18	0.014
Relative basal area (conifer) 0.16		0.029
P. ponderosa 0.15		0.030
Relative basal area (hard0.14 0.049 wood)		
Acer macrophyllum	-0.15	0.040
Quercus kelloggii	0.15	0.032
Salix lutea	-0.16	0.025
% Cover shrub species	No correlation	No correlation
Potentilla species	0.14	0.044
Rosa californica	0.13	0.066
Symphoricarpos acutus	-0.15	0.035

^a The designations (mature, pole, sapling, and seedling) refer to the density (#/hectare) of each size class.

Table 2 Variables correlated to distance from the thalweg ^a

Correlation with ln(distance)	z-score	<i>P</i> -value
% Canopy (conifer)	0.67	<0.001
% Canopy (total)	-0.36	< 0.001
Mature (total)	0.36	< 0.001
Mature (con)	0.44	< 0.001
Abies concolor	0.31	< 0.001
Pinus lambertiana	0.18	0.011
Pinus ponderosa	0.22	0.003
Mature (hardwood)	-0.24	< 0.001
Populus fremontii	-0.28	< 0.001
Poles (total)	0.16	0.029
Poles (con)	0.21	0.004
Abies concolor	0.25	< 0.001
Pinus contorta	-0.22	0.003
Poles (hardwood)	No correlation	No correlation
Alnus rhombifolia	-0.18	0.013
Populus fremontii	-0.16	0.023
Quercus kelloggii	0.17	0.020
Quercus wislizinii	0.17	0.020
Saplings (con)	0.33	< 0.001
Abies concolor	0.33	< 0.001
Calocedrus decurrens	0.18	0.010
Saplings (hardwood)	-0.29	< 0.001
Alnus rhombifolia	-0.25 -0.25	< 0.001
Populus fremontii	-0.20	0.006
Salix lutea	-0.20 -0.19	0.009
Seedlings (con)	0.28	< 0.001
Abies concolor	0.18	0.010
Calocedrus decurrens	0.26	< 0.001
Pinus lambertiana	0.18	0.010
Pinus ponderosa	0.22	0.002
Pseudotsuga menziesii	0.20	0.002
Seedlings (hardwood)	No correlation	No correlation
Quercus wislizinii	0.21	0.003
~		
Basal area (total)	0.45	<0.001
Relative basal area (conifer)	0.47	<0.001
Abies concolor Calocedrus decurrens	-0.44	<0.001
	0.20	0.005
Pinus contorta	-0.22	0.002
Pinus lambertiana	0.18	0.010
Pinus ponderosa	0.22	0.002
Pseudotsuga menziesii	0.18	0.014
Relative basal area (hardwood)	-0.44	<0.001
Alnus rhombifolia	-0.26	<0.001
Populus fremontii	-0.30	<0.001
Quercus wislizinii	0.17	0.021
Salix lutea	-0.21	0.004
Basal area (total)	0.46	< 0.001
% Cover shrub species Ceanothus integerrimus	No correlation 0.15	No correlation 0.034

^a The designations (mature, pole, sapling, and seedling) refer to the density (#/hectare) of each size class.

measure of conifer density and dominance there was a highly significant positive correlation with "ln(distance)" across all size classes. In addition, individual conifer species were strongly correlated with "ln(distance)" in terms of density and dominance. This phenomenon is particularly pronounced with regard to relative basal area. Every species of conifer that existed on the sample plots exhibited a positive correlation, with the exception of *Pinus contorta* which had an inverse correlation due to its tolerance of riparian conditions.

There were also significant correlations for "ln(distance)" with the density and dominance with of hardwoods in general as well as for individual hardwood species. The relative basal areas of *Alnus rhombifolia*, *Populus fremontii*, and *Salix lutea* were all negatively correlated. In contrast *Quercus wislizinii*, a dry upland species showed a positive correlation.

4. Discussion

The purpose of this study was to determine what physical factors, both static and dynamic, influence the balance between conifer and hardwood dominance in the riparian zones sampled. Of the factors that were examined, distance from the stream channel showed the greatest influence on the composition and distribution of species. To a lesser extent the time since the fire was also shown to exert an influence on many of the same aspects of stand composition. The significance of these two factors was related to the relative importance of their ecological influence.

Within the Sierra Nevada mixed conifer forest, fire is often a dominant influence in stand structure and composition. In the stands examined in this study fire was influential to some degree, but was by no means dominant. The most important influence in these stands was the proximity to the stream. This measure carries with it a number of different connotations. The first, and perhaps most obvious, is the moisture regime. Relatively high soil moisture has the effect of favoring certain species. In the case of the mixed conifer forest many of the species, though not all, are hardwoods. The second important connotation of stream proximity is the occurrence of flood. Recurrent flood not only increases soil moisture but can damage standing trees through the movement of large woody

debris, and can suffocate the roots of flood intolerant species. The repeated occurrence of flood results in conditions quite different from those on upland sites, including more open canopy cover, less dense stands, and a reduced duff layer on the forest floor.

The community dynamics of riparian forest systems are more complex than those of their more xeric counterparts due to the interaction between these two ecological influences. The influence of the riparian zone affects forest structure and increases fuel moisture so that not only are community dynamics altered, but they are altered in such a way as to reduce the likelihood and impact of fire.

In summary, the influence of riparian conditions were dominant in the determination of stand composition, including the relative importance of conifers and hardwoods, within riparian zones. The influence of fire, though significant, was relatively small.

References

- Baker, W.L., 1992. Effects of settlement and fire suppression on landscape structure. Ecology 73, 1879.
- Barrett, S.W., Arno, S.F., 1988. Increment-borer methods for determining fire history in coniferous forests. USDA Forest Service. General Technical Report INT-244.
- Baltz, D.M., Moyle, P.B., 1984. The influence of riparian vegetation on stream fish communities of California. California riparian systems: ecology, conservation, and productive management, University of California Press, Berkeley, CA, pp.183–187.
- Bock, J.H., Raphael, M., Bock, C.E., 1978. A comparison of planting and natural succession after a forest fire in the northern Sierra Nevada. J. Appl. Ecol. 15, 597–602.
- Conard, S.G., Radosevich, S.R., 1982. Post fire succession in white fir (Abies concolor) vegetation of the northern Sierra Nevada. Madroño 29, 42–56.
- Gregory, S.V., Swanson, F.J., McKee, W.A., Cummins, K.W., 1991.
 An ecosystem perspective on riparian zones. Bioscience 41, 540–551.
- Holstein, G., 1984. California riparian forests: deciduous islands in an evergreen sea. In: California Riparian Systems: Ecology, Conservation, and Productive Management, University of California Press, Berkeley, CA, pp. 2–22.
- Kercher, J.R., Axelrod, M.C., 1984. A process model of fire ecology and succession in a mixed conifer forest. Ecology 60, 129–142.
- Knight, A.W., Bottorf, R. L., 1984. The importance of riparian vegetation to stream ecosystems. In: California Riparian Systems: Ecology, Conservation, and Productive Management, University of California Press, Berkeley, CA, pp. 160–176.
- Leighton, J.P., Risser, R. J., 1989. A riparian vegetation ecophysiological response model. In: Proceedings of the

- California Riparian Systems Conference, Davis, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.
- Lisle, T.E., 1989. Channel-dynamic control on the establishment of riparian trees after large floods in northwestern California. In: Proceedings of the California Riparian Systems Conference, Davis, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.
- Lunan, J.S., Habeck, J.R., 1973. The effects of fire exclusion on ponderosa pine communities in Glacier National Park Montana. Can. J. Res. 3, 574–579.
- Mahoney, D.L., Erman, D.C., 1984. The role of streamside bufferstrips in the ecology of asquatic biota. In: California Riparian Systems: Ecology, Conservation, and Productive Management, University of California Press, Berkeley, CA, pp. 168–176.
- McBride, J.R., Strahan, J., 1984. Establishment and survival of riparian species on gravel bars of an intermittent stream. American Midland Naturalist 112, 235–245.

- Meehan, W.R., Swanson, F.J., Sedell, J.R., 1977. Influence of riparian vegetation on aquatic ecosystems with particular reference to salminoids and their food supply. In: Symposium on Importance, Preservation and Management of Riparian Habitat, Fort Collins, Colorado, US Forest Service, Rocky Mountain Forest and Range Experiment Station.
- Murray, M., 1992. Suppression threatens subalpine meadows. Inner Voice 4, 10 pp.
- Phillips, D.L., Sure, D.J., 1990. Patch-size effects on early succession in southern Appalachian forests. Ecology 71, 204–212.
- Russell, W.H., McBride, J., Rowntree, R., 1998. Revegetation after four stand-replacing fires in the Lake Tahoe basin. Madroño 45 (1), 40–46.
- Weaver, J.E., 1960. Floodplain vegetation of the central Missouri valley and contacts to woodlands with prairie. Ecological Monographs 30, 37–64.