

Geostatistically modeling stem size and increment in an old-growth forest

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Geostatistics provides tools to model, estimate, map, and eventually predict spatial patterns of tree size and growth. Variogram models and kriged maps were used to study spatial dependence of stem diameter (DBH), basal area (BA), and 10-year periodic basal area increment (BAI) in an old-growth forest stand. Temporal variation of spatial patterns was evaluated by fitting spatial stochastic models at 10-year intervals, from 1920 to 1990. The study area was a naturally seeded stand of southwestern ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *scopulorum*) where total BA and tree density have steadily increased over the last decades. Our objective was to determine if increased stand density simply reduced individual growth rates or if it also altered spatial interactions among trees. Despite increased crowding, stem size maintained the same type of spatial dependence from 1920 to 1990. An isotropic Gaussian variogram was the model of choice to represent spatial dependence at all times. Stem size was spatially autocorrelated over distances no greater than 30 m, a measure of average patch diameter in this forest ecosystem. Because patch diameter remained constant through time, tree density increased by increasing the number of pine groups, not their horizontal dimension. Spatial dependence of stem size (DBH and BA) was always much greater and decreased less through time than that of stem increment (BAI). Spatial dependence of BAI was close to zero in the most recent decade, indicating that growth rates in 1980–1990 varied regardless of mutual tree position. Increased tree crowding corresponded not only to lower average and variance of individual growth rates, but also to reduced spatial dependence of BAI. Because growth variation was less affected by intertree distance with greater local crowding, prediction of individual growth rates benefits from information on horizontal stand structure only if tree density does not exceed threshold values. Simulation models and area estimates of tree performance in old-growth forests may be improved by including geostatistical components to summarize ecological spatial dependence.

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La géostatistique fournit les outils pour modéliser, estimer, cartographier et éventuellement prédire la distribution spatiale des arbres selon leur diamètre, leur surface terrière et leur accroissement périodique. La variation temporelle de la corrélation spatiale est évaluée entre 1920 et 1990 par période de 10 ans. Le peuplement étudié est une vieille futaie de *Pinus ponderosa* Dougl. ex Laws. du sud-ouest des États-Unis issue de régénération naturelle et dont la surface terrière et la densité ont augmenté de façon soutenue au cours des dernières décennies. L'objectif consiste à déterminer si, tout en réduisant l'accroissement des arbres individuels, l'augmentation de la densité modifie aussi leur corrélation spatiale. Le variogramme construit révèle que la structure spatiale de la futaie étudiée n'a pas changé entre 1920 et 1990. Il révèle aussi le regroupement des arbres par bouquets dont le diamètre moyen est de 30 m. Le diamètre des bouquets demeurant constant dans le temps, l'augmentation de la densité est donc causée par l'augmentation du nombre de paquets et non par l'augmentation de leur diamètre. La corrélation spatiale de la taille des arbres reste toujours supérieure à celle de leur accroissement. Elle diminue avec le temps, mais moins vite que celle de leur accroissement. La faible corrélation spatiale de l'accroissement observée à la dernière décennie montre que l'accroissement varie indépendamment de la localisation des arbres dans le bouquet. L'augmentation de la densité correspond non seulement à la diminution de la moyenne et de la variance de l'accroissement, mais aussi à la réduction de sa corrélation spatiale. Sachant que plus la densité augmente, moins l'accroissement de l'arbre individuel dépend des distances avec ses voisins dans le bouquet, l'apport de la distribution spatiale des arbres dans la futaie à la prédiction de leur accroissement devient nul lorsque la densité dépasse un maximum critique. Les modèles de simulation spatio-temporelle de la croissance des futaies peuvent être améliorés par l'intégration des informations sur la corrélation spatiale en faisant appel à la géostatistique.

[Traduit par la rédaction]

Introduction

Estimation and mapping of forest resources is an inescapable premise of management, planning, and research. Time and cost

constraints do not usually allow exhaustive measurements; hence, sampling schemes need to be designed and implemented to estimate population values (Husch et al. 1982). Because foresters deal with spatially distributed samples and variables, they have long been aware that spatial correlation violates common statistical assumptions, e.g., independence of observations (Matérn 1960; Clutter et al. 1983). Analyses of forest structure and dynamics that incorporate, rather than exclude, information on spatial variability are

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bound to provide a more accurate description of reality. Moreover, estimating the amount of variation due to spatial dependence at different scales provides a basis for designing effective experiments (Jeffers 1982). Mapping often requires interpolation of available sample points to estimate values at unsampled locations and compute spatial averages. Of all interpolation techniques, kriging is the best linear unbiased estimator. Kriging allows declustering of data points and it provides an estimate of mapping error. Most importantly, kriging incorporates information on spatial dependence, or continuity, of the variable being mapped, and is fully supported by regionalized variable theory, also known as geostatistics (Matheron 1963, 1965). Isaaks and Srivastava (1989) and Cressie (1991) provide details of geostatistical theory, methods, and applications.

Regionalized variables are spatially correlated to one another over short distances, but independent of one another over large distances. This approach has proven both flexible and powerful for answering research and management questions in the spatial domain. From its original application in ore exploration and mining (Krige 1966), geostatistics has found applications in a number of disciplines, including geology (Olea 1977), soil science (Burgess and Webster 1980a, 1980b), remote sensing (Carr and Myers 1984), pollution studies (Lefohn et al. 1987), ecology (Robertson 1987), phytopathology (Lecoustre et al. 1989), geography (Oliver et al. 1989a, 1989b), hydrology (American Society of Civil Engineers 1990a, 1990b), entomology (Liebhold et al. 1991), climatology (Bigg 1991), and meteorology (Hevesi et al. 1992a, 1992b). Rossi et al. (1992) provide an extensive review of geostatistical models to interpret spatial dependence in ecological studies. The potential of regionalized variable theory for forestry applications has not yet been fully exploited. Matérn (1960) supplied a rigorous and extensive treatment of the theory, and used correlograms to examine problems in forest sampling. Samra et al. (1989) used variograms to analyze spatial heterogeneity of tree height after 1, 2, and 3 years of growth in a *Melia azedarach* L. plantation. Cohen et al. (1990) analyzed conifer canopy structure by computing variograms from digitized aerial video images. Current research efforts on linking point processes to watershed and landscape processes include GIS (geographical information system) models (Band et al. 1991; Baker 1992), but have not yet employed geostatistical representations of forest structure. Mandallaz (1993) discussed geostatistical estimation methods to merge airborne observations and ground-truth measurements in forest inventories.

The space available for a tree to grow is determined by its position with respect to nearby trees (Weiner 1988). For instance, in southwestern ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *scopulorum*), intraspecific competition for resources reduces growth rates of dominant pines (Biondi et al. 1992) and makes them less responsive to environmental variations (Sutherland et al. 1991). However, does increased stand density simply reduce growth rates or does it also alter spatial interactions among trees? In this article, we used geostatistics to test for spatial trends, directional patterns, and temporal modifications of spatial dependence. We fitted spatial stochastic models to ground measurements of tree size and increment at 10-year intervals, from 1920 to 1990. The study area was a naturally seeded, old-growth forest undergoing endogenous modification of its horizontal and vertical structure.

Southwestern ponderosa pine stands have changed considerably since European settlement a few decades ago (Moir and Dieterich 1988). Until the end of the 19th century, stand dynamics in this relatively arid environment used to be primarily controlled by fire (Weaver 1951; Dieterich 1980). Frequent, low-intensity fires spread erratically and burned surface materials without reaching the canopy. Fire controlled vegetation structure by producing a patchy pattern of surviving trees across the landscape (Cooper 1960; White 1985). Mortality in old trees was caused primarily by lightning, a frequent phenomenon and a natural cause of fire in the Southwest (Schubert 1974). Around the 1870s, after European settlement, domestic livestock were introduced in the pine forest. Overgrazing and trampling by cattle and sheep depleted fuels and reduced competition of herbaceous understorey with pine seedlings. Lack of fuels and active fire suppression, which began at about 1910 in north-central Arizona, reduced the thinning effect that fire once had on pine regeneration (Madany and West 1983; Savage and Swetnam 1990). Reduced fire frequency, favorable climatic conditions, and good seed crops resulted in abundant pine regeneration during the 20th century (Pearson 1950). Today many old-growth ponderosa pine stands are multistoried, even though age or size classes still occur in a mosaic pattern (Kaufmann et al. 1992). The seedlings that established in the early 1900s have grown into dense pole stands where basal area exceeds 40 m²/ha, density reaches about 2000 stems/ha and total crown cover exceeds 70% (Covington and Moore 1991). Accurate knowledge of spatial and temporal patterns is needed to inform silvicultural guidelines and management decisions for long-term sustainability of these and other old-growth forests.

Materials and methods

Study area

The Gus Pearson Natural Area, located along U.S. Highway 180, about 15 km northwest of Flagstaff, Ariz., is one of the first Research Natural Areas established in the United States (Avery et al. 1976). It is included in the Fort Valley Experimental Forest, within the Coconino National Forest, Coconino County. Geographical coordinates for the approximate center of the area are 35°16'11"N and 111°44'30"W; elevation is 2230–2260 m. Climate, topography, soil parent material, soil type, biota, and disturbance history of the Gus Pearson Natural Area are relatively homogeneous (Avery et al. 1976; White 1985). Climate is characterized by cold and wet winters, late spring droughts, and cool summers with frequent thundershowers. Over the 82-year period from 1909 to 1990, annual precipitation at the study area averaged 573 mm and mean annual temperature averaged 6°C. Monthly precipitation averaged 15 mm in June, the driest month, and 83 mm in August, the wettest month. Based on mean monthly temperatures, January is the coldest month (average of -3.7°C) and July is the warmest (average of 17.0°C). Topography is level to very gentle, with an average slope and exposure of about 5% and 182°, respectively. Bedrock is formed by late Tertiary lava flows and soils consist of montmorillonitic clay-loams with high moisture-holding capacity. Some small rock outcrops are present, but the area has the potential of being fully covered by trees.

The Gus Pearson Area is an unthinned, unburned, uneven-aged, pure, old-growth stand of southwestern ponderosa pine. It is an 800 × 400 m permanent plot divided in twenty-nine 100 × 100 m subplots plus five smaller subplots. Only plots 1–29 were considered because plots 30–34, the ones closest to the Fort Valley Experiment Station, had been thinned in the past. When it was established in 1920, all pines with diameter at breast height (1.3–1.5 m; DBH) above 8.9 cm (3.5 inches) were

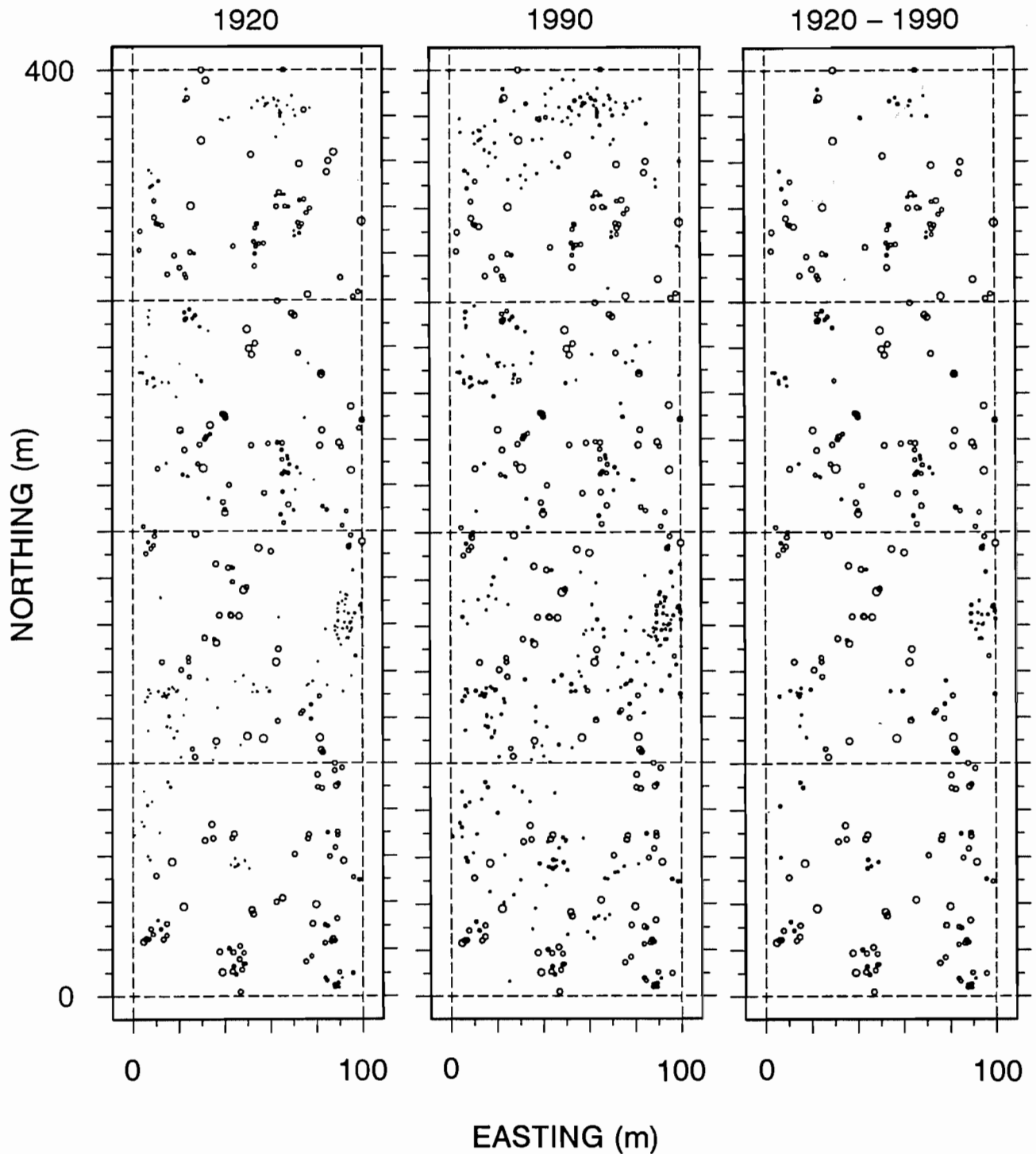


FIG. 1. Map of pines included in the 1920 ($N = 424$) and 1990 ($N = 590$) forest inventory of the study area. Circle diameter is proportional to stem diameter and is on a scale different from stem coordinates. The location of pines included in all the 1920–1990 forest inventories is also shown ($N = 308$; circle diameter is proportional to stem DBH in 1990).

identified by a metal tag with plot and tree number. The Forest Service has remeasured stem diameter at tag level every 5 years from 1920 to 1960, and every 10 years from 1960 to 1990. The 1920–1970 inventories of plots 1–14, 16, and 27 have already been published (Avery et al. 1976). On those plots, ingrowth was measured from 1925 to 1960 by placing new tags on pines whose DBH had exceeded 8.9 cm since the last inventory. In 1970, the minimum diameter for inclusion in the inventory was raised to 15.2 cm (6 inches) and ingrowth was measured only on plots 15, 17, 23–26, and 28–29, where ingrowth had not been

measured since 1940. Because of budget constraints, no ingrowth was measured in 1980 and 1990. Three different kinds of tags can be found on some large trees: current tags were first used in 1970. At that time, pines already dead were given the last numbers for the plot and their original number was assigned to a new, nearby tree. Although this did not affect the data, it made it impossible to obtain coordinates of trees that died before 1970.

At present, the inventory data base includes 12 DBH measurements per tree, repeated throughout a 70-year period on a total of 5724 pines. Data were converted from English to metric

TABLE 1. Statistics of stem diameter (DBH; cm)

Year	N	Mean	Variance	CV ^a (%)	Minimum	Median	Maximum	a ^b (m)	C ₀ ^c	C ₁ ^d	SPD ^e (%)
Estimates based on all available trees for each year											
1920	424	36.4	455.7	59	7.9	37.3	88.6	30	40	450	92
1930	479	35.9	458.1	60	9.1	31.2	91.4	30	55	440	89
1940	505	36.9	444.5	57	9.4	30.5	94.0	30	60	420	88
1950	567	35.6	456.3	60	9.1	29.2	95.8	30	80	400	83
1960	605	36.1	441.2	58	10.4	29.7	97.5	30	90	380	81
1970	605	37.8	420.7	54	14.5	31.2	99.8	30	90	360	80
1980	594	38.6	399.5	52	15.2	32.0	100.8	30	90	330	79
1990	590	39.9	381.4	49	15.5	33.7	102.4	30	90	310	78
Estimates based on the same trees for each year											
1920	308	43.5	352.1	43	15.2	43.4	88.6	30	70	310	82
1930	308	46.0	333.8	40	16.5	45.7	91.4	30	70	280	80
1940	308	48.0	320.5	37	17.5	47.8	94.0	30	75	270	78
1950	308	49.5	313.6	36	18.5	49.2	95.8	30	80	255	76
1960	308	51.0	304.4	34	19.1	50.8	97.5	30	90	240	73
1970	308	52.1	302.6	33	19.3	52.2	99.8	30	95	230	71
1980	308	52.8	298.8	33	19.3	53.0	100.8	30	100	220	69
1990	308	53.8	296.2	32	19.3	54.0	102.4	30	100	215	68

^aCV, coefficient of variation.^ba, range of sample variogram.^cC₀, nugget of sample variogram.^dC₁, sill of sample variogram.^eSPD, spatial dependence, given by the ratio 100C₁/(C₀ + C₁).TABLE 2. Statistics of stem basal area (BA; cm²/π)

Year	N	Mean	Variance	CV ^a (%)	Minimum	Median	Maximum	a ^b (m)	C ₀ ^c (×10 ³)	C ₁ ^d (×10 ³)	SPD ^e (%)
Estimates based on all available trees for each year											
1920	424	445.5	202 432	101	15.6	347.8	1962.5	30	16	220	93
1930	479	436.7	211 691	105	20.7	243.4	2088.5	30	23	220	91
1940	505	451.4	218 961	104	22.1	232.6	2209.0	30	30	210	88
1950	567	431.6	221 310	109	20.7	213.2	2294.4	30	40	200	83
1960	605	435.5	223 653	109	27.0	220.5	2376.6	30	45	200	82
1970	605	461.4	229 368	104	52.6	243.4	2490.0	30	45	205	82
1980	594	472.4	226 256	101	57.8	256.0	2540.2	30	45	200	82
1990	590	493.1	225 753	96	60.1	283.1	2621.4	30	45	195	81
Estimates based on the same trees for each year											
1920	308	561.7	191 977	78	57.8	470.9	1962.5	30	33	185	85
1930	308	611.8	202 598	74	68.1	522.1	2088.5	30	40	190	83
1940	308	655.0	210 069	70	76.6	571.2	2209.0	30	45	195	81
1950	308	689.5	216 630	68	85.6	604.0	2294.4	30	50	195	80
1960	308	724.9	221 678	65	91.2	645.2	2376.6	30	55	195	78
1970	308	754.6	228 204	63	93.1	681.2	2490.0	30	60	198	77
1980	308	772.2	229 681	62	93.1	701.0	2540.2	30	65	195	75
1990	308	796.2	233 927	61	93.1	727.7	2621.4	30	70	195	74

NOTE: See Table 1 (notes a-e) for definitions of statistics.

units and checked for errors and inconsistencies. Stem basal area (BA; cm²/π) and 10-year periodic basal area increment (BAI; cm²/π) were computed from the repeated measurements of stem DBH (cm). Negative increments were used to identify errors. The original DBH values were also checked when either the 5-year BAI exceeded 100 cm²/π or the 10-year BAI exceeded 200 cm²/π. Pre-1980 abnormal values on plots 1-14, 16, and 27 were compared with values listed in Avery et al. (1976). Whenever possible, abnormal 1990 values were verified in the field. If a pine was missing in 1980 and measured in both 1990 and 1970, the missing value was estimated. In 1990, maximum tree

size was 114.3 cm and the largest number of annual rings counted on a single increment core was 615.

Subplot corners at the Gus Pearson Natural Area were accurately mapped in 1991 by two registered surveyors using an electromagnetic distance measuring (EDM) system (Whyte and Paul 1985). The subplot corners were then used as reference points to map all the tagged ponderosa pines included in a 100 × 400 m, north to south area formed by subplots 5, 12, 13, and 20. Stem coordinates were first obtained as polar coordinates using a staff compass and a measuring tape. They were later converted into x-y coordinates using as reference point

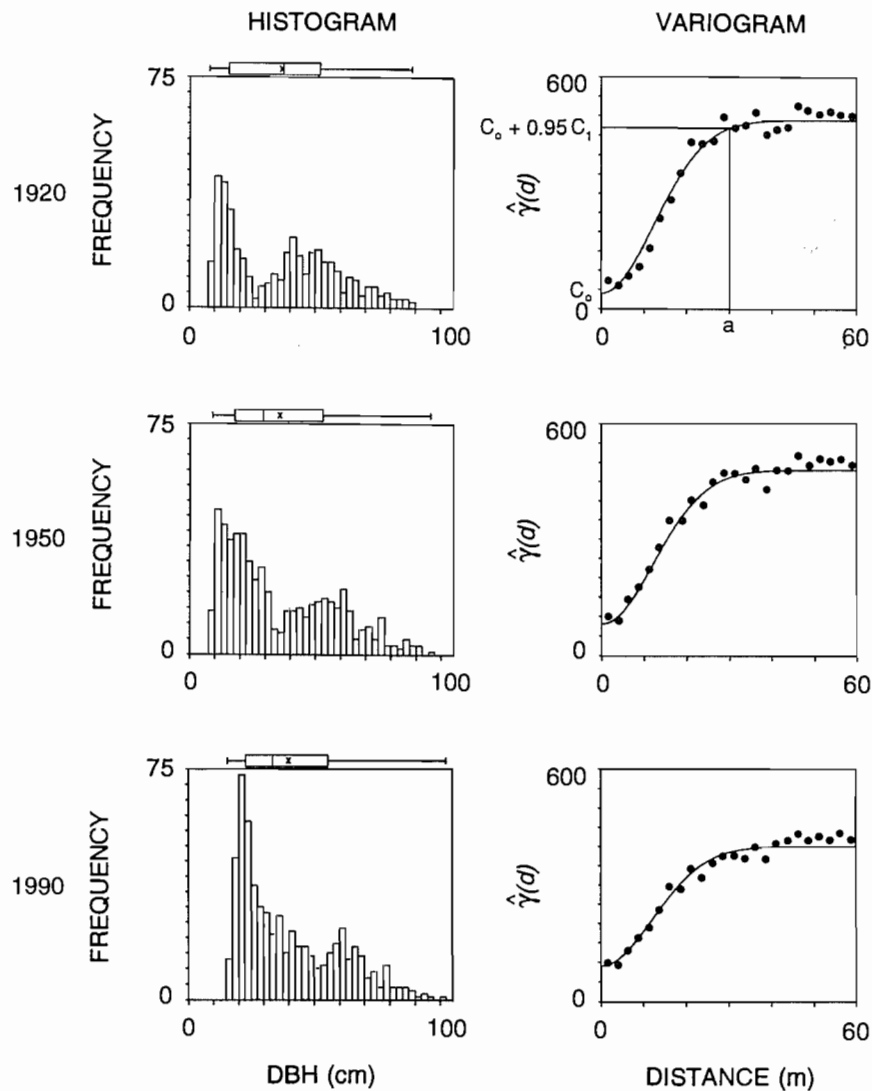


FIG. 2. Absolute histogram, box plot, and omnidirectional sample variogram for stem diameter (DBH) of pines included in the 1920 ($N = 424$), 1950 ($N = 567$), and 1990 ($N = 590$) forest inventory. The Gaussian variogram model for 1920 includes a graphical representation of its nugget (C_0), range (a), and total sill ($C_0 + 0.95C_1$).

the southwest corner of the area. The Forest Service defined subplots simply as a grid of smaller land units that did not differ in terms of vegetation-forming factors (Major 1951). Hence, the four subplots were merged together in the final analysis. Stem maps were checked in the field for possible errors and were found accurate, on average, to the nearest meter. Maximum intertree distance was 410.5 m among a total of 183 921 pairs.

Geostatistical analyses

Geostatistical methods are based on a fundamental assumption: if a variable is observed at several spatial locations, its estimate at any unsampled location should be most dependent on the nearest observations. In other words, the correlation between observations for pairs of locations decreases with increasing distance between the locations. Dependence on nearby data locations and estimation uncertainty are expressed mathematically by a random function model (Myers 1991). Let $Z(x)$ denote the value of the spatial variable at location x , x being a point in two- or three-dimensional space. Each $Z(x)$ is a random variable, and the collection of such random variables (for every x in a region of interest) is a random function. The spatial dependence of these random variables is assumed to be a function of the separation vector. Mathematically, the assumptions imposed on $Z(x)$ are

$$E[Z(x + d) - Z(x)] = 0$$

$$0.5\text{var}[Z(x + d) - Z(x)] = \gamma(d)$$

where E denotes expectation, d is the separation vector, var means variance, and $\gamma(d)$ is the variogram of $Z(x)$. If $\gamma(d)$ depends on the length of d but not on its direction, then $Z(x)$ and $\gamma(d)$ are said to be isotropic. The use of random function models for interpolating spatial data was introduced by Matérn (1960) and Matheron (1963, 1965). Matérn referenced the variogram, but used the covariance function and the correlogram, graphical representations of the spatial (auto)covariance and (auto)correlation, respectively. Matheron placed much more emphasis on the variogram, which is based on weaker stationarity assumptions (Myers 1989). The variogram is easier to estimate than the covariance function or the correlogram because it does not require a value for the mean of $Z(x)$.

To clarify, $Z(x)$ is a "model" for the variable of interest, and $\gamma(d)$ is a "parameter" of the model. In general $\gamma(d)$ is not known a priori and must be estimated from the data. The sample variogram is the simplest estimator of $\gamma(d)$ (Isaaks and Srivastava 1988; Myers 1991). The sample variogram is computed after sorting all possible pairs of locations into classes by distance and direction. The sample variogram value for a certain distance and direction is the sum of squared differences between all pairs

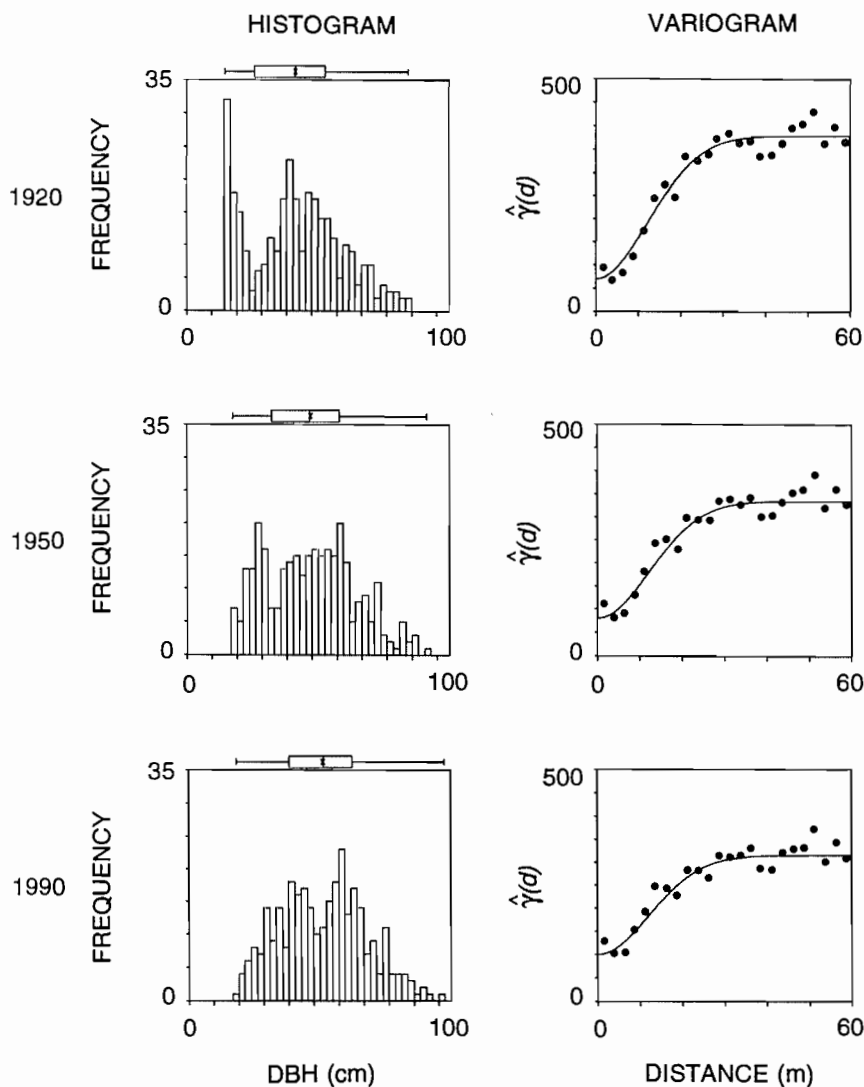


FIG. 3. Absolute histogram, box plot, and omnidirectional sample variogram for stem diameter (DBH) of pines always present in the 1920–1990 inventories ($N = 308$).

of observations, x_i, x_k , which belong to the distance class r and angle window θ , as follows:

$$\hat{\gamma}(r, \theta) = \frac{0.5}{N(r, \theta)} \sum_{i,k}^{N(r, \theta)} [Z(x_i) - Z(x_k)]^2$$

Directional sample variograms are usually computed for θ equal to 0, 45, 90, and 135° with an angle tolerance of $\pm 22.5^\circ$. The omnidirectional sample variogram is computed for θ equal to 0° with an angle tolerance of $\pm 90^\circ$. Sample variograms are then plotted against distance to examine directional dependence (anisotropy) and to choose a model for the variogram. Variogram models are needed to solve the ordinary kriging equations; hence, they must satisfy a form of positive definiteness. Valid variogram models include the nugget, spherical, exponential, Gaussian, and linear model; positive linear combinations of these models may also be used. The distance at which the variogram model reaches a constant value is called the range, and the constant value is called the sill. The Gaussian and exponential models reach the sill asymptotically; hence, their range is defined as the distance at which the variogram value is 95% of the sill. The linear model does not have a true range and sill but, rather, the ratio of these two parameters is the slope of the line. The nugget model corresponds to no spatial dependence, i.e., pure randomness (Isaaks and Srivastava 1989).

The ordinary kriging estimator of a regionalized variable at any unsampled location is a weighted sum of values at nearby locations. The form of the estimator is the same for estimates at a single point (point kriging) or for estimates of the average value over an area (block kriging). The kriging weights are a function of the unsampled location and are determined by imposing two conditions on the estimator: (i) unbiasedness, and (ii) minimum variance of the estimation error. While all sampled locations could be used to produce all estimates, it is customary to specify a search neighborhood that identifies data closest to the unsampled location. The kriging variance, i.e., the minimized variance of the estimation error, can be computed using the kriging weights and represents a relative ranking of model reliability. Public domain software (Englund and Sparks 1989) makes geostatistical tools accessible and inexpensive.

Spatial dependence of stem size and increment was analyzed using two-dimensional variograms and ordinary block kriging. Stem DBH, BA, and BAI were studied at 10-year intervals, from 1920 to 1990. To model both short- and long-range spatial dependence, sample variograms were computed (i) for 1-m lags up to a maximum distance of 24 m, (ii) for 2.5-m lags up to a maximum of 60 m, and (iii) for 4-m lags up to 96 m. Each sample variogram was computed twice, first using all available trees (N ranging from 424 in 1920 to 605 in 1960) and second using only trees always present from 1920 to 1990 and with DBH

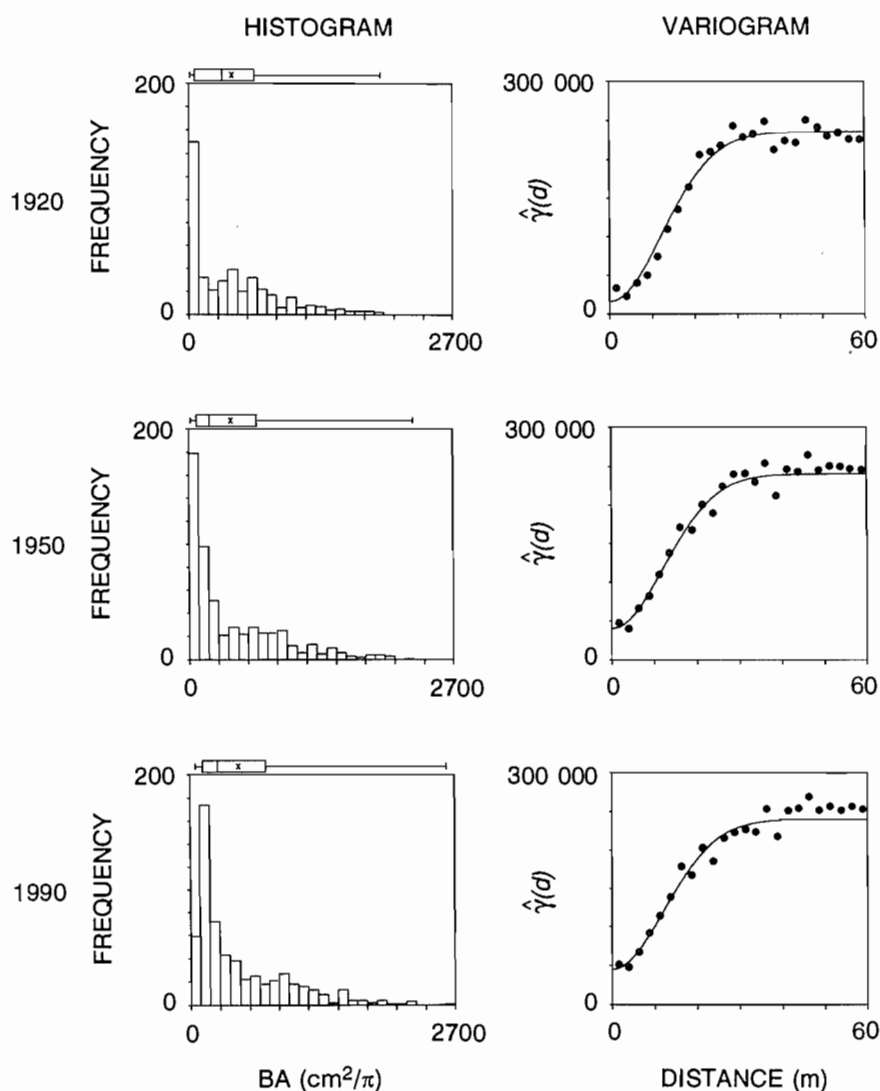


FIG. 4. Absolute histogram, box plot, and omnidirectional sample variogram for stem basal area (BA) of pines included in the 1920 ($N = 424$), 1950 ($N = 567$), and 1990 ($N = 590$) forest inventory.

larger than 15.2 cm in 1920 ($N = 308$). Because accurate ingrowth records were lacking after 1960, we defined the restricted sample to eliminate thickets of small pines from the analysis. Then, by comparing results obtained using the general and the restricted sample we evaluated the influence of ingrowth, i.e., increased number of small pines, on spatial dependence of stem size and increment. Ordinary block kriging was used to estimate average values over 5×5 m blocks. The search neighborhood allowed a maximum of 20 and a minimum of three nearest data points within a circular search area with maximum search radius of 30 m (Englund and Sparks 1989).

Spatial and temporal variability were analyzed separately. Because data were both spatially and temporally distributed, it might seem that modeling space-time trends jointly would be more appropriate. As pointed out in Rouhani and Myers (1990), there are fundamental differences between spatial dependence and temporal dependence that hamper modeling the joint correlation structure. Because of the lack of a distance measure in space-time, it is usually necessary to treat either the spatially dependent variable separately at each time or the temporally dependent variable separately at each location. In the case of this data set, with many spatial locations but relatively few time points, it was more reasonable to focus on the spatial variability at each time point. The parameters of spatial variability were estimated at each time using a nonrandom sample from a single

realization of the spatially dependent variable. Knowledge of the parameter distribution required strong assumptions, which could not be statistically tested from the data. The nonparametric, univariate Mann-Kendall test (Kendall and Gibbons 1990) was used to evaluate monotone temporal trends of model parameters. Assessing temporal dependence in geostatistical parameters by means of the Mann-Kendall test provided a numerical value for visually persistent tendencies with respect to time.

Results and discussion

Stand density increased between 1920 and 1990 (Fig. 1). Estimates of stem size and increment based on all available observations were affected by ingrowth records. Influx of small pines increased the number of observations and decreased median tree size from 1920 to 1950 (Tables 1 and 2). Mortality and lack of ingrowth records were mostly responsible for the decreasing number of observations and increasing average tree size from 1960 to 1990 (Tables 1 and 2). The Mann-Kendall test for N , mean and median of DBH and BA from 1920 to 1990 was not highly significant ($p > 0.034$). Temporal trends in stem size were not affected by ingrowth when described by DBH (Table 1) and BA (Table 2) of trees always present and with DBH greater than

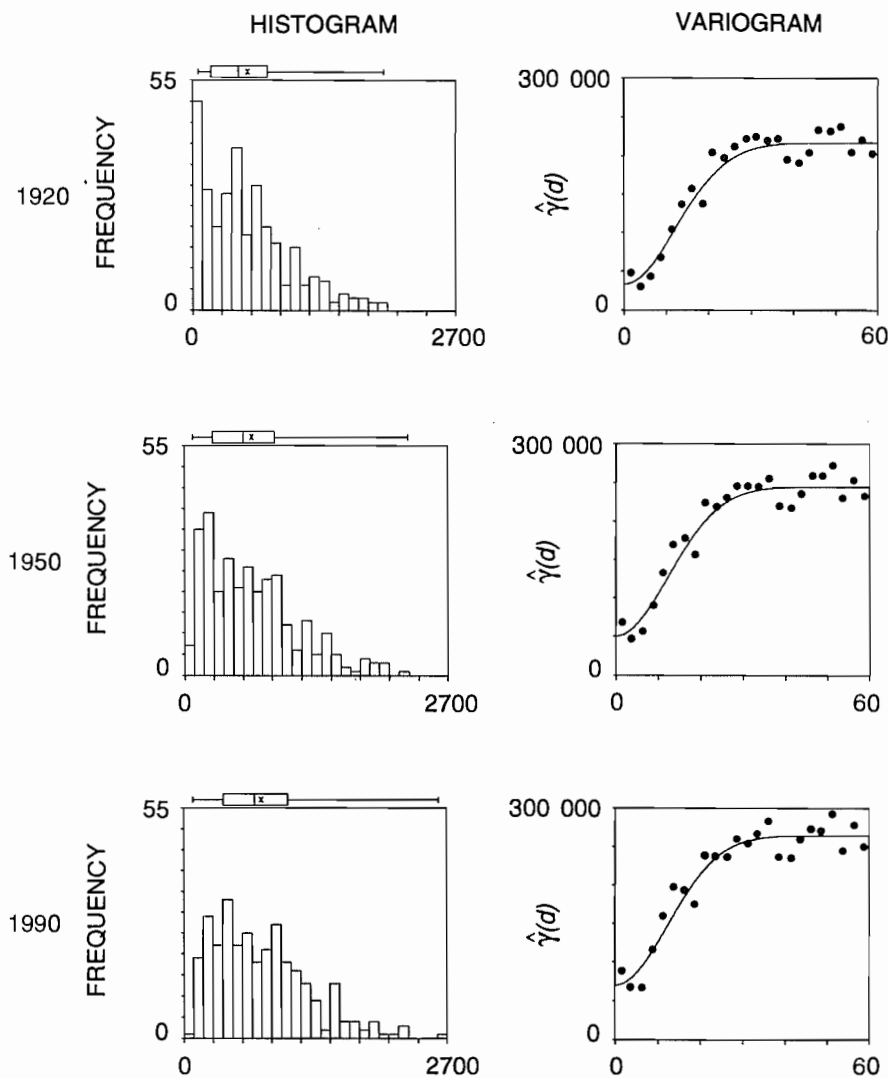


FIG. 5. Absolute histogram, box plot, and omnidirectional sample variogram for stem basal area (BA) of pines always present in the 1920–1990 inventories ($N = 308$).

15.2 cm in 1920 (the restricted sample, with $N = 308$ at all times). Average size of the restricted sample constantly increased from 1920 to 1990: the Mann–Kendall test for mean and median of DBH and BA was equal to 1.00 ($p = 0.0005$). Size variability of the restricted sample steadily decreased: the Mann–Kendall tests for the coefficients of variation of DBH and BA were -0.98 ($p = 0.0008$) and -1.00 ($p = 0.0005$), respectively.

Stem size distributions were analyzed using absolute histograms and box plots (Tukey 1977; Figs. 2–5). Although minimum size increased between 1920 and 1990 (Mann–Kendall test, $p \leq 0.0018$), the histogram shape for DBH remained both bimodal and skewed to the right when based on all available observations (Fig. 2). Ingrowth of small pines in the 1930–1960 inventories contributed to maintaining skewness of size distributions. When based on the restricted sample, the histogram shape for DBH gradually changed through time (Fig. 3). It was bimodal and skewed to the right in 1920 because of a large amount of small pines. It became more symmetrical, albeit slightly bimodal, in 1990 because diameter increment was greater in smaller trees, thus producing faster outgrowth from the smallest size classes. Interestingly, the bimodal feature of the DBH

histogram in 1920 (Figs. 2 and 3) was caused by a large number of pines with DBH from 10 to 20 cm. This peak in size frequency suggested that strong regeneration pulses must have occurred in southwestern ponderosa pine forests long before the “excellent 1919 seedling crop over most of the Colorado Plateau” (Schubert 1974). Histogram shapes for basal area (Figs. 4 and 5) were unimodal, but showed changes in skewness that were consistent with those observed for DBH.

Spatial dependence explained a large amount of stem size variability. The directional and omnidirectional sample variograms did not show evidence of spatial trend or anisotropy (Isaaks and Srivastava 1989). At all times from 1920 to 1990, a Gaussian model plus nugget very closely represented the omnidirectional sample variograms for DBH (Figs. 2 and 3) and BA (Figs. 4 and 5). In all cases, the model was able to fit sample variograms computed using either 1.0-, 2.5-, or 4.0-m distance classes. For brevity, only figures of sample variograms computed using 2.5-m classes were included in this article. The variogram model was defined as

$$\gamma(d) = \begin{cases} C_0 + C_1 [1 - \exp(-3d^2/a^2)] & \text{if } d > 0 \\ 0 & \text{if } d = 0 \end{cases}$$

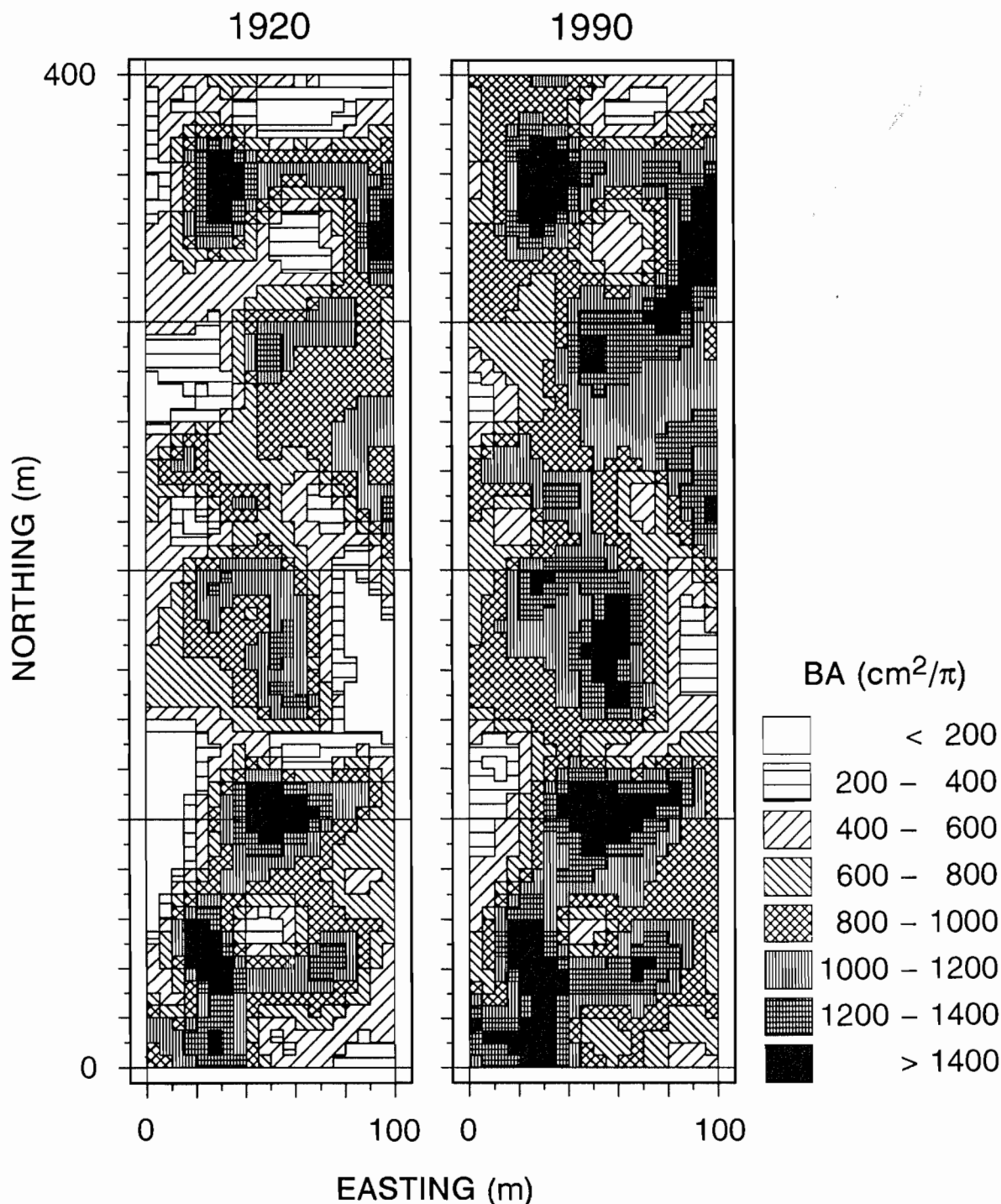


FIG. 6. Ordinary kriging estimates, on 5×5 m blocks, of stem basal area (BA) in 1920 and in 1990, based on pines always present ($N = 308$).

where $\gamma(d)$ is the variogram value for the inter-tree distance d , C_0 is the nugget, C_1 is the sill of the Gaussian component, $C_0 + C_1$ is the total sill and a is the range of the variogram (Fig. 2). The Gaussian model is usually best suited for extremely continuous phenomena (Isaaks and Srivastava 1989). Hence, pines located less than 5–10 m from one another had extremely similar sizes. The parabolic behavior near the origin and the presence of an inflection point are unique to the Gaussian model. Using 1-m lags to increase resolution at short distances, it was possible to notice a stronger parabolic behavior near the origin, pro-

duced by the variogram reaching a minimum after 3–5 m, and increasing at longer as well as shorter distances.

For modeling and simulation purposes, it was remarkable how well the same variogram model could represent spatial dependence of stem size, either DBH or BA, at different spatial scales and at different points in time. Overall, variogram models were affected marginally by ingrowth records, and only in terms of nugget and sill estimates, not of model type or range. The range of variograms for DBH and BA was always 30 m (Tables 1 and 2, Figs. 2–5). Ordinary kriging estimates of average BA over 5×5 m blocks

TABLE 3. Statistics for 10-year basal area increment (BAI; cm²/π)

Years	N	Mean	Variance	CV ^a (%)	Minimum	Median	Maximum	a ^b (m)	C ₀ ^c	C ₁ ^d	SPD ^e (%)
Estimates based on all available trees for each year											
1920–1930	424	43.8	787.0	64	0	39.0	181.3	30	410	370	47
1930–1940	479	37.4	586.3	65	0	33.0	177.8	30	350	230	40
1940–1950	505	29.6	467.6	73	0	24.4	142.2	30	280	180	39
1950–1960	567	30.3	411.9	67	0	26.7	125.4	30	300	120	29
1960–1970	605	25.9	351.4	72	0	22.9	113.4	30	220	120	35
1970–1980	593	18.7	203.5	76	0	17.3	82.6	30	160	50	24
1980–1990	589	23.7	306.3	74	0	21.8	115.5	30	260	60	19
Estimates based on the same trees for each year											
1920–1930	308	50.1	806.0	57	0	45.3	181.3	30	530	240	31
1930–1940	308	43.2	648.0	59	0	39.0	177.8	30	410	220	35
1940–1950	308	34.5	566.1	69	0	31.1	142.2	30	400	170	30
1950–1960	308	35.4	507.5	64	0	31.4	125.4	30	400	110	22
1960–1970	308	29.7	492.7	75	0	26.0	113.4	30	400	100	20
1970–1980	308	17.6	243.6	89	0	15.0	82.6	30	220	30	12
1980–1990	308	24.0	403.0	84	0	21.5	115.5	30	400	10	2

NOTE: See Table 1 (notes a–e) for definitions of statistics.

(Fig. 6) showed clearly the horizontal patchiness of the stand, caused by a mixture of pine groups. Each group is roughly even sized, i.e., formed by trees with similar size, but nearby groups are uneven sized. The variogram range measured the average dimension of these pine groups. Although pine density increased through time, the average dimension of a pine group remained the same, being about 30 m in 1990 as it was in 1920. The consistency through time of variogram models for DBH and BA, with or without ingrowth records, provided strong evidence that size distributions maintained basically the same spatial patterns from 1920 to 1990. Tree density increased by increasing the number of pine groups, not their horizontal dimension.

The nugget, C₀, of variogram models quantifies spatial variability at near-zero distances, whereas the sill of the Gaussian model component, C₁, quantifies spatial dependence. In variogram models of stem size, the nugget was always much less than the sill of the Gaussian component (Tables 1 and 2, Figs. 2–5). Because all variogram models had a finite sill, it was possible to compute the percentage of spatial variance explained by spatial dependence. This percentage was computed from the ratio C₁/(C₀ + C₁) and provided a relative value of spatial dependence, useful for making comparisons. Spatial dependence (SPD) of DBH ranged from 68–78 to 82–92%, slightly less than SPD of BA, ranging from 74–81 to 85–93% (Tables 1 and 2). Whenever such a large spatial dependence exists, point and area estimates of tree size greatly benefit by including information on horizontal stand structure.

Spatial dependence of stem size gradually decreased between 1920 and 1990 (Tables 1 and 2). The Mann–Kendall test for SPD of DBH and BA ranged from –0.94 (p = 0.0015) to –1 (p = 0.0005). The time-related decrease in SPD of stem size was mostly an effect of increasing nugget (Mann–Kendall test, p ≤ 0.0035) and of decreasing sill (Mann–Kendall test for C₁ of DBH was equal to –1.00, p = 0.0005). Small ponderosa pines form dense groups, or thickets, where many intertree distances are less than 2.5 m, the distance lag used in Figs. 2–5 and 7–8. An increase in the number of small pines corresponded to an increase in near-

zero intertree distances, which presumably increased the nugget term of variogram models. The increase in spatial variability at near-zero distances with clustering of trees had already generated the parabolic behavior observed in sample variograms computed for 1.0-m distance classes.

Temporal patterns of stem growth rates (Table 3) estimated using all available observations (Fig. 7) were similar to those estimated using always the same trees (Fig. 8). Individual growth rates decreased over time: the Mann–Kendall test for mean and median BAI was –0.81 (p = 0.0107). In the last decade, 1980–1990, mean and median BAI of the restricted sample were less than half of those in the first decade, 1920–1930 (Table 3). Variance of 10-year periodic basal area increment also decreased over time (Mann–Kendall test = –0.90, p = 0.0043). Because mean BAI decreased more through time than its variance, the coefficient of variation for BAI increased over time (p ≤ 0.0243). This was reflected by increased asymmetry of the data distribution from 1920 to 1990 (Figs. 7 and 8). As shown by BAI histograms based on trees always present (Fig. 8), skewness to the right became stronger as growth rates of more and more pines became smaller. The same pattern appeared in BAI histograms based on all available trees (Fig. 7) even though new, small pines kept entering the inventories between 1930 and 1970 (Figs. 1–3, Table 1). Therefore, the reduction of individual growth rates over time was tied to increased pine density, which usually intensifies intraspecific competition for resources (Biondi et al. 1992). Kriged estimates of average basal area increment over 5 × 5 m blocks (Fig. 9) showed that reduction of growth rates from 1920–1930 to 1980–1990 was not spatially clustered and was common to the entire stand.

Directional and omnidirectional sample variograms of BAI showed no evidence of spatial trend or anisotropy. A nugget plus Gaussian variogram model adequately described spatial dependence of stem increment at all times and distance lags (Figs. 7 and 8). Competitive interactions in southwestern ponderosa pine forests concentrate below ground (Cooper 1960, 1961) and are usually symmetrical, i.e., small trees compete with large trees (Biondi et al. 1992).

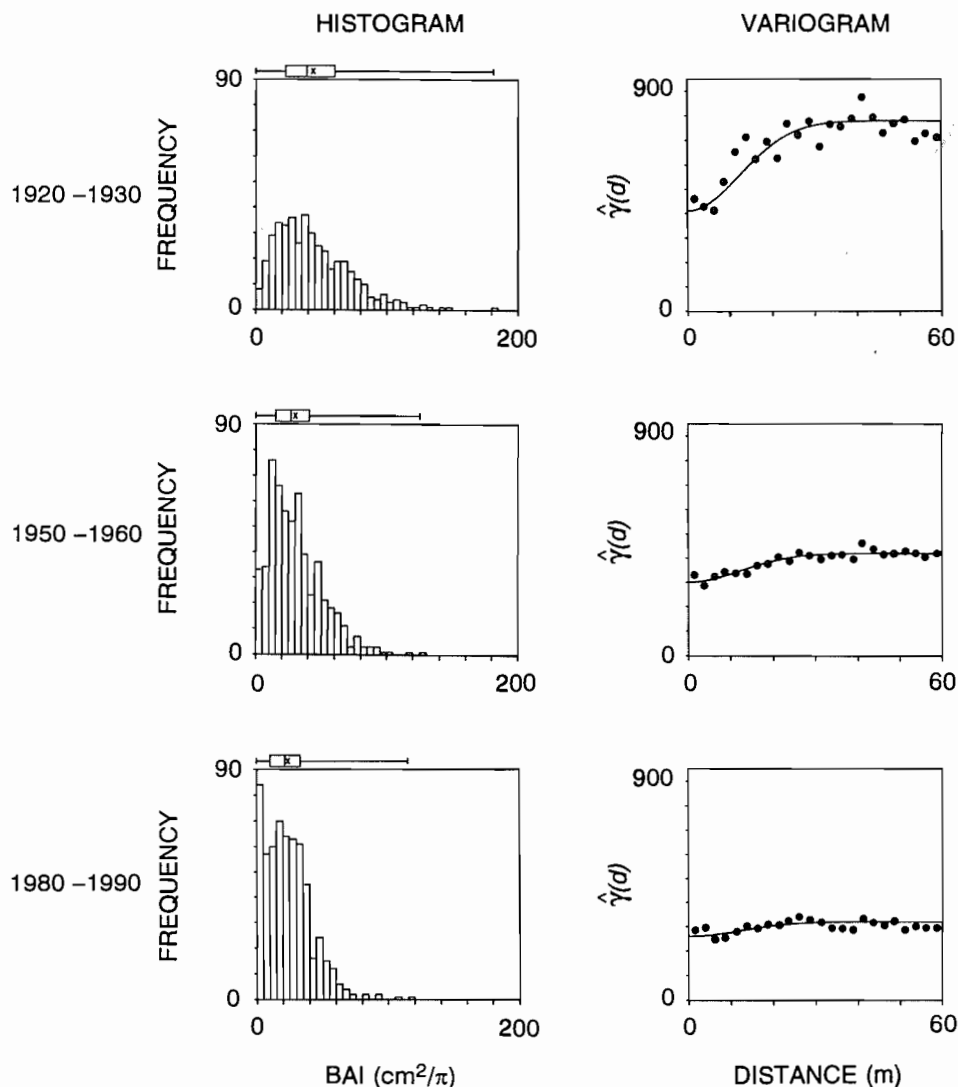


FIG. 7. Absolute histogram, box plot, and omnidirectional sample variogram for 10-year basal area increment (BAI) of pines included in the 1920–1930 ($N = 424$), 1950–1960 ($N = 567$), and 1980–1990 ($N = 589$) forest inventories.

Presumably, the isotropic structure of root systems in ponderosa pine and the ground flatness determined isotropic competitive interactions, resulting in isotropic spatial dependence of growth rates. The range of variogram models for BAI was always 30 m, but even shorter ranges could be considered, partly because of the limited amount of spatial dependence. Considering that spatial variation of growth rates was being modeled, the variogram range could be used to represent the maximum distance spanned by intertree competitive interactions. Therefore, average competitive radius did not exceed average patch size. The absence of spatial dependence beyond 30-m distances suggested a lack of spatial variation in soil properties, which were found to be responsible for spatial dependence in tree growth at scales larger than any reasonable competitive radius (Samra et al. 1989).

Spatial dependence of stem increment was smaller and decreased more through time than that of stem size (Table 3, Figs. 7 and 8). Spatial dependence of BAI was 31–47% in 1920 and 2–19% in 1990. Omnidirectional sample variograms for BAI “flattened out”, i.e., showed a decrease in spatial dependence, after 1950. The nugget component of variogram models for BAI was always greater than the sill of the Gaussian component (Table 3). This indicated that

growth variation at short distances was not much different from growth variation at long distances. The variogram model for the 1980–90 period was almost a pure nugget model, because the Gaussian component was quasi nonexistent (Figs. 7 and 8). A pure nugget variogram model entails a complete lack of spatial dependence, i.e., “the data value at any particular location bears no similarity even to very nearby data values” (Isaaks and Srivastava 1989, p. 307). In these situations, knowledge of sample location does not improve estimation of point values or area averages. In other words, prediction of stem increment becomes independent of mutual tree position.

Geostatistical models of stem increment, especially when compared with models of stem size, indicated that increased stand density during the 1900s not only reduced the magnitude of stem growth rates but it also altered its spatial patterns. At high densities, resources available to each pine are not only a function of its mutual position with respect to surrounding pines but also of its ability to compete, depending, for instance, on the sociological status of the tree, on its genetic potential, and on its microsite, within or on the edge of a patch. Separating the effects of competition, tree vigor, microsite, etc. on growth variation was not the objective of

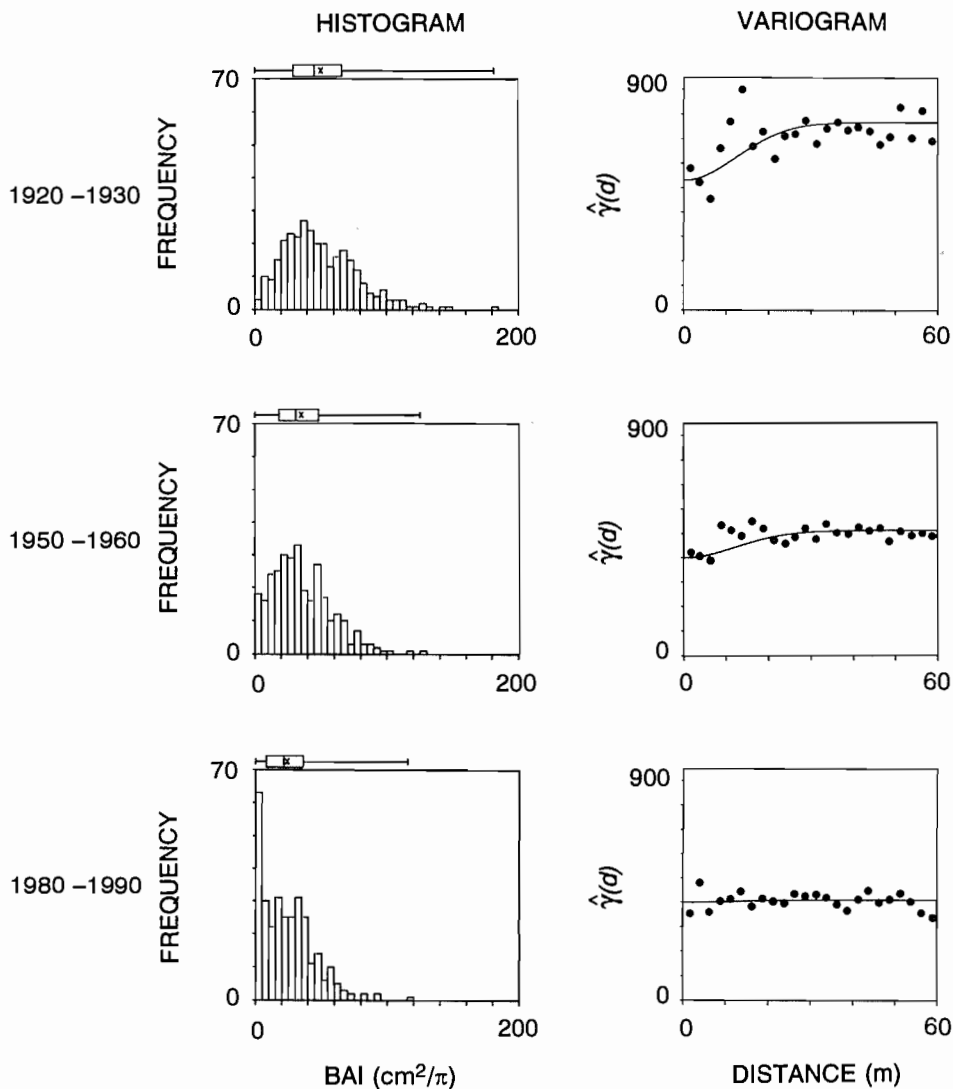


FIG. 8. Absolute histogram, box plot, and omnidirectional sample variogram for 10-year basal area increment (BAI) of pines always present in the 1920–1990 inventories ($N = 308$).

our study. However, reduced spatial dependence of BAI with increasing stand density strongly suggests that growth variation is a function of intertree distance only when local crowding does not exceed threshold values. Because crowding reduced the dependence of growth variation on mutual tree position, prediction of individual growth rates cannot rely on intertree distances alone. Further research should estimate the time needed for a modification in spatial dependence of growth rate to affect spatial patterns of tree size.

Conclusions

Geostatistical models provide tools to quantify spatial scales of ecological patterns and processes. Spatial knowledge is crucial to define unit areas of forest ecosystems that are homogeneous with respect to a given variable or set of variables. Definition of homogeneous areas leads to designing optimal sampling schemes, applying efficient silvicultural treatments, and reducing management costs, especially in old-growth forests. Investigations on spatiotemporal trends of tree size and increment in natural forests provide information to form the basis of principles to guide general forest management for protecting and improving biodiversity as well as long-term forestry sustainability. For instance, deter-

mination of characteristic patterns of old-growth stand structure is useful in enhancing and restoring old-growth ecosystems within managed landscapes (Mladenoff et al. 1993). Furthermore, most ecological theories and models of vegetation composition and productivity assume, explicitly or not, some spatial structuring. Much better simulations and predictions can be obtained by including spatial dependence itself among the predictive variables (Legendre 1993). Simulation models and area estimates of tree size and increment in naturally seeded forests will benefit by including geostatistical components to summarize ecological spatial dependence.

Modeling spatial dependence helped understanding the mechanisms of site occupation in old-growth ponderosa pine forests. In the last century, the structure of ponderosa pine stands in the American Southwest has changed from an open forest with scattered large trees to a more closed forest where the gaps between and around large trees have been occupied by thickets of small trees. In this study, spatial dependence of tree size and increment was mostly related to stand density because climate, topography, geology, soil and vegetation type, disturbance history, and anthropic manipulation were homogeneous over the study area. We found that stem

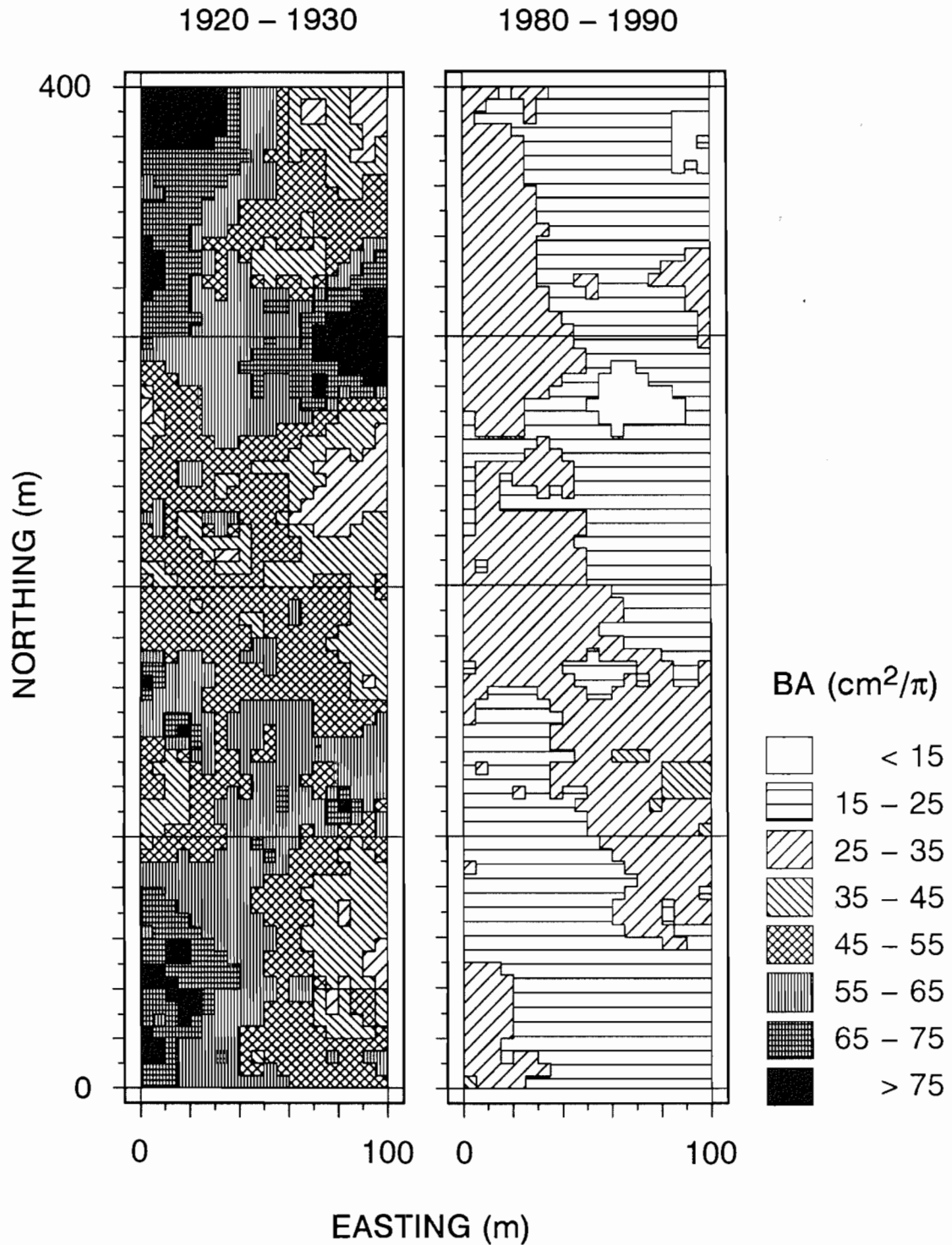


FIG. 9. Ordinary kriging estimates, on 5×5 m blocks, of 10-year basal area increment (BAI) in 1920-1930 and in 1980-1990, based on pines always present ($N = 308$).

size of ponderosa pine behaves as a regionalized variable and that the spatial distribution of stem size is autocorrelated over distances no longer than 30 m. The consistency through time of variogram models used to represent spatial dependence of DBH and BA provided strong evidence that size distributions maintained basically the same spatial patterns from 1920 to 1990. Tree density increased by increasing the number of pine groups, not their horizontal dimension.

Variogram models indicated that spatial dependence from 1920 to 1990 decreased more for stem increment than for

stem size. Increased density was associated with decreased mean and variance of individual growth rates, as well as with lower spatial dependence of stem size and increment. In particular, BAI between 1980 and 1990 showed almost no spatial dependence, indicating that trees grew at different rates regardless of their proximity. Since growth variation was less affected by intertree distance with greater local crowding, prediction of individual growth rates cannot rely on intertree distances alone. We argue that increased tree density intensified competition for resources and that spatial

patterns of stem increment were disrupted by competitive interactions. In other words, our findings suggest that density-dependent limitation of tree growth does not necessarily generate distance-dependent growth rates. For simulation purposes, it was remarkable how well the same variogram model could represent spatial dependence of stem size at different spatial scales and over different time periods. The Gaussian model, which portrayed spatial dependence of tree DBH and BA over a large range of stand densities, was both empirically and theoretically meaningful. Although the features that distinguish spatiotemporal patterns of this old-growth ponderosa pine forest need to be examined elsewhere to determine their generality, finding other extensive permanent plots that have been maintained since 1920 in virgin forest may not be simple.

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