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TALL SHRUB DYNAMICS IN NORTHERN MINNESOTA ASPEN AND CONIFER FORESTS

James C. Balogh
and David F. Grigal

Tall shrubs are a dynamic component of upland forests in the Lake States (Balogh 1983, Dunn 1986, Ohmann and Ream 1971). They are an integral part of forest element cycles, competitors with overstory for growth and reproduction, essential to post-harvest site stabilization, and a source of wildlife cover and browse (Comerford and White 1977, Dunn 1986, Robinette 1972, Tappeiner 1971).

Most research on shrubs has been conducted in arid and semiarid ecosystems where they dominate (Johnson 1982, Louda 1982, Schlesinger and Gill 1978). Previous research on shrubs in north-temperate ecosystems has focused on single species or composite populations in a limited number of stands (Crow 1978, Reiners 1972), development of species biomass equations (Grigal and Ohmann 1977, Smith and Brand 1983), and shrubs as components of vegetation surveys and site classifications (Grigal and Ohmann 1975, Whittaker and Woodwell 1968). In the Great Lakes forests, few studies have quantitatively examined tall shrub dynamics and their relation to site characteristics.

The objective of this study was to quantitatively analyze age-density distributions of tall shrubs within conifer and aspen forests in northern Minnesota. We investigated the structure and implications of the age-density distributions, fit to both negative exponential and power function models and compared model characteristics, including slope and intercept, to overstory characteristics and soil resources. These analyses provide information regarding life-history strategies and autecology of tall shrubs in northern Minnesota forests.

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BACKGROUND

The number of stems of each age-class present in a population, or the age-density distribution, provides important information regarding age structure, mortality, and regeneration in forest communities (Hett and Loucks 1976, Lorimer 1980, Stewart 1986). Mortality and regeneration of members of a plant community regulate plant density and affect species survival strategies.

Age-density distributions have been well documented for overstory trees and long-lived woody plant species (fig. 1). In uneven-aged forests of late-successional species, the age-density distribution has an inverse-j shape (Leak 1975, Whipple and Dix 1979). A unimodal or Gaussian age-density distribution has been reported for stands of even-aged trees (Knowles and Grant 1983, Stewart 1986, Yarranton and Yarranton 1975). Irregular or random age-density distributions have been associated with species that grow on marginal habitats (Whipple and Dix 1979).

Age-density distributions are usually represented by three general mathematical models (fig. 2) (Deevey 1947). Type I, or the negative skewed rectangular distribution, models are rare in perennial plant populations (Sarukhàn and Harper 1973). Herbaceous plants often exhibit a Type II, or negative exponential distribution, with constant slope for all ages. Long-lived tree species demonstrate a Type III, or power function relation, with high initial slope that decreases with age class (Hett and Loucks 1971, 1976). Harper (1977) observed that some plant species exhibit both negative exponential and power function distributions. Mathematical fitting of age-density distributions to these two models has been used to determine the most appropriate model and to quantify slopes (Hett and Loucks 1976, Hibbs 1979, Monk 1981). Qualitative assessments of deviations from models along simple environmental gradients have also been reported (Hett and Loucks 1971, 1976; Leak 1975; Lorimer 1980; Whipple and Dix 1979).

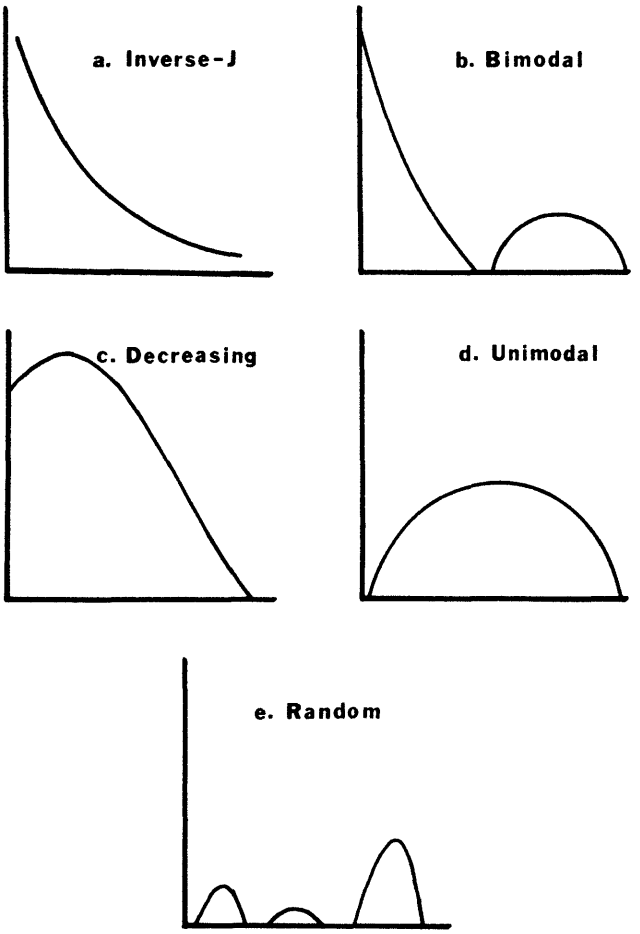

Figure 1.—*Five potential age-density distributions that may be observed in natural plant populations. The horizontal axis is age and the vertical axis is the density in an age class.*

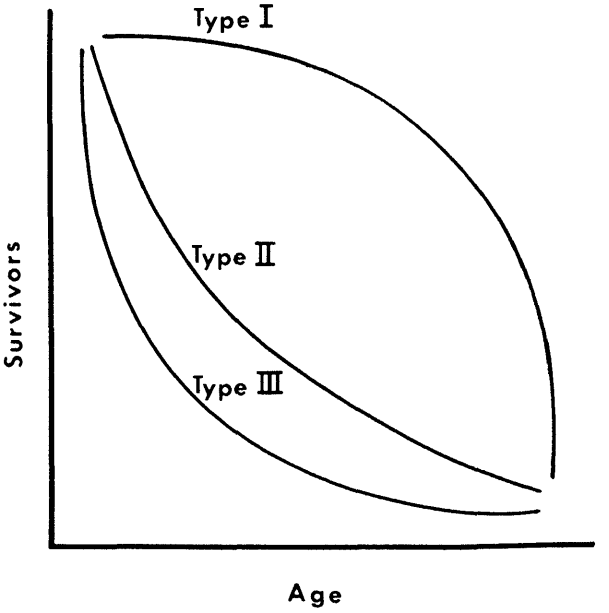

Figure 2.—*Generalized shape of three types of age-density distributions observed in natural populations. Type I is the negative skewed rectangular distribution, Type II is the negative exponential distribution, and Type III is the power function distribution.*

Research on shrub age-density distributions and their relations to site characteristics has been emphasized for arid and semiarid ecosystems (Barbour 1969, Crisp and Lange 1976, Johnson 1982, Louda 1982). Few studies of age-density distributions or life-history dynamics of tall shrubs in temperate forest communities have been reported (Hibbs 1979, Marks 1974, Tappeiner 1971). Age-frequency histograms presented by Ohmann *et al.* (1978) suggest that common tall shrub species in northeast Minnesota have inverse-j age-density distributions.

Few studies have compared age-density distributions of tall shrubs for a series of forest communities with different site characteristics. In many northern forests, high stem densities (Ohmann and Ream 1971, Tappeiner 1971) and the requisite intensive sampling have discouraged such work.

METHODS

Site Selection and Site Characteristics

Twenty-four upland forests were sampled in the Chippewa and Superior National Forests in north-central and northeastern Minnesota (centered at 47° N, 93° W) (fig. 3). Overstory trees were early-successional species including trembling and bigtooth aspen (*Populus tremuloides* Michx.; *Populus grandidentata* Michx.), red pine (*Pinus resinosa* Ait.), and jack pine (*Pinus banksiana* Lamb.). Sixteen of the stands were undisturbed and were randomly selected from USDA Forest Service cover-type maps. The remaining eight stands were multiple-study sites, including silvicultural treatments of thinning, fertilizing, and cutting. All treatments had been done more than 10 years before sampling. Portions of these latter stands that differed in treatment were sampled as separate substands, yielding a total of 34 sample locations (fig. 3; table 1).

The climate of the study area is continental with short, hot summers and cold winters. Normal annual

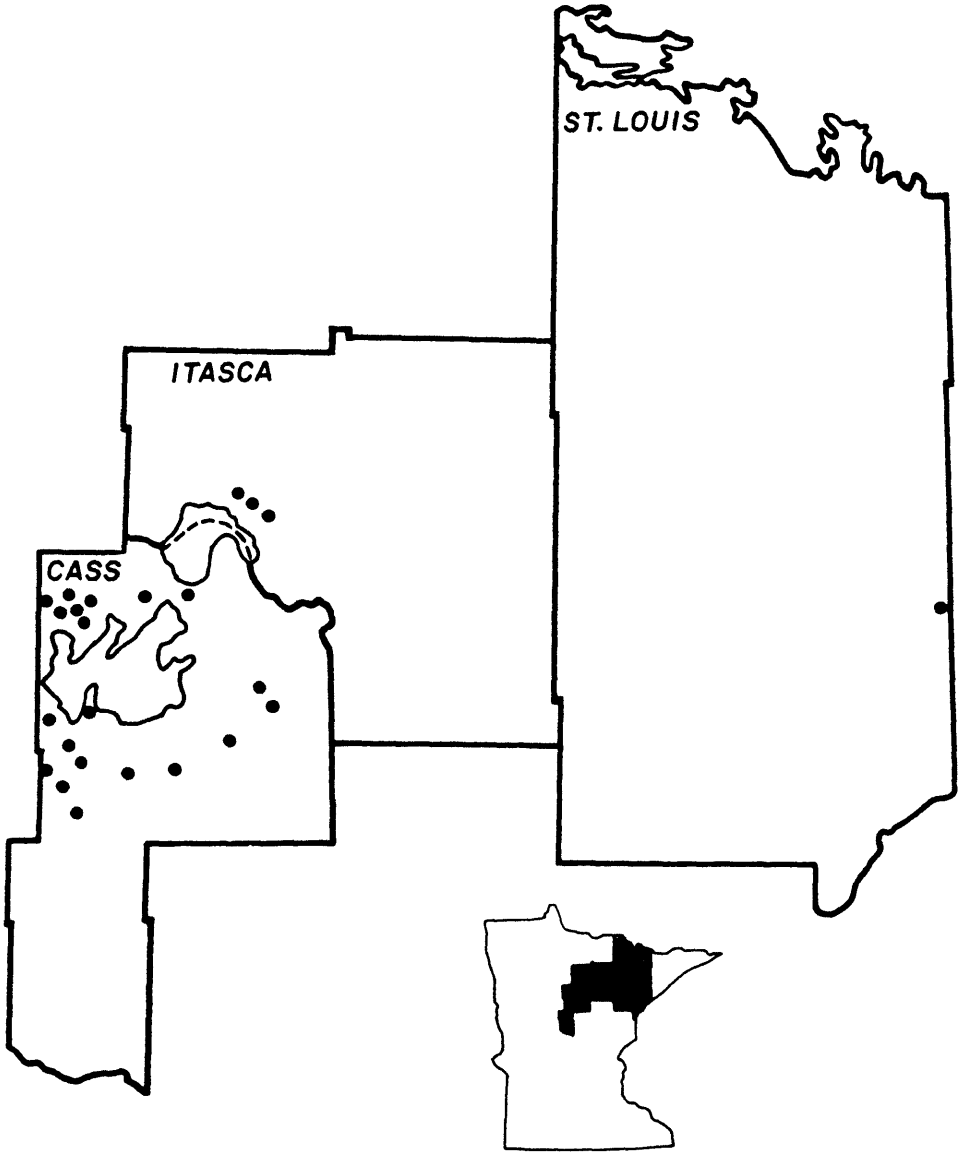

Figure 3.—*Location of study sites in north-central and northeastern Minnesota.*

temperature is 3.4° C, and normal annual precipitation is approximately 68 cm, about two-thirds of which falls during the growing season (Baker *et al.* 1985, Baker and Kuehnast 1978). Soil parent material is diverse and includes till, outwash, and lacustrine material deposited in the late-Wisconsin era (Cummins and Grigal 1981, Wright 1972). Soils in the Chippewa National Forest study area developed on material deposited in the Itasca moraine and Bemidji physiographic area. The Superior National Forest study area was located in the Toimi drumlin field deposited by the Rainy sublobe (Wright 1972).

Shrub, Overstory, and Soil

Vegetation was sampled systematically in each stand with a random start (Balogh 1983). A minimum of six, 5 m^2 plots were used to determine shrub characteristics. These plots were nested within a similar number of contiguous 70 m^2 plots that sampled the overstory. Shrub identification and nomenclature follows Gleason and Cronquist (1963). Common tall shrub species sampled included: *Acer spicatum* Lam., *Alnus crispa* (Ait.) Pursh., *Amelanchier* spp., *Cornus alternifolia* L. F., *Cornus rugosa* Lam., *Corylus americana* Walt., *Corylus*

Table 1.—*Overstory and site characteristics of sampled stands*

Stand	Overstory basal area	Potential overstory productivity	Stand age	High light index	Treatment	Shrub density	Dominant shrubs[1]
	m^2/ha	*m^3/ha/yr*	*Years*	*Percent*		*10^3 stems/ha*	
ASPEN COVER TYPE							
1	32.1	6.52	34	16	Natural	80	Ac sp, Co ru, Co co
2	74.6	6.52	42	25	Natural	41	Co co, Pr vi, Co am
3	25.5	5.25	56	29	Natural	83	Ac sp, Cr ru, Co co, Am
4	35.0	4.13	60	19	Natural	26	Co co, Cr ru, Vi ra, Pr vi
5	23.3	5.25	49	15	Natural	24	Co co, Sa
6	17.3	5.25	49	27	Natural	46	Co co
7	19.9	6.52	49	42	Natural	108	Co co, Cr al, Cr ru, Co am
8	22.0	6.52	18	13	Natural/Clearcut	61	Co co, Am Pr vi, Cr al
9a	33.1	6.52	38	11	Natural/Control	73	Co co, Co am, Am, Vi ra
9b	23.1	6.52	38	25	Natural/Thinned	60	Co am, Co co, Pr vi, Vi ra
10	16.1	7.15	18	17	Natural/Clearcut	83	Co co, Sa Cr ru
CONIFER COVER TYPE							
11	49.9	5.25	69	33	Natural/Red Pine	72	Co co, Am, Pr vi
12	40.1	4.13	70	27	Natural/Jack Pine	286	Co co, Ac sp, Al cr
13	42.7	4.13	87	36	Natural/Red Pine	15	Co co, Al cr, Co am, Am
14	54.3	4.13	84	22	Natural/Red Pine	36	Co co, Am, Pr vi, Sa
15	35.0	5.25	82	38	Natural/Red Pine	44	Co co, Cr ru, Ac sp, Pr vi
16a	28.2	5.25	45	24	Plantation/Red Pine Fertilized	45	Co co, Pr pe, Pr vi, Sa
16b	26.8	5.25	45	26	Plantation/Red Pine Fertilized	60	Co co, Sa, Am, Pr vi
16c	28.1	5.25	45	32	Plantation/Red Pine Control	32	Co co, Pr vi, Am, Pr pe
17a	25.9	5.25	69	23	Natural/Red Pine	29	Co am, Co co,

(Table continued on next page)

Table 1.—*Overstory and site characteristics of sampled stands (continued)*

Stand	Overstory basal area	Potential overstory productivity	Stand age	High light index	Treatment	Shrub density	Dominant shrubs[1]
	m^2/ha	m^3/ha/yr	Years	Percent		10^3 stems/ha	
					Thinned		Pr vi, Am
17b	29.7	5.25	69	18	Natural/Red Pine Thinned	22	Co co, Co am, Pr vi
18a	23.7	4.13	69	21	Natural/Jack Pine Control	82	Co co, Co am, Cr ru
18b	16.5	2.94	69	16	Natural/Jack Pine Thinned	81	Co co, Sa, Co am, Vi ra
19a	26.6	4.13	104	16	Natural/Red Pine Thinned	33	Co co, Sa, Cr ru
19b	26.9	4.13	104	12	Natural/Red Pine Thinned	74	Co co, Sa, Cr ru, Am
19c	33.4	4.13	104	19	Natural/Red Pine Thinned	114	Co co, Al cr
20a	33.4	6.52	39	24	Natural/Jack Pine Fertilized	48	Am, Sa, Al cr
20b	34.9	5.25	39	23	Natural/Jack Pine Fertilized	21	Sa, Al cr, Am, Co co
20c	35.1	5.25	39	22	Natural/Jack Pine Control	31	Sa, Al cr, Am
20d	—	—	8	50	Natural/Jack Pine Clearcut	41	Sa, Am, Al cr
21	33.3	9.18	44	30	Plantation/Red Pine	22	Co co, Pr vi, Cr ru
22	45.4	7.15	80	17	Natural/Red Pine	66	Ac sp, Co co, Co am
23	—	—	19	50	Natural/Jack Pine Clearcut	115	Al cr, Sa, Co co
24	—	—	10	72	Natural/Jack Pine Clearcut	104	Sa, Co co, Co am, Am

[1] Ac sp = *Acer spicatum* Lam., Al cr = *Alnus crispa* (Ait.) Pursh., Am = *Amelan chier* spp., Cr al = *Cornus alternifolia* L.f., Co am = *Corylus americana* Walt., Co co = *Corylus cornuta* Marsh., Cr ru = *Cornus rugosa* Lam., Pr pe = *Prunus pensylvanica* L.f., Pr vi = *Prunus virginiana* L., Sa = *Salix* spp., and Vi ra = *Viburnum rafinesquianum* Schult

cornuta Walt., *Prunus pensylvanica* L. F., *Prunus virginiana* L., *Ribes* spp., *Rosa acicularis* Lindl., *Rosa blanda* Ait., *Salix* spp., and *Viburnum rafinesquianum* Schult.

All tall shrub stems on each 5 m^2 shrub plot were cut at ground level. Tall shrubs are perennial plants having woody, permanent stems that branch from or near the ground. Mature shrub stems are between 0.5 m and 5 m tall. Stem age was determined by duplicate counts of annual rings in the field with a hand lens (magnification 10x). Additional 5 m^2 shrub plots were randomly established on the periphery of the main plot until at least 100 stems of the dominant shrub species had been sampled. Stand density of shrubs by 1 year age-classes, or the age-density distribution, was determined for each species and for the total shrub population. The total shrub population was determined as the sum of all species within each stand.

The above-ground stems of the shrubs in this study reproduce vegetatively (Tappeiner 1971). Therefore, the age distributions developed in this study refer to the age-density distributions of ramets, and not the distribution of genets. Management and analyses of shrub dynamics usually are based on the temporal and spatial distribution of shrub stems irrespective of mode of reproduction (Dunn 1986, Krefting and Ahlgren 1974, Tappeiner 1979). Forest management practices and attempts to simulate shrub abundance dynamics require information regarding the age distribution of all shrub stems.

The diameter at breast height (d.b.h.) of all trees with d.b.h. greater than 3 cm was recorded on each tree plot by species. Average basal area and density of the overstory were calculated. Height and age of one dominant tree per plot (six per stand) were measured, and site index was calculated (Lundgren and Dolid 1970). Site index was converted to annual productivity so different overstory species could be easily compared (table 1) (USDA Forest Service 1978). Annual productivity is the annual volume of wood accumulated on an area.

At the center of each shrub plot the overstory canopy was photographed with a 180° (fisheye) lens to provide an integrated estimate of crown opening (Harcombe and Marks 1977). An index of the amount of light penetrating the forest canopy was developed by computer analysis of the photo-digitized images (table 1). The canopy was considered to be open when it allowed more than 75 percent of maximum light to penetrate, intermediate when between 25 and 75 percent of maximum light penetrated, and dense when less than 25 percent of maximum light filtered through (Balogh 1983).

A soil pit was excavated in each stand. Profile descriptions followed standard terminology (Soil Survey Staff 1951, 1981). Soil taxa identified included Eutroboralfs, Glossoboralfs, Udorthents, Dystrochrepts, and Udipsamments (Soil Survey Staff 1975, USDA Soil Management Services 1985). Percent slope of the land surface was recorded with each profile description (table 2). Samples were taken from each horizon for particle size, moisture retention, and chemical analysis. Bulk density was determined by the core method (Blake 1965). Organic soil horizons

Table 2.—*Soil physical and chemical properties of sampled stands*

Stand number	Weighted moisture storage capacity to 150 cm	Slope	Weighted nutrients to 150 cm					Soil suborder
			N	P	K	Ca	Mg	
	cm	*Percent*	*kg/ha*					
1	6.86	2	12,740	100	780	8,490	1,780	Boralf
2	3.08	3	14,000	70	440	3,500	650	Boralf
3	2.39	34	8,870	100	160	2,780	200	Psamment
4	1.74	26	8,630	50	110	1,580	150	Psamment
5	3.44	3	9,890	10	230	2,960	480	Boralf
6	3.16	4	9,430	50	110	1,950	440	Boralf
7	4.34	10	15,190	80	430	6,000	1,340	Boralf
8	2.35	5	9,220	70	220	1,900	190	Boralf
9a,b	2.22	3	10,040	60	280	2,860	400	Boralf
10	1.84	2	8,030	50	190	1,750	190	Orthent
11	2.06	15	7,100	60	110	1,430	160	Orthent
12	1.32	35	10,590	60	110	1,910	240	Psamment
13	1.35	2	15,140	30	160	1,150	130	Psamment
14	2.49	10	5,880	60	130	1,920	210	Boralf
15	2.40	9	4,840	40	160	1,750	260	Boralf
16a,b,c	1.64	4	5,570	40	100	890	100	Psamment
17a,b	1.81	3	8,930	50	100	1,400	120	Psamment
18a,b	1.75	2	16,140	50	190	1,540	180	Boralf
19a,b,c	2.35	9	8,810	80	100	1,030	130	Psamment
20a,b,c,d	2.77	4	10,310	40	270	1,350	180	Ochrept
21	2.00	16	10,110	40	110	1,170	120	Boralf
22	1.76	40	9,570	50	170	1,120	140	Psamment
23	1.91	2	7,080	80	250	1,720	220	Orthent
24	1.18	2	10,630	20	140	1,080	140	Psamment

were sampled at the center of each 5 m^2 plot with a 12 cm-diameter brass ring. Soil from the control area was sampled in stands having several silvicultural treatments.

Particle size distribution was determined by a modified hydrometer method (Grigal 1973). Moisture content on soils with sandy texture was determined at 0.01 MPa and 1.5 and for finer-textured samples at 0.03 MPa and 1.5 MPa (Richards 1965). Moisture retention in organic horizons was estimated based on literature values (Balogh 1983). Water storage capacity was computed using moisture retention data, bulk density, thickness, and volume of coarse fragments. The site moisture pool was determined as a weighted average. Weighting was by an exponential function that decreased from a maximum value at the soil surface to near 0 at 150 cm (table 2) (Balogh 1983, Grigal and Arneman 1970).

Nitrogen content of mineral soil was determined by micro-Kjeldahl analysis (Bremner and Tabatabai 1972). Phosphorus was analyzed colorimetrically on soil extracted with Bray's No. 1 solution (Olsen and Dean 1965). Mineral soil samples were extracted with neutral 1*N* NH_4 OAc (Chapman 1965) and analyzed by an inductively coupled plasma spectrometer (ICP) to determine exchangeable bases, K, Ca, and Mg.

Forest floor samples were dried for 72 hours at 70° C and ground to pass a 20-mesh screen. Samples were ashed at 500° C for 12 hours, dissolved in 2*N* HCl, and K, Ca, Mg, and P were determined by ICP. Nitrogen in litter was estimated by regression on P, based on data from the literature (Balogh 1983).

Nutrient concentrations were converted to mass per unit area by adjustment for horizon thickness, bulk density, and coarse skeleton volume. Stand nutrients were summed to 150 cm using the exponential weighting method previously described (table 2).

Multivariate classification techniques were used to place sampled stands in groups along synthetic gradients of resources for plant growth (Balogh 1983). These techniques were used to eliminate problems of covariance when several resources were combined to produce a gradient. A general numerical procedure was used to objectively classify the stands into groups. Non-hierarchical cluster analysis was used on the variables related to nutrients to establish an initial group classification (BMDPKM; Dixon and Brown 1979). Group classification was statistically validated via a jackknifed stepwise discriminant analysis with Mahalanobis distance probability testing (BMDP7M; Dixon and Brown 1979). Incorrectly classified stands were reclassified into the "correct" group based on the minimum discriminant distance function. The best linear combination of multivariate data for classification (first discriminant canonical variate) was recorded as the synthetic variable for analysis.

Unlike univariate groupings, which increased in value from the the first to last group, multivariate groupings and gradients are not necessarily related to increasing means of any single variable. Multivariate stand groupings included a moisture grouping based on the site moisture pool and on slope; a nutrient grouping based on quantities of N, P, K, Ca, and Mg; and a light grouping based on the high and intermediate light index. Coefficients of shrub age-density models were related to positions along these gradients of plant growth resources.

Constructing Shrub Age-Density Distributions

For each sampled stand, age-density distributions for individual shrub species and for the entire population as the sum of all species were fit to both the negative exponential and power function models. Model fitting was by logarithmically transformed least square regression (Dixon and Brown 1979). The first model was the negative exponential distribution

$$Y = Y_0 e^{-bX} \quad (1)$$

which after transformation becomes

$$\ln Y = \ln Y_0 - bX \quad (2)$$

where b is the slope, Y is the density of stems at age-class X, and Y_0 is the density of age-class 0. The second model was the power curve function

$$Y = Y_0 X^{-b} \quad (3)$$

which after transformation becomes

$$\ln Y = \ln Y_0 - b \ln X \quad (4)$$

where the parameters are as previously defined, except Y_0 is the density of age-class 1.

Based on statistical significance, both models (2) and (4) usually fit the entire shrub population and the dominant shrub species in a stand. Significance was determined at the 0.05 level based on an F-test of the regression (BMDP1R, Dixon and Brown 1979). A few populations and species with low densities had random age-density distributions leading to non-significant model fits and were rejected (Whipple and Dix 1979).

Models were initially selected for further comparison if they met the following criteria: (a) they explained at least 50 percent of the variance in age-class density ($R^2 \geq 0.50$), (b) they were significant at the 0.05 probability level by the analysis-of-variance F-test, and (c) they confirmed the assumptions concerning model variance being constant, independent of age, and having a mean of zero. Bartlett's test was used to determine homogeneity of variance among the models for age distributions of individual species and the population (Snedecor and Cochran 1967). Current or 0 year age-class was not included in the analysis because all stems in that class were not sampled. The ephemeral survival of the 0 year age-class make it impossible to accurately sample (Harper and White 1974).

Observing the age-density distribution of a standing population is a time-specific technique used to develop stem depletion curves (Hibbs 1979, Leak 1975). In this method age structure is assumed to be constant. The assumption is met by constant input into the 0 year age-class and by the presence of a complete age distribution (Hett and Loucks 1976). Most of the stands in which shrubs were sampled had no evidence of external disturbance for at least 10 years, and probably had been undisturbed for longer. Without disturbance, *sans* weather fluctuations, the environmental conditions in the understory have probably remained constant. In the case of most of the shrub species, the age distributions had developed within 10 to 15 years of the sampling date. Therefore, most of the sampled shrub stems developed during a period of undisturbed stand conditions. Slopes of the age-density distributions are heavily influenced by data from stems less than or equal to 10 years old, and the data from older stems do not deviate markedly from these slopes. On that basis, we accepted the assumption of a constant age-structure for shrub stems spanning the age of stems forming the basis of best-fit models.

If the assumption of constant age-structure is accepted, the slopes of the age-density distributions are synonymous with mortality rates and the intercepts are synonymous with annual regeneration (Hett and Loucks 1976, Hibbs 1979). Because of the nonmobile status of plants, density in a given site is regulated by mortality and regeneration (Harper and White 1974). Species with a negative exponential mortality rate have a constant probability of death throughout their life span. Species showing power-function mortality have high initial rates of stem death that decrease with age (Harper 1977). Mathematical fitting of age-density distributions to these two models quantifies both mortality rates and annual regeneration of shrub stems.

Comparing Age-Density Distribution Models

The model with the smallest residual mean square [equation (2) or (4)], pooled across all acceptable regressions developed in individual stands, was considered to have the best fit for an individual species (Snedecor and Cochran 1967). This criterion was used because it could be quantitatively applied over all stands. If we had chosen a subjective criterion, such as a comparison of negative exponential and power function models, each stand would have to be considered individually. Age-density distributions were compared using the models with the best fit.

Equality of model slopes, or mortality rates, was tested with a slope comparison F-test (Snedecor and Cochran 1967) that also yields pooled slopes. The pooled estimates of slope and residual mean square are independent of individual model intercepts. Intercepts, or annual regeneration of shrub stems, were tested by one-way analysis of covariance of adjusted means (Snedecor and Cochran 1967). The 0.05 probability level was used in all cases as the criterion of statistical significance.

The relation between the model coefficients and overstory and soil characteristics was based on least square multiple linear regression. The dependent variable was either the intercept or slope from the model, and the independent variables were basal area of overstory trees, site productivity, stand age, percent high light (> 75 percent of maximum light), synthetic light gradient, site moisture pool to 150 cm, N and Ca content to 150 cm, the synthetic moisture gradient, and the synthetic nutrient gradient.

The regression models relating coefficients of the age-density models to overstory and soil characteristics were screened using Mallows' Cp criterion (BMDP9R; Dixon and Brown 1979). Relations were developed separately for aspen and conifer cover types to limit the confounding influence of overstory. Only coefficients for models of the entire population and *Corylus cornuta* had enough observations for meaningful regression analyses. The regression models had 0.05 probability significance for the overall regression (F-test) and for model coefficients (t-tests) and met the assumptions concerning regression model variance (Weisberg 1980).

RESULTS AND DISCUSSION

Developing Age-Density Distributions

Age-density models were developed for the entire population of shrubs and for *Corylus cornuta, Amelanchier* spp., *Acer spicatum, Cornus rugosa, Salix* spp., *Alnus crispa, Cornus alternifolia, Prunus virginiana, Corylus americana,* and *Viburnum rafinesquianum* (table 3) (Balogh 1983). In many stands, both negative exponential and power function models were significant at the 0.05 probability level (fig. 4, table 3).

As has been found in similar studies, some distributions deviated from the developed models (fig. 4) (Hett and Loucks 1976, Lorimer 1980). A review of the pattern of residuals among all age-density models did not reveal systematic deviations from either the negative exponential or power function distributions. The fact that the models explained more than 50 percent of the variation in the age-density distributions, and usually more than 70 percent (Balogh 1983), indicates that most of the deviations are random variation and are not clear trends. The best-fit models lessened this divergence. In some stands, especially those with few shrubs, age-density models did not meet all acceptance criteria. The low density of shrubs on these sites may indicate that the species were marginally adapted causing random excursions from regular age-density distributions to be more pronounced (Leak 1975, Whipple and Dix 1979).

Selecting the Best Age-Density Distribution Model

The model with the best fit to the distributions, independent of the intercept, was the one that minimized the pooled residual mean square (table 3). The total population, *Corylus cornuta, Amelanchier* spp., *Salix* spp., *Cornus alternifolia, Prunus virginiana,* and *Corylus americana* were best described by the negative exponential model. *Acer spicatum, Cornus rugosa, Alnus crispa,* and *Viburnum rafinesquianum* were best described by the power curve model.

The power curve model for *Acer spicatum* was similar to that found for other *Acer* spp. (Hett 1971,

Table 3.—*Pooled parameters for tall shrub survivor models by species and population*

Species	Model type[1]	Pooled mortality rate,b	Pooled residual mean-square	Models developed	Regeneration range; $\ln Y_0$	Best model fit[1]
				No.		
Total population	1	0.202	0.2456	33	8.04 - 10.99	1
	2	1.242	.4810	30	8.40 - 12.00	
Corylus cornuta	1	.221	.3287	21	7.59 - 10.63	1
	2	1.139	.5730	14	7.62 - 11.69	
Amelanchier spp.	1	.157	.2196	6	6.43 - 8.33	1
	2	.793	.2919	6	6.84 - 9.50	
Acer spicatum	1	.154	.3960	4	7.83 - 9.01	2
	2	1.237	.1999	4	9.38 - 9.95	
Cornus rugosa	1	.158	.4699	4	6.99 - 7.90	2
	2	.825	.3610	4	7.09 - 8.69	
Salix spp.	1	.129	.2800	4	6.75 - 8.26	1
	2	.782	.4371	3	6.59 - 8.57	
Alnus crispa	1	.055	.1722	2	6.92 - 7.04	2
	2	.592	.1501	2	7.52 - 7.68	
Cornus altenifolia	1	.074	.2485	1	7.41	1
	2	.556	.2673	1	7.79	
Prunus virginiana	1	.193	.1084	1	8.00	1
	2	.769	.1091	1	8.12	
Corylus americana	1	.090	.2639	1	7.70	1
	2			0		
Viburnum	1	.153	.4106	1	8.16	2
rafinesquianum	2	1.199	.3555	1	9.21	

[1] Model number; (1) negative exponential depletion and (2) power function depletion.

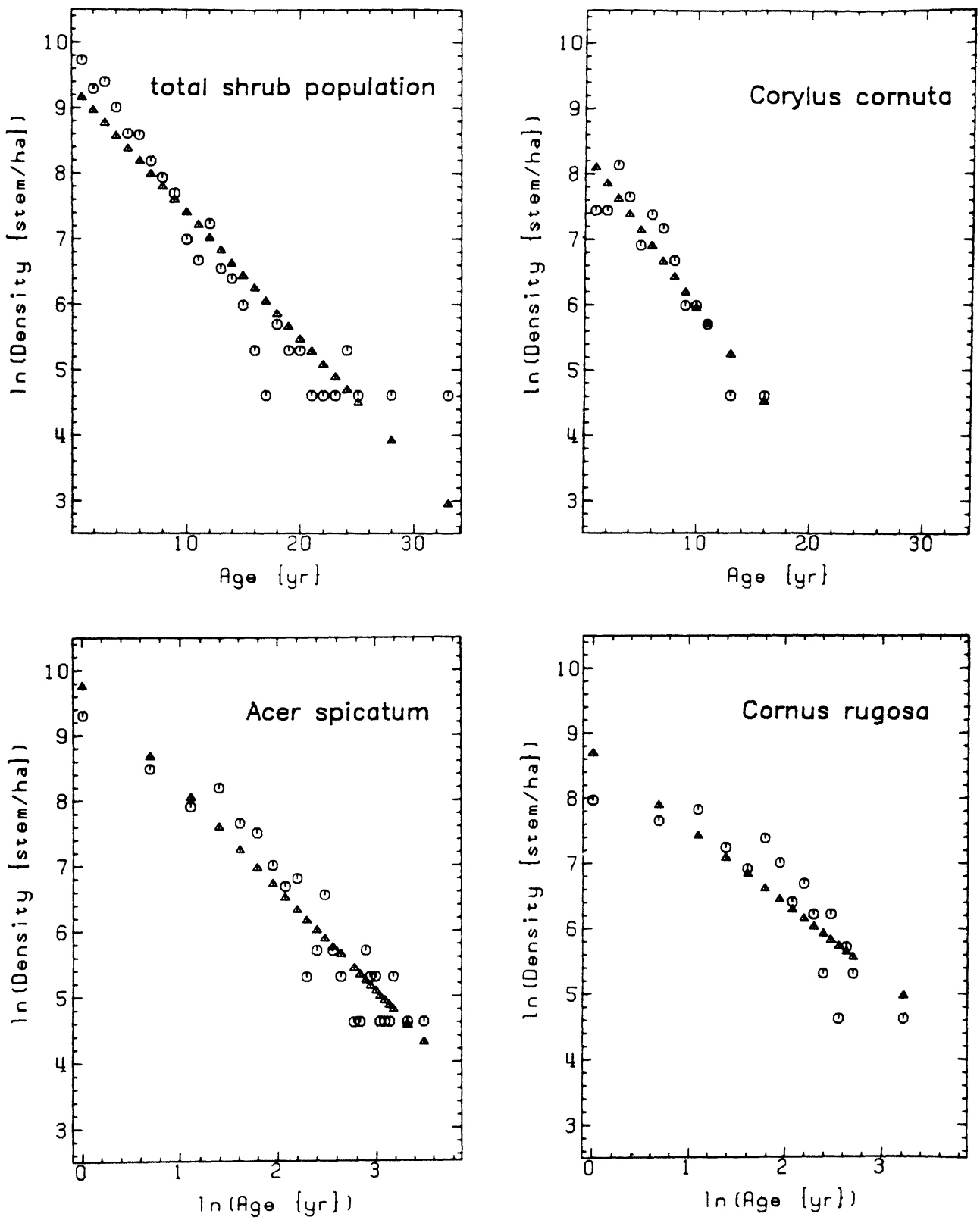

Figure 4.—*Observed (○) and predicted (▲) age-density distribution of tall shrubs in an aspen stand. The distributions of the entire population and* Corylus cornuta *were described by the negative exponential age distribution model. The distributions of* Acer spicatum *and* Cornus rugosa *were described by the power function model.*

Hett and Loucks 1971, Hibbs 1979). The negative exponential model has been reported for herbaceous plants (Harper 1977), small trees (Monk 1981), and semiarid grasses (Williams 1970). The random or irregular age-density characteristic of the species with low density was similar to that of some semiarid shrubs (Barbour 1969, Goldberg and Turner 1986).

Shrub Mortality Rates

We only compared age-density distributions for those shrubs with statistically significant models in more than one stand (table 3). Such comparison requires homogeneous variance (Snedecor and Cochran 1967); generally the variances among the models for dominant shrub species and for the entire shrub population were not statistically different (table 4). Homogeneous variance implies that fluctuations in age-density relations were similar for all stands.

Slopes of the age-density distributions did not differ significantly across stands for either model type (table 4). Therefore, the mortality rates for shrub stems are independent of total shrub density, overstory, and soil characteristics. Mortality rates for tall shrubs in the sampled stands are best described by the pooled slopes of the models (table 3).

Mortality was independent of stem density and age for the shrub population and those dominant species with negative exponential age-density distributions.

Table 4.—*Comparisons of tall shrub species and population age-density model presented as statistical probabilities*

Species	Model type	Homogeneity of variance X^2-probability	Slope equality F-probability	Intercept equality F-probability
Total population	1	0.064	> 0.250	< 0.005
Corylus cornuta	1	.047	> 0.250	< 0.005
Amelanchier spp.	1	.099	> 0.250	< 0.005
Acer spicatum	2	.411	> 0.250	< 0.005
Cornus rugosa	2	.036	> 0.250	< 0.005
Salix spp.	1	.914	> 0.250	< 0.005
Alnus crispa	2	.057	> 0.250	< 0.005

However, mortality was independent of density but dependent on age for a few species with power function models, including *Acer spicatum* (Hibbs 1979).

Shrub Regeneration

Intercepts of the models, or annual regeneration, could be tested because of homogeneous variance and equal slopes (table 3). Regeneration of shrub stems was significantly different across the range of sampled stands (table 4). With constant stem mortality, observed as constant slopes across age-density distributions, density of tall shrubs in the studied stands is determined by steady-state regeneration.

Regression analysis of the estimated intercepts (i.e., the annual regeneration of shrub stems) as a function of overstory and soil characteristics showed few significant relations (table 5). Only one regression model was significant for stem regeneration of the entire shrub populations in conifer stands, an inverse relation to site productivity and the synthetic moisture gradient. As conifer site quality, an integration of site resources, and soil moisture decreased, regeneration of shrub stems increased. Shrubs have a rooting morphology that is advantageous for acquiring limited resources (Buckman 1964). Under conditions of limited resources, especially soil moisture, regeneration of the shrub population was favored.

In aspen stands also, only one regression model for the shrub population was significant. This was an inverse relation of the age-density model intercept to aspen basal area. As aspen basal area increased, shrub regeneration decreased. Seedlings and shrub sprouts are sensitive to competition with the deciduous aspen overstory.

The relations shown for *Corylus cornuta* regeneration were similar to those of the total shrub population (table 5). Regeneration of *Corylus cornuta* stems in conifer stands was inversely related to moisture status and overall site productivity. As with the total shrub population, annual regeneration of *Corylus cornuta* increased with moisture stress and depressed site quality. A positive relation of regeneration to conifer basal area appears to contradict this interpretation, but the positive trend is apparently linked to older poor-quality stands with high basal areas in the data set (Balogh 1983) (table 5).

Only one significant regression model for *Corylus cornuta* regeneration was found for aspen stands. Regeneration had an inverse relation to the synthetic gradient of soil nutrients, possibly because of the adaptive surface rooting morphology of *Corylus cornuta* for acquiring limited resources (table 5).

Table 5.—*Total shrub population and* Corylus cornuta *regeneration as related to selected overstory and soil characteristics in aspen and conifer stands*

Shrub	Cover type	Variable	Coefficient	Coefficient t-probability	Residual mean square	Regression F-probability	R^2
Total population	Conifer	Intercept	10.574		0.356	0.017	0.380
		Site productivity	-0.289	0.016			
		Moisture gradient	-0.094	0.018			
Total population	Aspen	Intercept	9.638		0.084	0.022	0.502
		Basal area	-0.016	0.022			
Corylus cornuta	Conifer	Intercept	9.317		0.431	0.039	0.430
		Moisture gradient	-0.145	0.039			
Corylus cornuta	Conifer	Intercept	10.922		0.346	0.040	0.600
		Basal Area	0.068	0.027			
		Site productivity	-0.852	0.024			
Corylus cornuta	Aspen	Intercept	8.820		0.300	0.410	0.471
		Nutrient gradient	-0.194	0.041			

Soil moisture and the integrated suite of nutrients are critical for plant growth and development (Boyer 1982). Site growth resources are linked to annual recruitment of shrub stems, but regeneration was not significantly related to either overstory age or light penetration. Regeneration of shrub stems was related to overstory basal area. In aspen stands shrub regeneration appeared to compete directly with the deciduous overstory, but it did not compete with the coniferous overstories. The relation of shrub regeneration to conifer and aspen overstories is mediated through long-term site productivity and soil moisture and nutrients.

CONCLUSIONS

Both the entire population of tall shrubs and of individual dominant species demonstrated clearly defined age-density distributions in most of the sampled stands. Less-frequently occurring species also showed similar distributions in stands where they were abundant. The negative exponential function best described the age-density relation of most species and of the entire tall shrub population. The age-density distribution of a few species was best described by a power function.

For any species, the slopes of age-density distributions, synonymous with mortality rates (Hett and Loucks 1976, Hibbs 1979), were equivalent and can be characterized by a single pooled slope. This common slope or rate occurs within the sampled stands representing a range of sites in northern Minnesota. The rate was independent of shrub density and site characteristics, and can be assumed to apply when stand conditions are stable. Mortality rates of the shrub population and of those dominant species with negative exponential distributions can be inferred to be independent of both stem density and age. The few species with power function stem depletion, including *Acer spicatum*, have mortality independent of density but dependent on age (Hibbs 1979).

Intercepts of the shrub age-density distributions, synonymous with annual regeneration (Hett and Loucks 1976, Hibbs 1979), were significantly different across the range of sampled stands. Because of the constant mortality rate, the wide range of tall shrub densities in the sampled stands is therefore determined by steady-state regeneration (table 1). Regeneration of shrub stems was independent of most overstory characteristics. The only exception to this conclusion was a relation of shrub regeneration to basal area. The deciduous shrub community competes with the deciduous overstory in aspen stands, but not in conifer stands. The relation of the shrub stratum to the conifer overstory may be mediated by competition for soil moisture. In conifer stands, regeneration had an inverse relation with overall site quality and soil moisture. In aspen stands, regeneration was inversely related to site nutrients. Situations in which soil moisture and nutrients were limiting appeared to favor regeneration. Tall shrubs are strong competitors under conditions of limiting moisture and nutrients.

The results of this study, and especially the inability to detect statistical differences among the mortality rates of shrub stems, suggest an interpretation that integrates both the ecological concept of density-mortality relations and theories concerning self-thinning in plant populations (Harper 1977, Hutchings 1983, Smith 1983). Based on the observed relation between dry weight and density for a wide range of plants (Hutchings 1983, White and Harper 1970, Yoda *et al.* 1963), tall shrubs in all but one of the sampled stands fall below densities where density-dependent mortality rates should be manifested. Shrub mortality rates were statistically equivalent in stands with a wide range of total stem densities (15,000 to 286,000 stems per ha), and in many of the stands shrub densities were very high (table 1); higher densities are difficult to conceive. If density were to increase, however, mortality may become related to density. It is possible that the statistical comparison of mortality rates failed to detect differences rather than demonstrated that no differences exist.

This study aids understanding of the dynamics of tall shrubs in conifer and aspen understories. We conclude that shrub abundance is controlled by annual regeneration, not mortality rate. Therefore, those factors that affect the regeneration of shrub stems—such as the overstory, soil water and nutrients, and random historical or climatic fluctuations—will affect shrub abundance. In this analysis we considered the dynamics of tall shrubs for approximately one shrub generation. For longer time periods, where overall stand structure shifts to favor or inhibit shrub regeneration (Marks 1974, Taber and Hanley 1979, Tappeiner 1971), changing species and population densities will respond directly to those factors inducing changes in regeneration of shrub stems.

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1988. Tall shrub dynamics in northern Minnesota aspen and conifer forests. Res. Pap. NC-283. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 15 p.

Tall shrub dynamics were examined in upland stands in northern Minnesota. Mortality rates of shrub stems did not differ among the stands. Shrub stem regeneration did differ among the stands and was related to overstory characteristics, soil moisture, and soil nutrients. Stem density was regulated by annual regeneration.

KEY WORDS: Inverse-J distribution, understory, soil.