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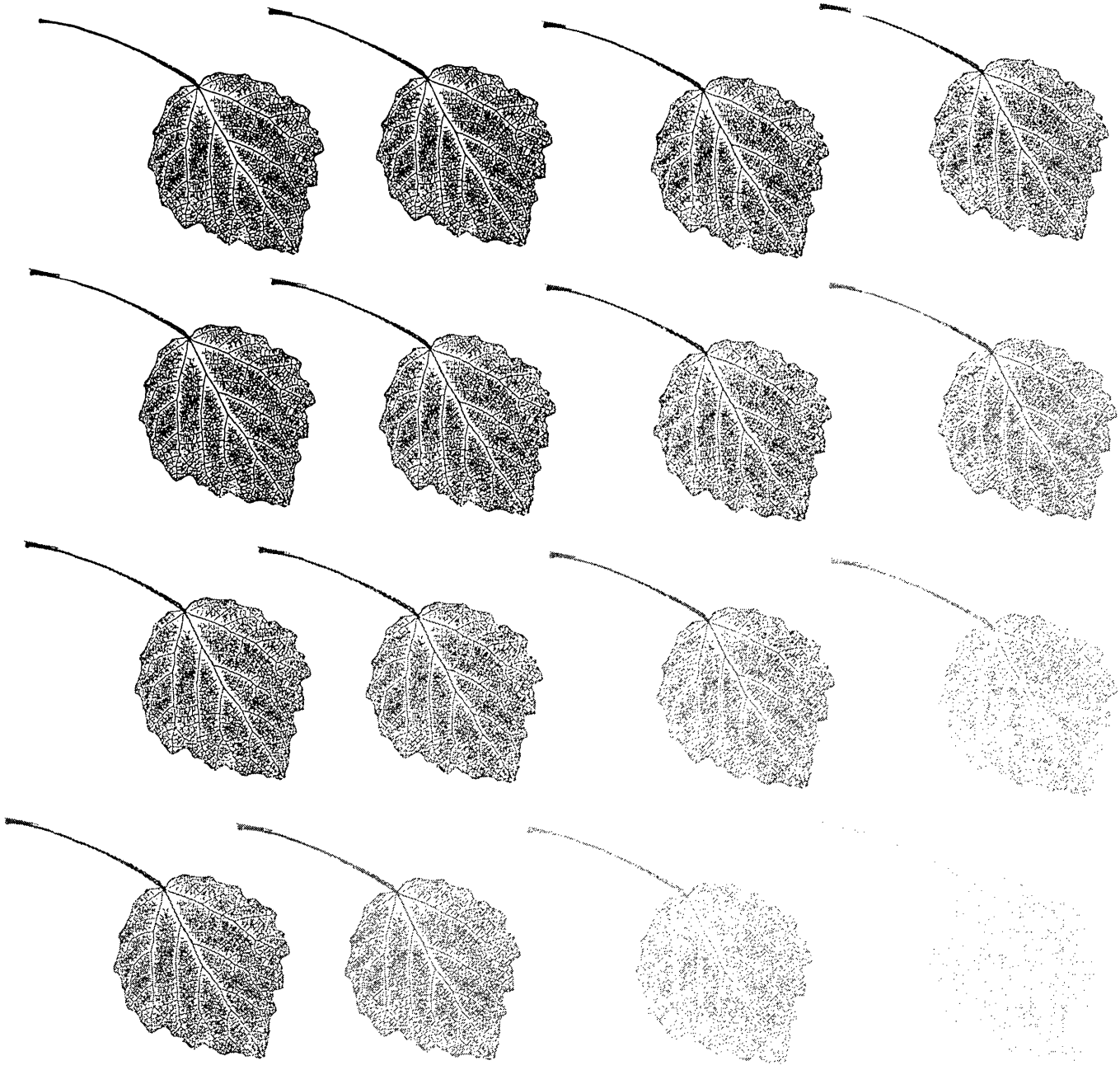

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Self-thinning and Stockability of the Circumboreal Aspens (*Populus tremuloides* Michx., and *P. tremula* L.)

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The North American trembling aspen, *Populus tremuloides* Michx., and its Eurasian counterpart, *P. tremula* L., dominate extensive tracts in boreal, montane, and north temperate ecosystems (Larsen 1980). These two species are so similar they lack traits to clearly differentiate them and arguably could be considered one circumboreal super species (Harper *et al.* 1985). They inhabit a broad array of soils and plant communities across a complex climatic spectrum, and endure a myriad of pathogens and herbivores. The aspens are genetically diverse, and respond to stress by expressing highly variable morphology, longevity, and rapidity of growth (Borset and Haugberg 1960, DeByle and Winokur 1985, Perala 1990). Consequently, mensurational data are highly variable and seemingly contradictory. To advance our understanding of aspen biology and management, we attempt here to reconcile the productivity of these wide-ranging species using general self-thinning models, some of which have been applied successfully to other even-aged monocultures (e.g., *Pinus radiata* D. Don (Drew and Flewelling 1977), *P. contorta* Dougl. (Flewelling and Drew 1985), *P. resinosa* (Smith 1986, Smith and Brand 1988), *Pseudotsuga menziesii* (Mirb.) Franco (Drew and Flewelling 1979, O'Hara and Oliver 1988), *Alnus rubra* Bong. (Smith 1986, Hibbs 1987), *Thuja plicata* Donn. (Smith 1989), and *Eucalyptus grandis* (Hill) Maiden (Bredenkamp and Burkhart 1990).

D.A. Perala (retired), USDA Forest Service, North Central Research Station, 1831 Highway 169 East, Grand Rapids, MN 55744.

R.A. Leary (retired), USDA Forest Service, North Central Research Station, 1992 Folwell Ave., St. Paul, MN 55108.

C.J. Cieszewski, Assistant Professor, School of Forest Resources, University of Georgia, Athens, GA 30602.

We feel the aspens should follow self-thinning relations of other even-aged monocultures because they typically regenerate 10,000 to 100,000 root sprouts (suckers) per hectare when the parent stand is killed by fire or logging, yet by maturity, in a half a century or so, will have less than 1,000 stems (Borset and Haugberg 1960, DeByle and Winokur 1985). Until maturity, background mortality caused by pathogens or other external influences is common but usually slight compared to intraspecific competition (Pollard 1971, Perala 1984). In gross analysis, background mortality appears to complement rather than supplement competition-induced mortality. Mortality proceeds steadily, mostly among the lesser crown classes, and more or less proportional to stocking, although sometimes it can be episodic (Graham *et al.* 1963).

In our analysis, we ask three questions:

1. Do circumboreal aspens self-thin in a consistent manner? (If available evidence forces us to answer negatively, questions 2 and 3 are inappropriate.)
2. Do the sites where these aspens grow support generally the same level of tree density for a given average tree size?
3. If the levels are different, can generally available local climate information account for the differences?

SELF THINNING RELATIONS IN GENERAL

We treat as a self-thinning relation any of the bivariate relations among properties of even-aged stands that include density (stems per unit area). The resulting group can be shown in a single row and column of the modified Bakuzis Matrix (Leary 1987). When attention is focused on the ordering of properties (x-axis or "causal" property, y-axis or "resultant"

property), self-thinning relations fall into three categories:

a. time - density
b. size - density, and
c. density - size

We discuss each of these relations below.

Time - density: The relation, called the Sukatchev effect (Gause 1934, Harper 1977), is that self-thinning occurs faster on good sites than on poor sites. Because our interest is bivariate relations where relations are the result of growth and/or death, we do not consider this relation further.

Size - density: Size - density relations have a size property on the x axis and density on the y axis. As trees increase in height, they require additional growing space to secure resources to produce thicker stems that provide physical support for the crown and upper stem. Inadequate space may lead to very large height-diameter ratios for trees and increased likelihood of stem breakage. The relation between mean height and tree density in unthinned stands may approach a limiting form given by equation [1].

$$N = k_0 \bar{h}^{k_1} \qquad [1]$$

where: N designates stem frequency,
$\bar{h}$ designates mean top height,
k_0 denotes a species-dependent parameter (larger for tolerant species), and
k_1 is about -2.0

Intertree distance divided by mean height (imperial units), $\left(\sqrt{\frac{43560}{N}}\right)/\bar{h}$, gives spacing percent, a practical measure of density useful in thinning and crop planning. Spacing percent seems more widely used in Europe than North America (Czarnowski 1947, 1961). However, Wilson (1946, 1951, 1955, 1979) thinned the Star Lake red pine plantation using spacing percent factors, and Day (1985) uses the spacing percent concept and other methods to plan thinnings and to develop crop plans.

Frothingham (1914) first noticed that stand density and quadratic mean stand diameter at breast height (d.b.h.) are self-limiting. Reineke (1933) further explored the concept, finding that for several hardwood and conifer species growing in even-aged stands, the slope of the relation ln (stand density) over ln (quadratic d.b.h.) is about -1.6. Reineke advanced these findings of an asymptotic density-mean d.b.h. relationship, or simply the "limiting relationship," to form his stand density index (SDI). Reineke's rule is:

$$N = l_0(\bar{d}_q)^{l_1} \qquad [2]$$

where: N designates stem frequency,
d_q designates quadratic mean diameter
l_1 denotes the slope, usually -1.6, and
l_0 denotes the level of the relation.

Additional claims of Reineke's rule are that l_1 is independent of site and age, and l_0 expresses the level of stem density, or packing, and is species dependent. Reineke's Stand Density Index, $N = l_0(x)^{l_1}$, gives stem frequency for the often-used standard mean tree diameter x, where x is often 10 inches at breast height.

Density - size: Density - size relations are expressed with density as the predictor property and size as the dependent property.

The relation between weight and tree frequency forms the basis for the widely studied Yoda's rule. Yoda *et al.* (1963) determined that the mean weight of a wide variety of herbaceous and woody plant populations undergoing self-thinning was limited by population density, the slope being -1.5 for ln (mean weight per individual) as dependent variable and ln (mean stand density) as independent variable. From this, the relationship became known as the "-3/2 power law of self-thinning." Mathematically, the relation is expressed:

$$\bar{W} = m_0 N^{m_1} \qquad [3]$$

where: $\bar{W}$ designates mean plant weight,
N designates stand density,
m_1 denotes the slope, usually -3/2, and
m_0 denotes the level of the relation.

An additional claim of Yoda's rule is that m_1 is independent of species, site, and age. Yoda's rule as written in [3] is fundamentally different from the rules in [1] and [2]. In the latter two, the continuous or growth property (height and diameter) occurs on the right-hand side of the equation, and the discrete property (stem frequency) is the dependent stand property. Thus, Yoda's rule as written in [3] is a purely descriptive, correlative statement: "When lots of plants are present, they don't weigh much, on average, but when there are few plants present, they weigh more on average."

We chose Reineke's rule, eq. [2], to be the basis for our stand dynamics model for philosophical, theoretical, and practical reasons.

Philosophically, stand dynamics models should bear some isomorphism with the real system. Reineke's rule is analogous to the basic gas laws: the event of trees in stands becoming larger increases the intensity of competitive "pressure" that results from plants seeking further resources to support an increased size. When the intensity of competitive "pressure" on trees seeking further resources exceeds the capability of individuals to expand crown and roots at a rate equivalent to neighbors, individual trees fall behind and die. The surviving neighbors expand their crowns and roots into the space no longer occupied, where they capture newly available resources.

The *theoretical* basis for Reineke's rule has been argued by Zeide (1991) on the basis of horizontal and vertical crown closure. Horizontal crown closure determines the number of trees and shape of the self-thinning line, and decreases with time. Vertical crown closure varies as the inverse of horizontal closure. It increases as horizontal crown closure decreases to maintain a constant leaf area in stands. Horizontal crown closure occurs first in young aspen stands. However, density in relation to size continues to increase because vertical crown closure does not occur until light extinction causes respiration in the lowest canopy leaves to exceed photosynthesis. These leaves die, and the canopy moves upward as trees grow in height.

The underlying mechanism controlling self-thinning seems to be the attainment of an upper limit of foliage, and the redistribution of this fixed amount among a declining number of larger survivors (Westoby 1977, Long and Smith 1984). Long and Smith (1984) argue that since cross-sectional sapwood area is directly proportional to foliar area (Grier and Waring 1974), the ultimate size-density relationship is between sapwood basal area and population density with a slope of -1.0.

The *practical* reason we chose Reineke's rule is that we have quadratic mean diameter and stand density (stems per unit area) for all data sources. Mean plant weight or mean height were available for only a small fraction of our data.

SCIENTIFIC HYPOTHESES ON SELF-THINNING RELATIONS FOR CIRCUMBOREAL ASPEN

Our study is concerned with two scientific hypotheses that deal with self-thinning as already noted in even-aged stand development of other species, and in aspen as well (Perala *et al.* 1995). We test these hypotheses against what stands of circumboreal aspens are like as determined by observations.

The power relations in equation [2] are generally accepted, so our hypotheses are directed at the values of parameters.

H_1: The need for additional space and resources for growth as *P. tremuloides* and *P. tremula* increase in size (measured by quadratic mean diameter) causes trees to succumb according to the following relation:

$$N = 1_0(\bar{d}_q)^{1_1} \qquad [4]$$

where terms are as defined for equation [2].

We hypothesize only that 1_1 is not significantly different among circumboreal aspen species. Recall, Reineke (1933) argued that 1_1 is independent of site and age, and is approximately -1.6 for a wide variety of species growing in even-aged stands.

H_2: The environmental conditions at sites where *P. tremuloides* and *P. tremula* stands grow determines stockability.

The magnitude of 1_0 is a measure of site "stockability" (DeBell *et al.* 1989), i.e., how

many trees can be packed into a given physical area. The "stockability" concept has also been referred to as "carrying capacity (Strub and Bredenkamp 1985, Harrison and Daniels 1988), and "average mass density" (Verwijst 1989).

HYPOTHESIS TESTING STRATEGY

Observational data suitable for testing the hypotheses proposed above for trembling aspen, Eurasian aspen, and their hybrids were extracted from the published literature, along with some observational data previously unpublished or limited in distribution (table 1).

Stand data: Minimum stand data needed were stem density (all trees taller than 1.37 m), quadratic mean d.b.h., total age (but not younger than attainment of self-thinning, usually 2 years), and site index. Because much data were extracted from the literature, there were some inconsistencies in how data were presented[1]. The test data consisted of point observations of aspen stand properties reported from unmanaged full density stands (fig. 1). These observations were usually control plots or initial conditions before experimental treatment.

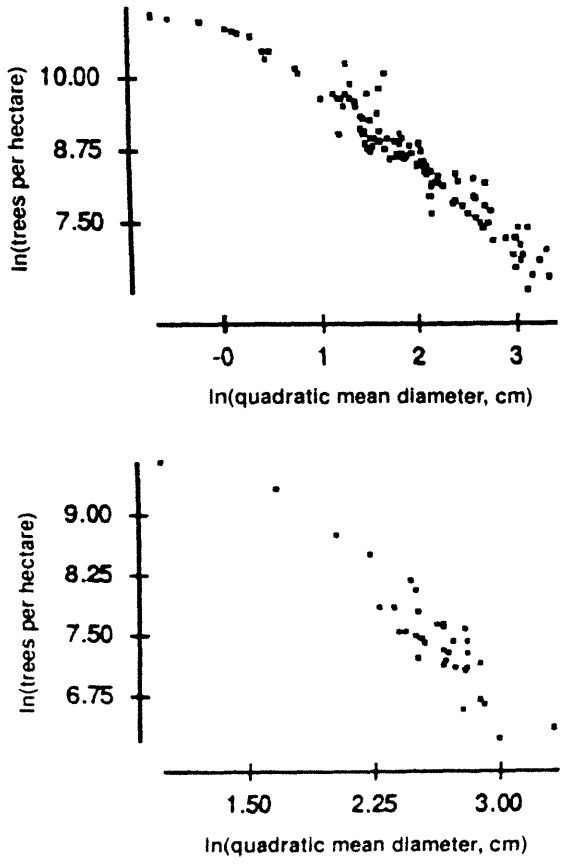

Figure 1.—*Test data sets for* P. tremuloides *(top) and* P. tremula *(bottom) available for use.*

Environment data: Because the observational data sets are geographically dispersed, we postulated that latitude, longitude, elevation, and other environmental variables might represent regional environmental differences. Unfortunately, the edaphic environment was seldom adequately described in the published literature, but climatic data were sometimes given or could be inferred from other sources, *viz.*

- total annual solar radiation, MJ/m^{2}y (Budyko 1982)
- mean July air temperature, °C (Hambidge 1941, Anon. 1984)
- total annual precipitation, mm (Hambidge 1941, Anon. 1986)
- annual runoff, mm (Geraghty *et al.* 1973, Pearse *et al.* 1985)

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[1] If either tree number or d.b.h. was missing, it was derived from given basal area according to

$$(1) \qquad D = (12732 \frac{B}{N})^{0.5}$$

where: D is mean d.b.h., cm
B is stand basal area, m^{2}ha^{-1}
N is stem density, stems ha^{-1}

If site index was missing or given in a base year other than 50, it was estimated from accompanying or local tabular or graphical values. If these were unavailable, we estimated site index from the following relationship (Lundgren and Dolid 1970):

$$(2) \qquad S = \frac{H_d}{1.48[1-\exp(0.0214\ A)]^{0.9377}}$$

where: S is site index, m at 50 years,
H_d is total height of dominants and codominants, m
A is stand age, years

Table 1.—*Data sources by species and provenance*

Author	Number of cases	Variable and range		
		Site index	Age	Mean d.b.h.
		m @ 50 yrs	*Year*	*cm*
		P. tremuloides		
Prairie Provinces				
Bella (1975)	9	20	3-6	1-2
Pike (1953)	4	17-18	35-55	8-16
Steneker (1969)	10	19-21	14-30	4-15
Steneker (1974)	29	16-21	11-44	3-23
Rocky Mountains				
Bartos and Lester (1984)	3	8-10	54-82	13-21
Crouch (1981)	1	17	66	20
Jones and Trujillo (1975)	6	12-20	22	4-5
Kemperman and Barnes (1976)	2	9-15	100-105	23-28
Schier (1975)	5	9-12	70-92	15-23
Schier and Smith (1979)	1	18	67	21
Walters *et al.* (1982)	3	13-19	60-70	21-28
Great Lakes				
Barnes (1969)	3	12-19	16-36	4-13
Day (1958)	7	18-24	10-25	3-11
Hubbard (1972)	4	27	7-24	3-14
Noreen (1968)	9	24	4-20	1-10
Perala (1978)	7	23-25	13-53	4-31
Perala (1979)	2	23-24	4-8	1-3
Perala (1984)	2	23-27	12	5
Perala (data on file)	6	24	15-39	5-17
Perala and Alban (1982)	2	21-22	40-49	18-24
Schlaegel (1975)	1	24	40	18
		***P. tremula* and hybrids**		
Scandinavia				
Haugberg (1958)	34	16-26	22-68	11-29
Vuokila (1977)	2	22-23	11-48	3-25
Total	152			

Published climatic data were based on long-term—often 30 year—averages. From the above climatic data, the following environmental variables were derived: total annual precipitation (mm), mean July temperature (°C), and effective annual precipitation (precipitation - runoff, mm). The distribution of environmental variables is given in figure 2.

Test of Hypothesis 1

Recall, hypothesis 1 claims the following is true for circumboreal aspens:

H_1: The need for additional space and resources for growth as *P. tremuloides* and *P. tremula* increase in size (measured by quadratic mean diameter) causes trees of both species to succumb according to the following rule:

$$N = l_0(\bar{d}_q)^{l_1} + e_i \text{ or} \quad [5]$$

$$N = l_0(\bar{d}_q)^{l_1} e_i. \quad [6]$$

A finding from our data sources that (a) parameter l_1 is not different for *P. tremuloides* and *P. tremula*, and (b) there is no pattern to the residuals, e_i, will be taken as evidence that H_1 is true.

Method

We first checked the standard deviations of number of trees across quadratic mean diameter classes as prescribed by Baskerville (1972). Our findings showed that the logarithmic transformation stabilized the variances in number of trees. Thereafter, we worked with the model:

$$\ln(N_i) = \ln(l_0) + l_1 \ln(\bar{d}_{i_q}) + \ln(e_i). \quad [7]$$

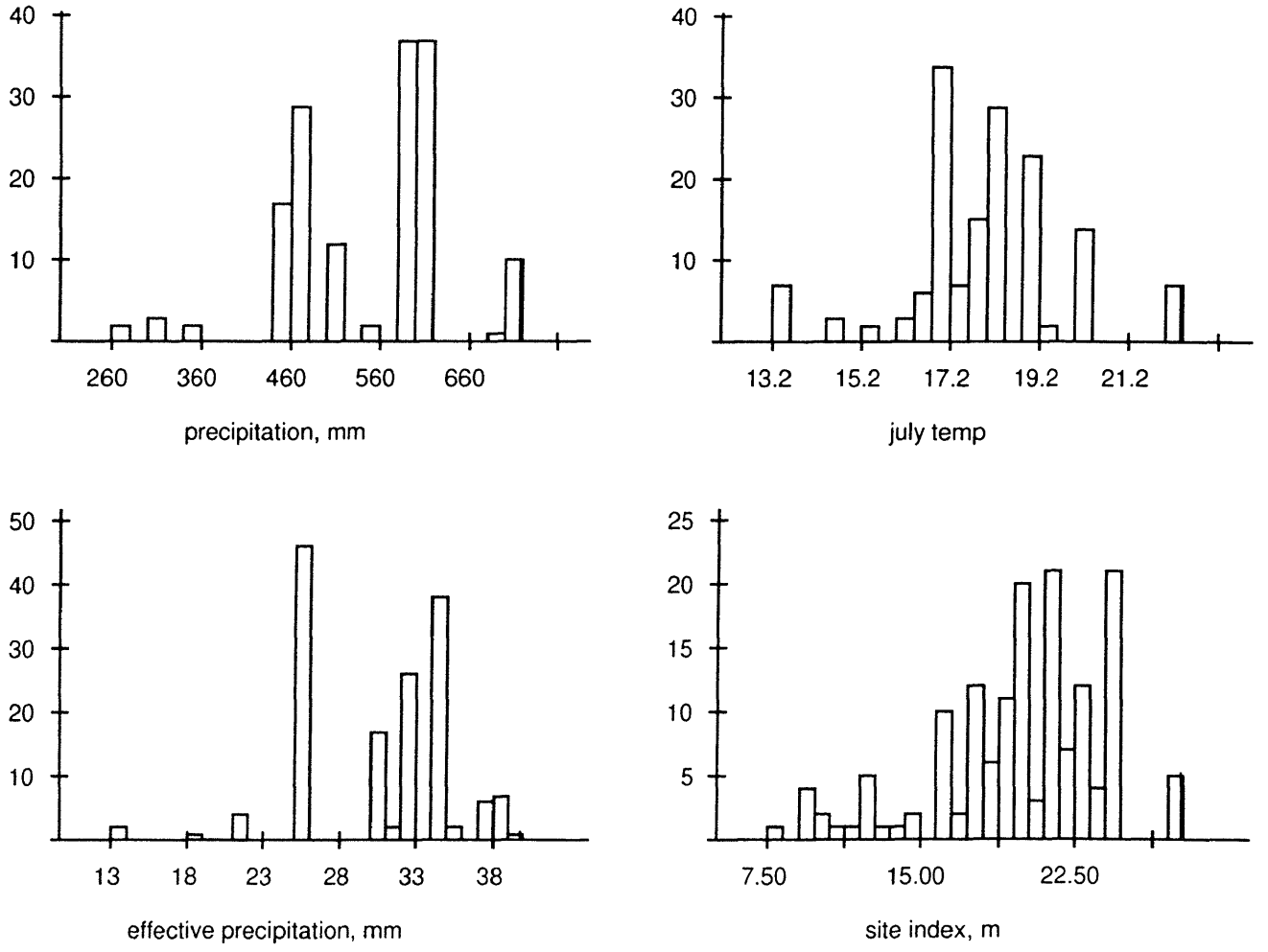

Figure 2.—*Frequency distributions of environmental variables for all data sources.*

We fit equation [7] separately to the test data set for *P. tremuloides* and *P. tremula*. We then used a dummy variable model with the combined data. Both analyses were made using Data Desk® statistical software package (Velleman 1992). Results of each regression analysis were tested for patterned relations with site index and stand age. Several regression diagnostics were run to analyze the residuals and to check for highly leveraged points and other regression assumptions. If observations significantly violated the regression assumptions, they were removed and the analyses were redone.

Results

Populus tremuloides regression analysis results are shown in row 1 of table 2 for the complete test data set. The overall regression models are, as expected, significant. However, the estimated slope, -1.24, is considerably different from Reineke's expectation. A further analysis of the *P. tremuloides* regression showed that four observations had high leverage values. Three of the four were also the extreme values using the DFFIT and Cook measures (Velleman 1992). The *P. tremuloides* test data set was therefore trimmed so that the DFFIT values were more normally distributed. The four observations removed came from stands with the smallest quadratic mean diameters. The regression was rerun, with results given in row 2 of table 2. The reduced data set better met the assumptions for regression analysis and the residual mean square was reduced by about 16 percent (table 2). The slope of the self-thinning line increased to -1.34. Analysis for the reduced trembling aspen yield data set showed no significant relation among residuals and site index but a near-significant relation with age.

The analysis was repeated for the yield data for *P. tremula* (row 1, table 3). Only 36 observations were available. Notice the exponent in equation [2] for *P. tremula* is much larger than for *P. tremuloides*, and approaches the -1.6 value suggested by Reineke. One observation had extreme leverage on the predicted values. We removed the one observation and repeated the analysis (row 2, table 3). Following removal of one observation, our estimate of the slope of the self-thinning line ballooned to 1.91. When analyzed, residuals were found not to be related to site. However, they were close to being significantly related to stand age, as was noted above for trembling aspen.

Table 2.—*Result of fitting equation [7] to the point observation (yield) data sets for* P. tremuloides

Data set	Number of observations	Model F ratio	Mean square	$\hat{I}_1$	Standard error of estimate of I_1	t	Prob. > t
All yield data	116	1,333	0.0966	-1.24	0.034	-36.5	≤0.0001
Linear DFFITS	112	1,325	0.0813	-1.34	0.037	-36.4	≤0.0001

Table 3.—*Result of fitting equation [7] to the point observation (yield) data sets for* P. tremula

Data set	Number of observations	Model F ratio	Mean square	$\hat{I}_1$	Standard error of estimate of I_1	t	Prob. > t
All yield data	36	174	0.0855	-1.65	0.125	-13.2	≤0.0001
Linear DFFITS	35	143	0.0749	-1.91	0.160	-12.0	≤0.0001

When equation [7] was fit separately to the *P. tremuloides* and *P. tremula* data sets, the self-thinning slopes appeared to be quite different. We used a model with dummy variables to analyze both species together:

$$\ln(N) = \ln(a_1) + d\ln(a_2) + a_3\ln(\bar{d}_q) + a_4 d\ln(\bar{d}_q) + \ln(e), \quad [8]$$

where d denotes a dummy variable (1 for *P. tremuloides* and 0 for *P. tremula*), and other variables are as defined previously.

Our statistical hypothesis is that neither a_2 nor a_4 is statistically significant. However, we found that *P. tremuloides* and *P. tremula* have both different intercept terms and self-thinning slope coefficients (models 2, 3, and 4, table 4).

Discussion

Based on separate analyses described above, it appeared the self-thinning slopes for *P. tremuloides* and *P. tremula* could be significantly different. Indeed, the dummy variable analysis, summarized in table 4, showed that not only are the slopes different, but so are the intercepts. Thus, we are faced with evidence that contradicts our scientific hypothesis.

It is standard practice in science, when a favorite hypothesis has not fared well, to look for culprits in the assumptions that surround every hypothesis, or in the data used to test the hypothesis, before re-evaluating the core hypothesis. We try to follow that strategy here as well, focusing on the test data set.

Two dimensions of the test data set are suspect: (1) in the analyses reported above, we found an important, but marginal, relation between the residuals and stand age (for quaking aspen but not for Eurasian aspen), and (2) it was assumed, although not checked, that the test data sets for *P. tremula* and *P. tremuloides* are approximately the same in all important dimensions, hence represent comparable stands. We conducted further analyses to examine the two questions about the test data set:

1. Does the estimated self-thinning coefficient l_1 change with stand age for *P. tremuloides*?

To answer this question, we rank ordered the *P. tremuloides* measurements and divided the entire range into fifths based on age. There were 116 usable observations, about 23 in each class. We then fit equation [8] separately to each of the five data sets (table 5).

Table 4.—*Summary of dummy variable analysis for* P. tremuloides *and* P. tremula. *Variable symbol 'd' denotes the dummy variable. In each analysis listed below, 147 observations were used. The estimated constant term is the natural logarithm of* a_1 *in equation [8].*

Model	Variables	Coefficient value	S.e. of coefficient	t-ratio	Prob. > t
1	constant	11.26	0.0774	145	≤0.0001
	$\ln(\bar{d}_q)$	-1.41	0.0349	-40.5	≤0.0001
2	constant	11.00	0.108	102	≤0.0001
	d	0.205	0.062	3.31	0.0012
	$\ln(\bar{d}_q)$	-1.36	0.037	-37.0	≤0.0001
3	constant	11.19	0.076	147	≤0.0001
	$\ln(\bar{d}_q)$	-1.44	0.034	-42.0	≤0.0001
	d $\ln(\bar{d}_q)$	0.203	0.054	3.76	0.0002
4	constant	12.43	0.434	28.6	≤0.0001
	d	-1.28	0.441	-2.90	0.0043
	$\ln(\bar{d}_q)$	-1.91	0.165	-11.6	≤0.0001
	d $\ln(\bar{d}_q)$	1.32	0.389	3.39	0.0009

Table 5.—*Results of fitting equation [7] to the* P. tremuloides *test data set in a piecewise manner. The distribution of plots was divided up into five age classes having approximately the same number of members. For each class, the regression itself was highly significant.*

Class	Age range	Estimated I_0	Estimated I_1	S.e. of coeff.	t	Prob. > t
1	≤22	10.7	-1.00	0.073	147	≤0.0001
				0.079	-12.7	≤0.0001
2	>22, ≤46	11.2	-1.41	0.337	33.2	≤0.0001
				0.216	-6.53	≤0.0001
3	>46, ≤69	12.7	-2.09	0.471	27.0	≤0.0001
				0.259	-8.06	≤0.0001
4	>68, ≤91	11.4	-1.47	0.639	17.9	≤0.0001
				0.285	-5.15	≤0.0001
5	>91	12.1	-1.67	0.772	15.7	≤0.0001
				0.263	-6.35	≤0.0001

Except in class 3, there is a monotonic increase in self-thinning slope with increasing stand age. The self-thinning slope of the oldest age class (-1.67) is approaching that of *P. tremula*. It has a substantial standard error, and may not be significantly different from that for *tremula*.

2. Are the *P. tremuloides* and *P. tremula* test data sets similar with respect to their age and size class distributions?

Graphical comparisons of plot frequency by age and quadratic mean diameter suggest the test data sets for the two species represent different kinds of stands (fig. 3). The distribution of *P. tremuloides* plots in the yield data set is strongly skewed toward younger stands. Comparable ranges of the two species age distributions begin at about 30 years, and extend to about age 60, with mean diameters ranging from about 9 to 22 cm. Test data set plots in these ranges are comparable and should have formed the basis for a comparison of self-thinning line intercepts and slopes. The regression analysis was repeated for pooled data, with species as a dummy variable (see equation [8] on previous page). Species in the range of quadratic mean diameters 9.0 to 22.0 gave the results in table 6. The terms involving the dummy variable are not significant, indicating there is not a significant difference between the two species in the 9 to 22 cm range.

These results indicate that for stands of circumboreal aspens with trees of comparable size, neither the intercepts nor self-thinning rates differ between species. Therefore, the available evidence does not invalidate a slight modification of the first hypothesis:

H_1: The need for additional space and resources for growth as circumboreal aspens increase in size from 9 to 22 cm causes trees of both species to succumb according to the following relation:

$$N = 12.54\ \bar{d}_q^{-1.96}, \qquad [9]$$

where terms are as defined previously.

Test of Hypothesis 2

Hypothesis 2 makes the following claim:

H_2: Environmental conditions where *P. tremuloides* and *P. tremula* grow determine stockability (i.e., the value of I_0).

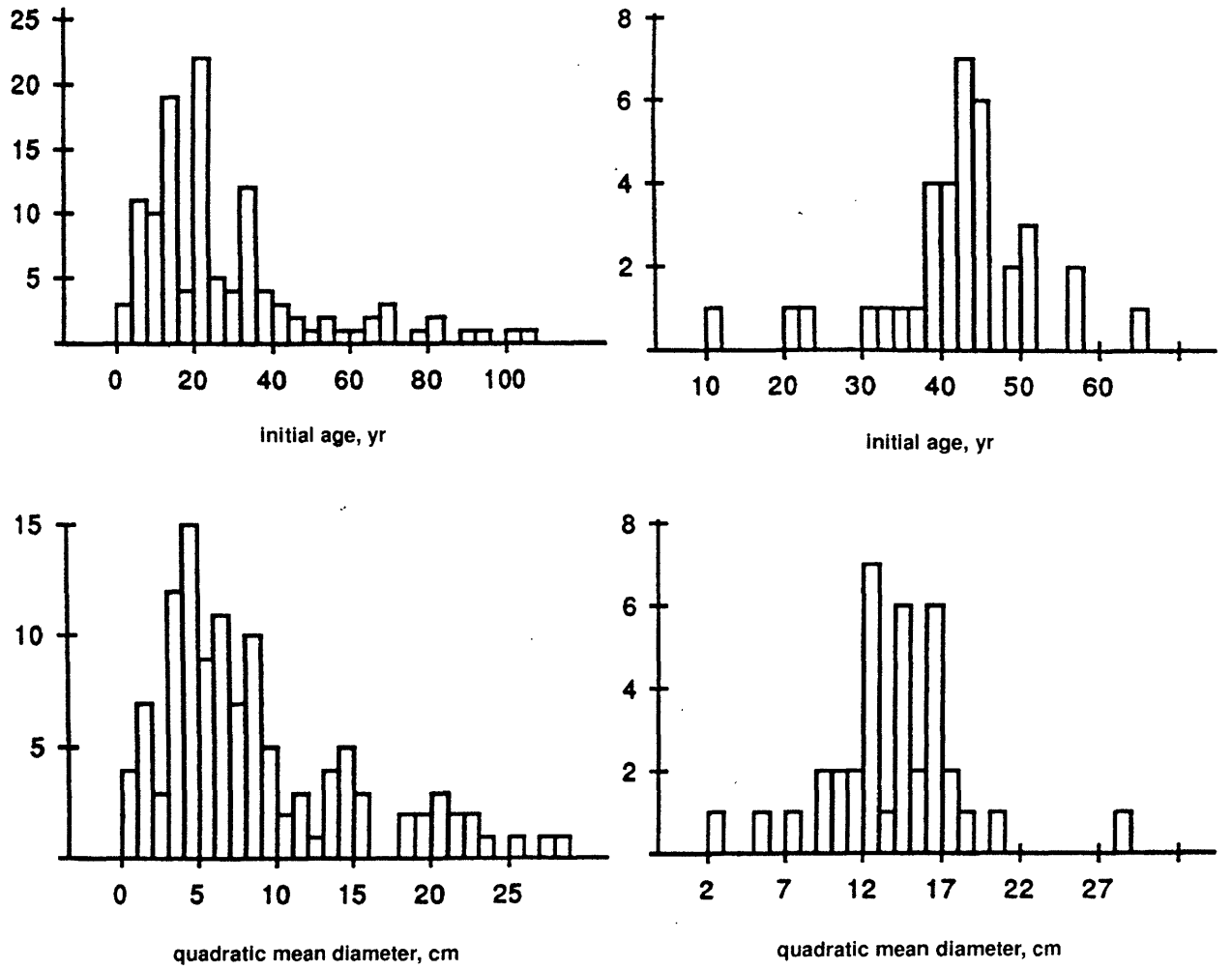

Figure 3.—*Age and size distributions of plots for* P. tremuloides *(left) and* P. tremula *(right).*

Table 6.—*ANOVA from fitting equation [8] to the 9 to 22 cm* $\bar{d}_q$ *data for* P. tremuloides *and* P. tremula; *d designates the dummy variable (1 for trembling aspen)*

R squared = 73.4% **R squared (adjusted)** = 72.0%
s = 0.2570 with 64 - 4 = 60 **degrees of freedom**

Source	Sum of squares	df	Mean square	F-ratio
Regression	10.9184	3	3.63946	55.1
Residual	3.96292	60	0.066049	

Variable	Coefficient	S.e. of coefficient	t-ratio	prob. > t
d	-0.917952	0.7810	-1.05	0.2992
d $\ln(\bar{d}_q)$	0.839069	0.6786	1.38	0.1715
Constant	12.5441	0.6399	19.6	≤0.0001
$\ln(\bar{d}_q)$	-1.96009	0.2419	-8.10	≤0.0001

If we find from our restricted test data set that no location variable, E_l, is statistically significant in the equation,

$$\ln(N_i) = [\ln(E_{ij}) + \ln(l_0)] + l_1 \ln(\bar{d}_{i_q}) + \ln(e_i), \quad [10]$$

where: E_{ij} represents the i th observation of the j th environmental variable, and other variables are as described for equation [2],

we will take that fact as evidence in support of H_2. Square brackets were used around the first two terms in equation [10] to make clear our strategy to develop an expanded intercept term.

Method

We fit equation [10] to the pooled yield data set for *P. tremuloides* and *P. tremula* using Data Desk® (Velleman 1992). Four environmental variables were tested for inclusion in the intercept term: total annual precipitation (mm), mean July temperature (°C), effective annual precipitation (mm), and site index. We discovered, however, that by limiting the plots to those with diameters >9 and <22 cm, we had limited the *P. tremula* data sources to a single study (Haugberg 1958). While the study had a range of site index values, it had a limited spatial range and the other environmental variables took single values. Further, the frequency of observations from this data source dominated all others in all regression analyses we planned to conduct. To alleviate this problem, we selected a systematic sample of half the values spread evenly through the site index classes of the Hamburg data source to include with plots from the *P. tremuloides* data sets. This reduced the number of observations available from 65 to 48. We then conducted regression analyses appending, in turn, the four candidate environmental variables to the restricted test data set that produced the final model summarized in table 7.

Results

When each environmental variable was in turn included in the regression model, we found their effects on the overall model mean square values differed greatly (table 7).

Stockability of *P. tremuloides* and *P. tremula*, as expressed by the term in square brackets in equation [10], is significantly related to several environmental variables. In general, stockability seems more sensitive to precipitation than to temperature, and more sensitive to climate than to soil conditions as summarized in the site index variable. Of course, the environmental variables are correlated in the constrained test data set we are analyzing, e.g., that between total precipitation and effective precipitation is 0.86 (Pearson product-moment), but lower for July temperature and site index. Because of these correlations, we did not attempt to estimate relations with two environmental variables to predict stockability.

Reflecting on Hypothesis 2, we find a restatement is in order:

H_2: Environmental conditions vary where *P. tremuloides* and *P. tremula* grow. Local climate information accounts for some of the differences in stockability.

Table 7.—*Regression results from using different environmental variables in equation [10]. Note that all climatic variables are statistically significant. However, total precipitation and effective precipitation perform much better than July temperature or site index.*

Environmental variable	Mean square error	M.s.e. percent reduction	Coefficient estimate	t-value	Prob. > t
None	0.0669				
Total precipitation, mm	0.0420	37.2	-0.861	-5.31	≤0.0001
Effective precipitation, mm	0.0487	27.2	-0.833	-4.27	0.001
July temperature, °C	0.0623	6.9	-0.866	-2.09	0.043
Site index, m	0.0643	3.9	-0.225	-1.70	0.097

Discussion

The model resulting from our analysis has the following arithmetic form:

$$N = l_0 P^{-.861} \bar{d}_q^{-1.96}, \qquad [11]$$

where: l_0 takes the value exp (17.436),
P designates total annual precipitation, in millimeters, and other variables are as described above.

Because the exponent of total precipitation is negative, high precipitation areas would have fewer stems for a given quadratic mean diameter. This stands to reason in light of Sukatchev's claim that stands of the same age will have fewer trees on good sites than on poor sites. Here, of course, we are speaking of growing conditions in general. In another more comprehensive analysis, from a more balanced data set (Perala *et al.* 1995), we found July temperature was a better predictor than precipitation was.

The predicted stem density was corrected for bias using the method described in Baskerville (1972) (fig. 4). Precipitation and quadratic mean diameter values are from the restricted data set used in our stockability analysis.

MODEL VERIFICATION

We found ourselves in the position of having used all available data to fit the self-thinning model and to analyze stockability, leaving no independent data set for testing. We verified our model using the PRESS strategy—systematically removing each data point in turn, calibrating the model on the remaining data set, and predicting the stem density for the omitted plot. Results from the PRESS analysis are given in table 8.

Table 8.—*PRESS analysis for final model, equation [11]*

Mean observed trees per hectare	2,225
Sum of differences (observed - predicted)	-218.9
Average difference	-4.6
Average absolute difference	374
Standard deviation of differences	500.4
Range of absolute differences	1,352.8 - 2.4

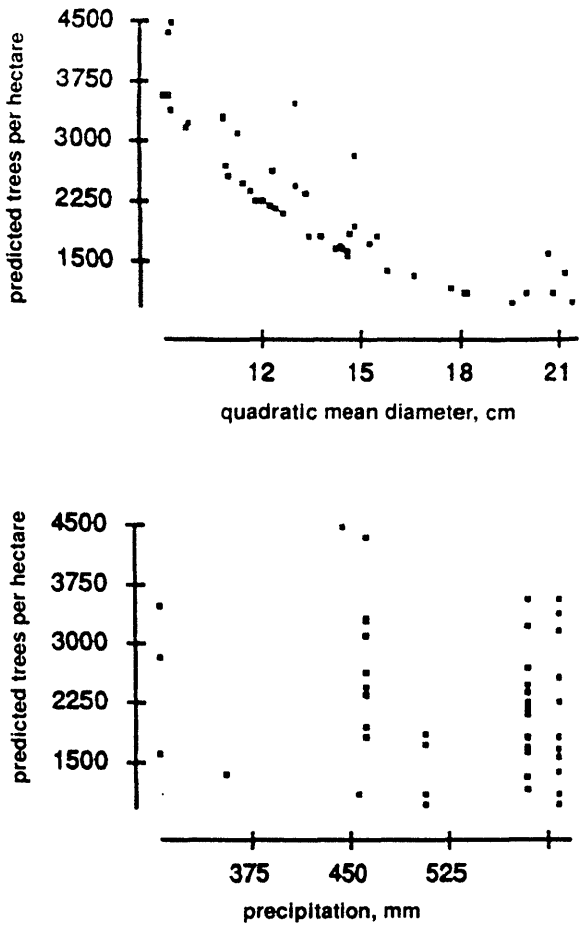

Figure 4.—*Predicted number of trees per hectare for combinations of quadratic mean diameter and total annual precipitation in the restricted yield data set.*

The average arithmetic difference of -4.6 trees is strong evidence that our model is unbiased. The average absolute difference and standard deviation of the differences between observed and predicted trees of 374 and 500 trees per hectare, respectively, suggest that the model is moderately precise. An examination of prediction errors showed that the largest errors, both positive and negative, occurred when predicting *P. tremula* stem density. Recall, all *P. tremula* were given the same precipitation values because information was not available on the spatial location of each of these plots. The size and distribution of the prediction errors by data source suggest that using a single precipitation value may have prevented the model from being more precise.

CONCLUSION

P. tremuloides and *P. tremula* trees are morphologically similar in a number of ways. We found also that stands of these two species of the same quadratic mean diameter are not different in the size - density relationship. Stockability differs between the two species, but the differences appear to vary with climate, most notably precipitation (or temperature, Perala *et al.* 1995), and not site as expressed with site index. A much larger database from throughout the range of *P. tremula* is needed to adequately test the circumboreal similarity of these aspens.

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Examines the stand diameter-density relationship of aspen across North America and Scandanavia, and how the level of this relationship might be climatically influenced.

KEY WORDS: size-density, limiting relationship, carrying capacity, average mass density.