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Comparison of an empirical forest growth and yield simulator and a forest gap simulator using actual 30-year growth from two even-aged forests in Kentucky

Daniel A. Yaussy*

USDA Forest Service, Northeastern Research Station, 359 Main Rd., Delaware, OH 43015-8640, USA

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Abstract

Two individual-tree growth simulators are used to predict the growth and mortality on a 30-year-old forest site and an 80-year-old forest site in eastern Kentucky. The empirical growth and yield model (NE-TWIGS) was developed to simulate short-term (<50 year) forest growth from an industrial perspective. The gap model (ZELIG) is based on the theory of growth processes and has been used to simulate long-term (100 years and greater) forest succession. Based on comparisons of species specific diameter distributions, biomass, and board-foot and cubic-meter volumes, NE-TWIGS performed better for both sites than did ZELIG. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: NE-TWIGS; ZELIG; Validation

1. Introduction

Scientists have simulated forest tree growth from two different viewpoints: empirical and theoretical. Those interested in timber production usually had access to repeated measurements of variables from trees on permanent plots. These variables, such as diameter at 1.37 m (DBH) and height, were the results of tree growth processes that could be used to empirically estimate these measurements and, therefore, timber values in the future. On the other hand, scientists interested in the plant processes and mechanisms involved in the growth and development of forests approached the matter from a theoretical viewpoint. Their models reflect the influence of perturbations in light, climate, weather, and moisture availability on the growth of trees.

These two groups seldom interacted until recently (Desanker et al., 1994; Sievanen and Burk, 1994). Both modeling approaches could benefit from some aspects of the other. The empirical models need to become more sensitive to changes in the environment. The assumption of many empirical models that site characteristics are fixed, hampers their ability to account for changes in growth due to extreme weather events. Many empiricists harbor the perception that predictions of tree growth from theoretical models are

*Tel.: +1-740-368-0093; fax: +1-740-368-0152.
E-mail address: dyaussy/ne_de@fs.fed.us (D.A. Yaussy).

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not sufficiently accurate to support economic management decisions. This study compares the predictive ability of a forest succession model, ZELIG, and an empirically based growth and yield model, NE-TWIGS, to accurately simulate the 30-year development of two plots in eastern Kentucky.

Many of the published uses of gap-phase models (Shugart and West, 1977; Busing, 1991; Solomon and Bartlein, 1992) report successional changes in forests due to changing environments over long periods of time (100–500 years). There are few examples of these models being used for periods of <100 years (Colbert and Sheehan, 1995). One of the reasons Rastetter (1996) finds no adequate method to validate models of ecosystem response to global change is because the predictive ability of models covering large time steps may not be accurately evaluated with data collected for shorter time periods. However, Botkin (1993) devotes an entire chapter to using JABOWA-II for natural resources management in which he reports findings at time periods from 10, 30, and up to 90 years. He also used 50 and 60 year growth data from the Hubbard Brook forest to verify his model. Botkin, the originator of the gap-phase model, sets no limitation to the time frames for which gap models are appropriate. This indicates that the accuracy of gap-phase models has and should be evaluated for time scales of <100 years.

Comparing these two models to actual data is a step in providing validation for both. Proper validation of these models would require long-term growth plots from all areas within the models' spatial and temporal range.

2. Models

2.1. ZELIG

ZELIG (Urban, 1990) was developed to simulate forest dynamics based on the light made available to the forest floor from gaps in the canopy caused by individual-tree mortality. It is termed a 'gap' or 'gap-phase' model. ZELIG is a refinement of previous gap models, starting with JABOWA (Botkin et al., 1972) and progressing through FORET (Shugart and West, 1977), FORENA (Solomon, 1986), LINKAGES (Pastor and Post, 1986), and other derivations. ZELIG was intended to be a 'generic' gap model eliminating many of the built-in site-specific conditions of the previous models while retaining the underlying structure. By specifying species- and site-specific parameters, the model can be applied to a wide variety of locales. The gap models are stochastic and are to be run many times to develop a pattern of typical behavior.

As stated above, Botkin used 50–60 year forest records to verify the JABOWA model. Lindner et al. (1997) evaluated the gap model, FORSKA, on 120 years of stand development data from a beech forest in Bavaria. They found the mortality algorithms to be inadequate and substituted a prescribed thinning routine analogous to the observed stand development. This modified version appropriately projected stand level values of biomass, mean diameter, and height, but individual tree dimensions and stand structure were quite unrealistic. Projections improved after substitution of a different height growth function. The authors were not familiar with any other study which used long-term forest observation data to calibrate and validate a gap model.

ZELIGs strength lies in its ability to modify tree growth based on the interaction of yearly climate variables and specific site variables. In this way, growing degree days and annual precipitation interact with soil fertility and soil moisture holding capacity to increase or decrease tree development. A tree's competition for light is based on solar variables and adjacent tree heights. Tree growth is determined by the tree's ability to obtain needed light, temperature, nutrients, and water.

Criticisms of the gap models include what may be invalid assumptions of growth rates related to realized niche. In gap models, the best growth of a species occurs in the middle of its range, then decreases to the north or south of this middle point. The regeneration algorithm of gap models typically allows all species listed to be available for establishment in gaps. This may be unrealistic if the species is heavily seeded and does not occur in the surrounding forest. This is not as critical with wind disseminated species.

Even though ZELIG was not designed to report typical growth and yield values (merchantable cubic-meter and board-foot volumes), it does maintain an individual tree list with DBH and height measurements from which these commercial volumes may be derived.

2.2. NE-TWIGS

NE-TWIGS (Hilt and Teck, 1989) is a growth and yield model based on data collected by the Forest Service's Forest Inventory and Analysis unit (FIA) from the 1950s through the 1980s. NE-TWIGS is the northeastern version of the four 'TWIGS' programs which include: LS-TWIGS (Lake States, Brand, 1981), CS-TWIGS (Central States, Shifley, 1987), and SE-TWIGS (Southeast, Meldahl, 1991). The TWIGS models are personal computer versions of a mainframe program originally designed to project regional forest inventories for Renewable Resource Assessments (USDA Forest Service, 1979). The algorithms of the TWIGS family of simulators have all been incorporated with algorithms from other simulators in the Forest Service's Forest Vegetation Simulator in use on the National Forests (Teck et al., 1996).

STEMS, a precursor of the TWIGS family of models, has been compared to earlier versions of STEMS and alternative stand and individual-tree growth and yield models with results favorable to the latest version of the model (Crow, 1986; Holdaway and Brand, 1983; Holdaway and Brand, 1986). CS-TWIGS was validated on 20-year growth data from Illinois forests by Kowalski and Gertner (1989) with acceptable prediction errors for mean stand diameter, basal area, and survival. The survival and basal area growth components of the NE-TWIGS model were deemed acceptable when validated using every fourth plot of the FIA data set used to develop these algorithms (Hilt and Teck, 1988; and Teck and Hilt, 1990). Schuler et al. (1993) compared four growth and yield simulators, including NE-TWIGS, using independent data from across the northeastern U.S. NE-TWIGS was found to be a suitable simulator for all forest types in the region, except spruce-fir, based on predictions of basal area, stand diameter, and number of trees.

As will be discussed in the Data Requirements section, the TWIGS models use typical data collected by foresters in the field, such as species, DBH, height, and site index. Models based on actual data, as opposed to theoretical relationships, are often assumed to be more accurate than theoretical models for the range of data on which they were developed. Because the TWIGS models are empirical, they should not be used to project forest dynamics much beyond the scope of the data, ca. 30 years. The deterministic equations used in NE-TWIGS provide a single result and no information on the possible range of future conditions.

3. Data requirements

3.1. ZELIG

The ZELIG model requires parameters to describe the site of the simulation and the growth characteristics of the tree species that may possibly occupy the site. The site is typified by variables describing location, light availability, soils, and climate. These variables may be easy or quite difficult to obtain. Easy variables include latitude, longitude, elevation, typical canopy height, and direct and diffuse radiation measures. The last two solar variables are easily derived with the SOLAR program included with ZELIG. SOLAR computes direct and diffuse solar radiation from latitude, elevation, aspect, slope, and an estimate of mean monthly cloudiness. Slightly harder to obtain are mean monthly temperatures, mean monthly precipitation, and the standard deviations of those means for the sites in question. These can be inferred from long-term records from nearby weather stations as can the mean monthly cloudiness needed for the SOLAR program. The soil variables of field capacity, wilting point, and soil fertility (represented by maximum Mg/ha/year of aboveground biomass) are very site specific and are not typically measured by any agency.

The growth and development characteristics of individual species are quantified by maximums of age, DBH, and height; a growth constant to determine the inflection point of the diameter growth curve over age, such that a tree will reach two thirds of its maximum diameter by half its maximum age (Botkin, 1993); range of growing degree days at which a species is found; and relative indices of shade tolerance, drought resistance, nutrient stress resistance, and the likelihood of producing viable seedlings. Species parameters were available from compilations of Solomon (1986) and Pastor and Post (1986) (original parameter set). Some of these parameters specifying maximum age, DBH, and height, did not agree with similar estimates found in Harlow and Harrar (1969) (modified parameter set). In development of the modified parameter set, new growth constants were calculated as described by Botkin (1993).

The ZELIG program allows a simulation to start from bare ground or with existing trees. To use the latter option, individual tree measurements of species, DBH and height to the base of the live crown (HBC) must be recorded for every tree on the plot.

3.2. NE-TWIGS

The TWIGS programs require less initial data, which also accounts for the inability to respond to climatic variation. The only site characteristic required is site index for the major species group present on the plot. This site index is then converted to site indices for the other 27 species groups. Site index indicates the height a tree, that has always been dominant, will reach by age 50. This implies that site index is a catch-all variable that accounts for all micro- and macro-site variations including solar radiation, slope, aspect, water availability, soil fertility, and climate. Site index is usually considered static over time in most applications. NE-TWIGS cannot start from bare ground and is designed to project an existing 0.405 ha (1 acre) of forest; so, species group, DBH, and number of trees per 0.405 ha represented by each tree in a plot are required as individual-tree inputs to the program. Crown ratio is estimated by the program if not supplied by the user.

4. Test data sets

Two sites in the Daniel Boone National Forest of Kentucky have been used for long-term thinning experiments. These sites near Baldrock and McKee, Kentucky, included control plots on which no thinnings occurred. These plots are used as the initial conditions for this study. Tree corings determined the age of the dominant and codominant trees at the Baldrock site to be ≈80 years in 1961. The trees at the McKee site were determined to be ≈30 years old. Measurements of DBH have been taken 20 times since 1961, with those taken in 1991 being used for this study. For graphical presentation, species were grouped as: white oak (*Quercus alba*), black oak (*Q. velutina*), scarlet oak (*Q. coccinea*), red maple (*Acer rubrum*), hickory (*Carya* spp.), and other trees (*Liriodendron tulipifera*, *Nyssa sylvatica*, *Pinus echinata*, *Cornus florida, Tsuga canadensis*, *Fraxinus* spp., *Oxydendrum arboreum*, and *Amelanchier arborea*). A *Q. prinus* was included in the white oak group and a *Q. rubra* in the black oak group at the McKee site. Initial stand structures for the control plots (1961) are shown in Fig. 1. Site parameters used by the two models are listed in Table 1.

Table 1
Site parameters needed to execute the ZELIG and NE-TWIGS programs

Variable	Baldrock	McKee
Age	80	30
Site index (base age 50)	19.5 m	20.1 m
Aspect	90°	95°
Slope	20%	22%
Sun angle (Φ)	0.6479 radians	0.6526 radians
Direct-beam insolation	0.5877%	0.5937%
Diffuse insolation	0.4095%	0.4087%
Canopy height	25 m	26 m
Field capacity	27%	27%
Wilting point	9%	8%
Soil fertility	3.40 Mg/ha/year	3.43 mg/ha/year

Solar radiation for the plots was calculated by SOLAR provided with the ZELIG software. Latitude, aspect, slope, average number of cloudy days per month, and beginning and ending months of the growing season were used to determine sun angle, and direct and diffuse insolation. Expected canopy height of the surrounding stand is used to reduce the light from the top of the canopy to the forest floor and is not changed within the program over the course of the simulation. This value was determined using site-index curves by Hampf (1965) for 100-year-old white oaks.

Moisture availability is evaluated in terms of field capacity and wilting point. These variables had been determined for these sites in the mid-60s. ZELIGs measure of site productivity is in terms of the maximum megagrams per hectare (Mg/ha) of aboveground biomass that a site can produce in a year. Annual diameter increment indicated that the maximum growth on both sites occurred in 1964. Wiant (1978) green weight equations and the appropriate conversions were used to calculate the aboveground biomass values in Table 1 (representing soil fertility).

Mean monthly temperatures, precipitation, and standard deviations were calculated for Baldrock from

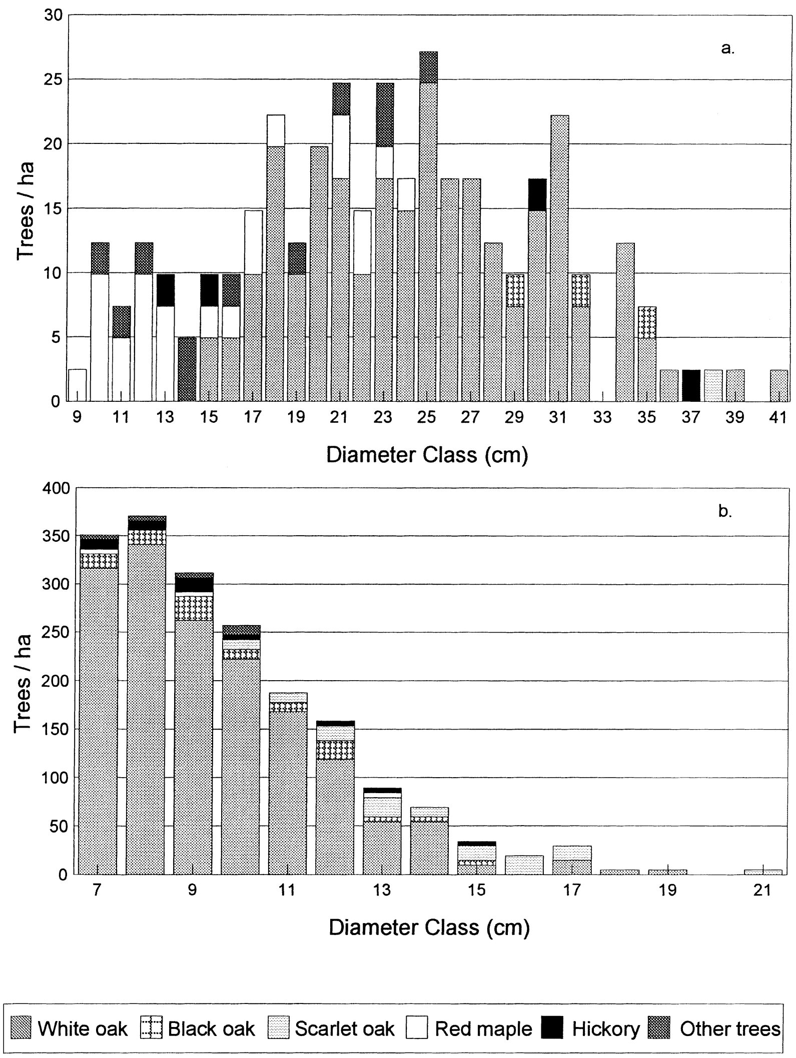

Fig. 1. Initial diameter distributions of the (a) 80-year-old Baldrock site and (b) the 30-year-old McKee site.

27 years of records collected at the London, Kentucky, airport. A weather station existed in McKee, Kentucky, until 1972, at which time the station was relocated to neighboring Grayhawk. Combined records from these two stations resulted in a data history of 29 and 40 years for temperature and precipitation, respectively.

The individual-tree measurements needed by ZELIG include HBC, which was not collected in 1961 on either of the sites. On trees that were large enough, merchantable height equations (Yaussy and Dale, 1990) were used to calculate height to 23 cm (nine inches) and 10 cm (four inches) top diameters. The HBC was then selected at a random point between these two points. If the tree was not larger than 23 cm DBH, then HBC was randomly chosen at some point between 1 m and the 10 cm diameter height. If the tree was smaller than 10 cm DBH, HBC was set to 1 m, the smallest value recognized by ZELIG.

Plot size for the ZELIG program is determined by the size of gap formed in the forest canopy when a typical dominant tree dies. In this case, the plot size was set to 0.05 ha (0.124 ac). The plot at Baldrock was 0.405 ha, and 0.202 ha (0.5 ac) at McKee. Therefore, the trees from the Baldrock site were randomly assigned to eight pseudo-plots for input into the ZELIG program, whereas four pseudo-plots were needed for the trees from McKee. NE-TWIGS requires a tree list on a 0.405 ha basis. So, each tree from the McKee site represented two trees per 0.405 ha, and no revision was required for the Baldrock site.

5. Methods

NE-TWIGS contains an optional ingrowth routine to predict new saplings that will occur in the stand. This routine adds trees of appropriate species, each with a 12.7 cm (five inches) DBH. To operate correctly, it eliminates all existing trees from the tree list with DBH below 12.7 cm. This option was not used when comparing the models, because almost all the trees from the McKee plot were <12.7 cm in DBH. ZELIG was, therefore, modified to identify which trees were initially present and which were ingrowth. All analysis was performed on initial trees only.

The ZELIG program was run 100 times to simulate growth for 30 years for each combination of site (Baldrock or McKee) and parameter set (original or modified). The initial trees that were present in the resulting tree lists were summarized into 1-cm DBH classes on a per-ha basis. ZELIG is stochastic, and 100 runs was considered adequate to quantify trends.

NE-TWIGS was run to simulate growth for 30 years, once for Baldrock and once for McKee, and the resulting tree lists were summarized into 1-cm DBH classes on a per-ha basis. The TWIGS programs are deterministic and more than one run would not change the results.

The actual 30-year data from Baldrock and McKee, excluding ingrowth, were also summarized as above. These actual diameter distributions were compared to the predicted distributions with Kolmogorov–Smirnov (KS) two-sample tests using number of stems of species groups within diameter classes. The KS test is used to detect broad differences between distributions. These differences can be in either location (mean) or spread (variance). However, if the hypothesis that the two distributions are similar is rejected, the test statistic gives no indication of whether the hypothesis was rejected because of differences in location, spread, or both.

In addition to the diameter distributions, the measures of aboveground biomass, cubic-meter volume to a 10 cm top diameter, and board-foot volume to a 25.4 cm top diameter were calculated for each of the eight data sets. There is no metric equivalent to the U.S. measure of board-foot volume; however this measure is of significant economic importance in the regions where the Twigs and ZELIG models were developed and for all of the United States. Mg/ha of aboveground biomass was calculated using Wiant (1978) equations and the appropriate conversion factors. The present author considered using the equation contained in ZELIG, but it is not species specific. Board-foot and cubic-meter volumes were determined using Scott (1979) and Scott (1981) equations. This required determinations of merchantable height to different diameters, which was accomplished using the equations by Yaussy and Dale (1990) and the site-index conversion equations contained in NE-TWIGS.

6. Results

Graphical comparison of the 1991 stand structure of Baldrock (Fig. 2) and McKee (Fig. 3) shows little similarity between actual and predicted values. Table 2 lists the two-sided probabilities (p-values) resulting from the KS tests comparing actual to predicted stem counts within diameter class by species. Total stem counts for each species are listed for comparison purposes. The KS procedure tests the hypothesis that the two distributions are the same. Smaller p-values indicate less similarity between the actual and predicted diameter distributions. Standard statistical practice is to choose an arbitrary α-level, $\alpha = 0.05$ for example, such that any test resulting in a p-value lower than α would indicate that the distributions were statistically different. Here, we are more interested in the similarity of the distributions, and so are interested in the larger p-values.

The KS tests indicated that the first run of the ZELIG program performed better than the average of 100 runs for both parameterizations. The effect of averaging smoothed the distributions. The KS tests detected this smoothing when compared to the more discrete actual distributions of the single plots. Therefore, results from the run of the ZELIG model which produced the highest KS-test p-value for the white oak

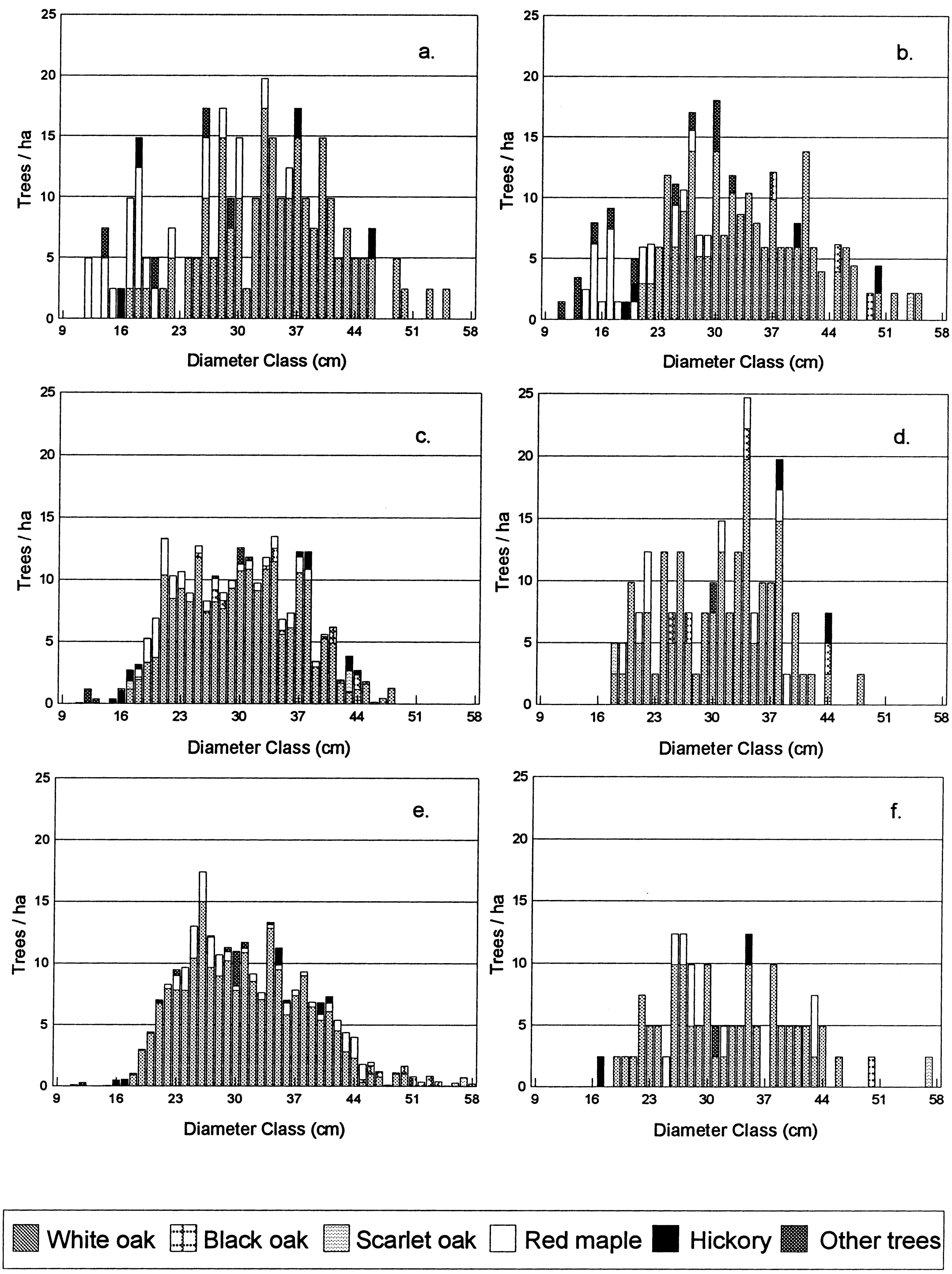

Fig. 2. Diameter distributions of the Baldrock site: (a) actual; (b) NE-TWIGS; (c) ZELIG original parameter set average of 100 runs; (d) ZELIG original parameter set best run; (e) ZELIG modified parameter set average of 100 runs; and (f) ZELIG modified parameter set best run.

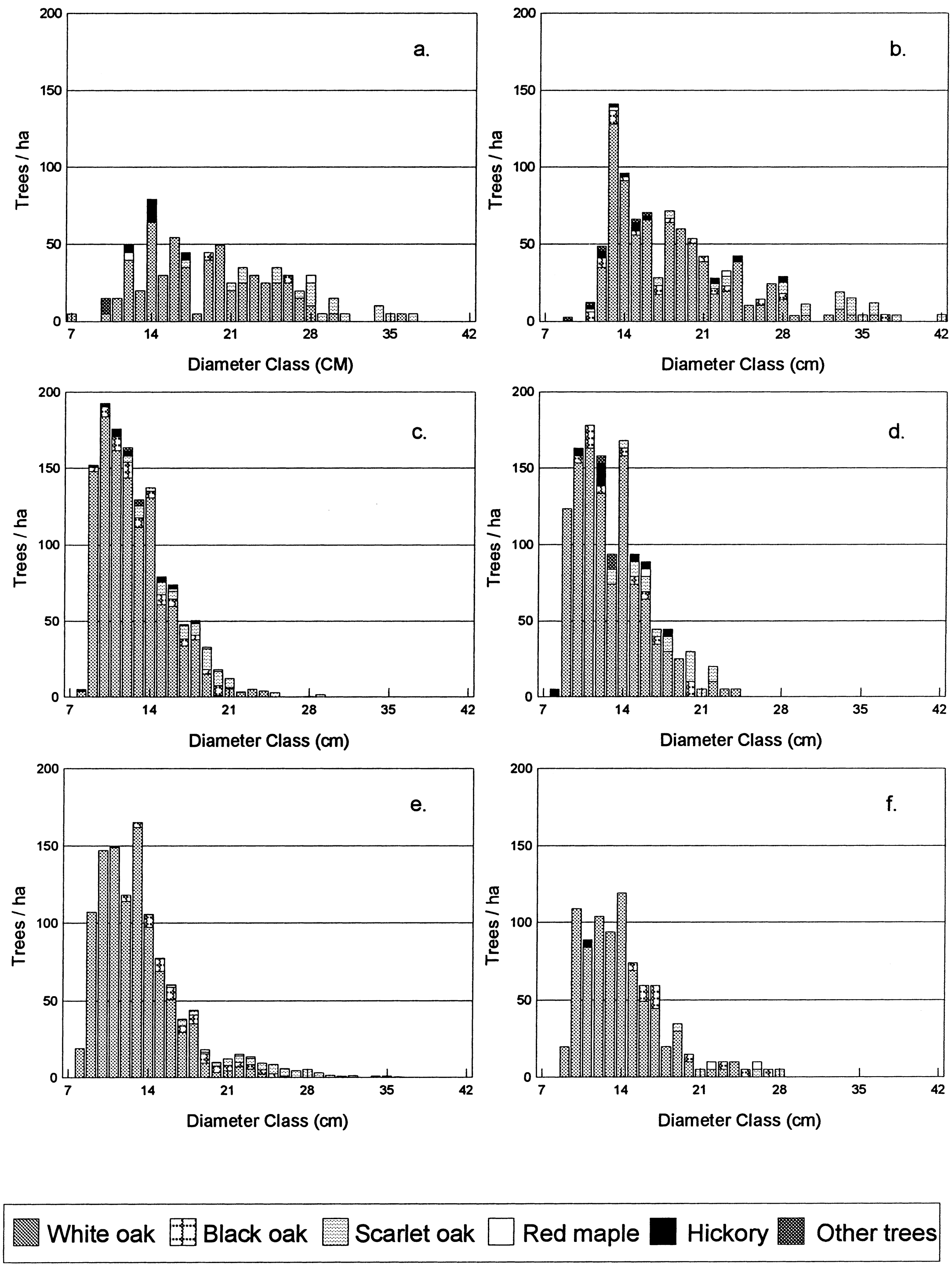

Fig. 3. Diameter distributions of the McKee site: (a) actual; (b) NE-TWIGS; (c) ZELIG original parameter set average of 100 runs; (d) ZELIG original parameter set best run; (e) ZELIG modified parameter set average of 100 runs; and (f) ZELIG modified parameter set best run.

Table 2
p-Value of Kolmogorov–Smirnov testing whether actual and predicted diameter distributions are different

Model	White oak	Black oak	Scarlet oak	Red maple	Hickory	Other trees	All trees
Baldrock (actual) trees/ha	217.45	0.00	0.00	54.36	9.88	7.41	289.11
ZELIG (original)	0.0020	0.0000	0.0000	0.0339	0.9978	0.9340	0.1301
100 runs	(196.25)	(6.97)	(2.64)	(24.46)	(6.08)	(2.72)	(239.12)
ZELiG (original)	0.0225	0.0000	0.0000	0.0231	0.4413	0.4413	0.1791
best run	(190.27)	(9.88)	(2.47)	(22.24)	(4.94)	(2.47)	(232.28)
ZELIG (modified)	0.0053	0.0000	0.0000	0.0038	0.9999	0.6065	0.2863
100 runs	(203.05)	(4.50)	(1.24)	(24.83)	(4.35)	(5.24)	(243.2)
ZELIG (modified)	0.0883	0.0000	0.0000	0.0086	0.8928	0.4413	0.4353
best run	(133.44)	(2.47)	(2.47)	(19.77)	(4.94)	(2.47)	(165.56)
NE-TWIGS	0.4845	0.0000	0.0000	0.9368	0.7946	0.8653	0.6693
	(199.17)	(7.41)	(0.40)	(37.06)	(7.16)	(19.27)	(271.57)
McKee (actual) trees/ha	543.63	9.88	88.96	9.88	24.71	9.88	686.95
ZELIG (original)	0.0001	0.1464	0.0001	0.9883	0.6849	0.5464	0.0001
100 runs	(1107.97)	(68.40)	(76.40)	(6.57)	(20.90)	(7.46)	(1287.72)
ZELIG (original)	0.0001	0.2073	0.0001	0.9963	0.6347	0.1813	0.0001
best run	(1052.67)	(54.36)	(84.02)	(4.94)	(39.54)	(14.83)	(1230.59)
ZELIG (modified)	0.0001	0.4081	0.2399	0.9909	0.9999	0.9999	0.0001
100 runs	(1010.51)	(68.49)	(55.10)	(6.13)	(1.83)	(0.05)	(1142.12)
ZELIG (modified)	0.0001	0.5860	0.5376	0.9639	0.3752	0.0000	0.0001
best run	(770.97)	(49.42)	(19.76)	(9.88)	(4.94)	(0.00)	(854.99)
NE-TWIGS	0.1971	0.6159	0.4364	0.9811	0.6882	0.5220	0.1228
	(766.03)	(61.28)	(82.04)	(7.66)	(30.64)	(12.11)	(959.76)

Note: Numbers in parentheses are predicted trees/ha.

species group is also reported in Table 2. The white oak group dominated the actual and predicted diameter distributions of the plots to such an extent that the other species groups could not be used to determine which of the 100 runs of the program was 'best'.

There were no black or scarlet oak remaining in the actual Baldrock stand, so no tests could be run for those species. The small number of stems predicted by the models for those species was such that they should not be considered when evaluating the simulators. The same holds true for the prediction of no stems in the 'other trees' species group by the best run of the modified ZELIG parameterization. The *p*-values are determined by the number of stems and their diameter distribution. As the number of stems decreases, the statistical power decreases, and the harder it is to distinguish differences in the distributions. All models underpredicted the total number of stems that would survive for this plot. The total number of stems predicted by the simulators was much more than the number of stems in the actual plot at McKee, especially for the 'white oak' group. Overall, the NE-TWIGS model provided better predictions of the diameter distributions within species and for all trees.

Figs. 4 and 5 show similar results for 1991 biomass, cubic-meter volume, and board-foot volume estimates. The volumes predicted by NE-TWIGS were within 13% and 16% of the actual for the Baldrock site and within 3–9% for the McKee site. Whereas, the predictions for both parameterizations of the ZELIG

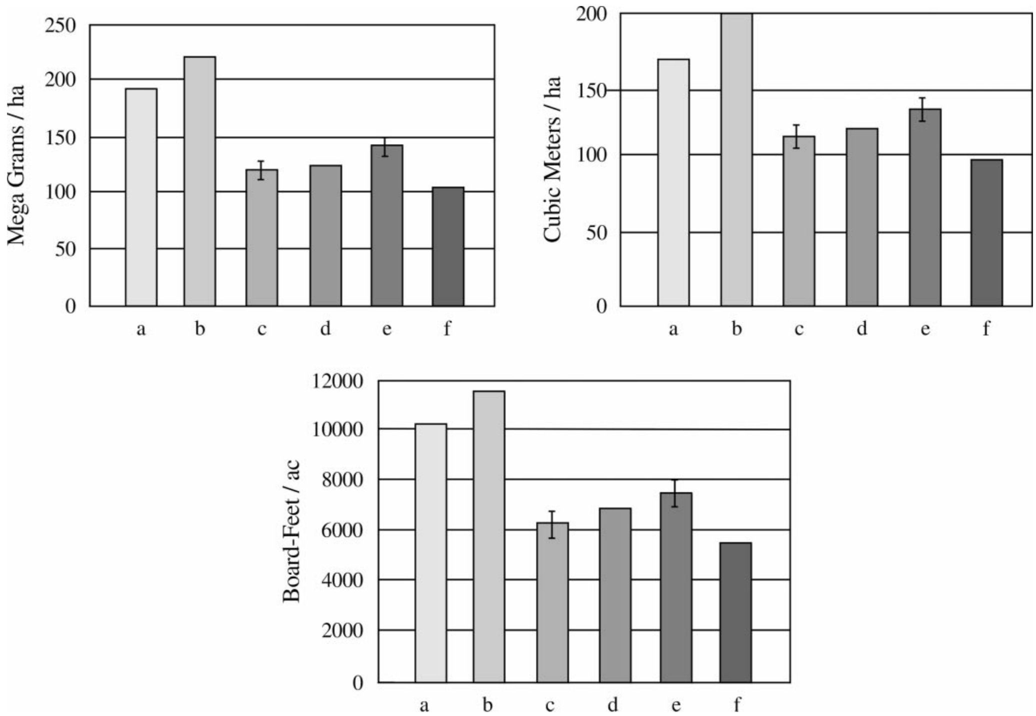

Fig. 4. Actual and predicted volumes of the Baldrock site: (a) actual; (b) NE-TWIGS; (c) ZELIG original parameter set average of 100 runs; (d) ZELIG original parameter set KS best run; (e) ZELIG modified parameter set average of 100 runs; and (f) ZELIG modified parameter set KS best run.

model were within 23–46% of the actual figures for the Baldrock site and 39–98% for the McKee plot. The average diameters predicted by the models for Baldrock were very close to the actual value with reasonable standard deviations (Fig. 6). The estimated trees per ha for the average of the 100 runs of the ZELIG model using both parameter sets and the NE-TWIGS model are within 20% of the actual values. The NE-TWIGS average diameter value for the younger McKee site is also very good; however none of the other simulations came within 20% for average diameter or trees per ha.

7. Discussion

The NE-TWIGS model performed better than the ZELIG based parameterizations on both stands. Although individual runs of the ZELIG model were better than the average of 100 runs based on KS tests of diameter distributions, they did not consistently improve the predictions of volume, average diameter, or trees per ha. Note that the ZELIG model overpredicted the number of stems for the McKee site (Fig. 6), but underpredicted the biomass and volumes (Fig. 5). This implies that the model does not grow the white oaks fast enough, as is seen in Fig. 3. The red maples, on the other hand, grew too fast and the white oaks incurred too much mortality in the ZELIG simulations of the Baldrock site (Figs. 1 and 2). Like Lindner et al. (1997), this evaluation found the projections of the unmodified gap model to be unrealistic. The small modifications in maximum diameter and maximum age did little to improve the projections. The results for NE-TWIGS compare favorably to those of Schuler et al. (1993) in which NE-TWIGS was found to be an adequate model for projecting development of hardwood forests of the central U.S.

The NE-TWIGS model cannot be easily altered to obtain better predictions for specific areas. One could annually adjust the site-index value based on seasonal temperatures and precipitation rates being above or below local averages (Woollons et al., 1997). NE-TWIGS was designed to work in the time frame and

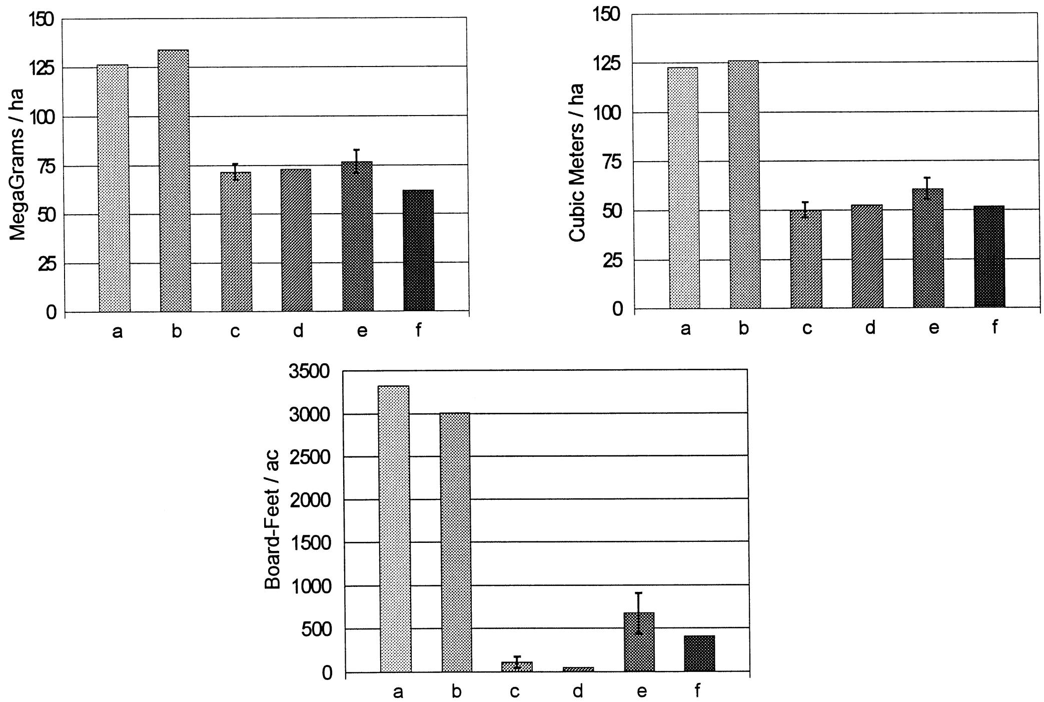

Fig. 5. Actual and predicted volumes of the McKee site: (a) actual; (b) NE-TWIGS; (c) ZELIG original parameter set average of 100 runs; (d) ZELIG original parameter set KS best run; (e) ZELIG modified parameter set average of 100 runs; and (f) ZELIG modified parameter set KS best run.

region used in this comparison; however, it is a generalized model, not developed, specifically for an even-aged, upland oak stand, as is OAKSIM (Hilt, 1985). For a comparison of NE-TWIGS, OAKSIM, and other empirical growth and yield simulators for the Northeast (see Schuler et al., 1993).

The species parameters in the gap models can be modified, which might produce better growth predictions. An adjustment of site-specific and species parameters was investigated for white oak on these data sets. White oak made up >75% of the stems at each site, and any improvement in prediction of the growth for this species would improve the overall predictions immensely.

Of the parameters required by ZELIG, the present author had the least confidence in his estimates of soil fertility. Whittaker (1975) states that net primary productivity for temperate deciduous forests range from 6 to 25 Mg/ha/year averaging 12 Mg/ha/year, much higher than was calculated for these sites (Table 1). Another parameter which might be altered is the species growth constant which changes the age at which a tree of that species puts on most of its diameter growth. A larger constant implies that trees of this species grow quickly early in their life and growth tapers as the tree ages. A lower constant allows trees of the species to grow in diameter evenly as they age (Botkin, 1993). The maximum age and diameter that a tree species can attain are parameters which determine many aspects of growth and mortality within the ZELIG model. Solomon (1986) used 400 years and 100 cm as the maximum age and DBH of white oak. Botkin (1993) lists 600 and 122, respectively, for these parameters. Harlow and Harrar (1969) give maximums of 600 years and 244 cm. The Wye oak in Maryland, the largest white oak reported in the United States, is assumed to be 450 years old and has a DBH of 302 cm, assuming a circular cross section (American Forestry Association, 1998). The present author set the maximum age for white oak to 600 years and the maximum diameter to 300 cm.

Systematic combinations of values within the ranges of the soil fertility parameter (2–24 Mg/ha/year) and the white oak growth constant parameter

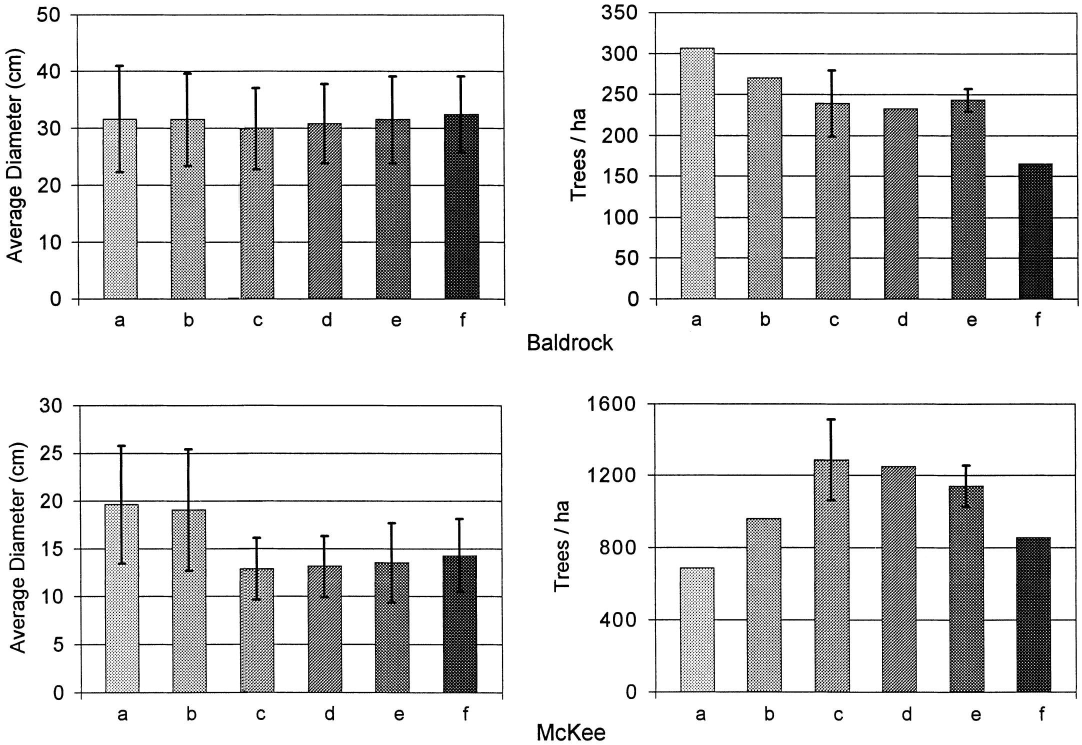

Fig. 6. Average diameter and trees/ha for the Baldrock and McKee sites: (a) actual; (b) NE-TWIGS; (c) ZELIG original parameter set average of 100 runs; (d) ZELIG original parameter set KS best run; (e) ZELIG modified parameter set average of 100 runs; and (f) ZELIG modified parameter set KS best run.

(50–300) were tested within the ZELIG framework seeking a combination that would improve the simulations of both stands. Graphs of the relationships between these parameters and average DBH, number of trees per hectare, and the volume measures showed that the volume measures and average DBH were not sensitive to soil fertility values above 10 Mg/ha/year. Number of stems on each site was quite sensitive to both parameters. Parameters were found for the 30-year-old site which satisfactorily predicted number of stems, average DBH, biomass, and cubic-meter volumes; however, the diameter distribution was such that the board foot estimates were still quite low (not enough large trees). These parameters simulated reasonable volume measures for the 80-year-old site, but the estimated average DBH and number of trees were not close to those of the actual site. No combination of parameters tested could produce enough trees for the 80-year-old stand. Reasonable average DBH estimates for the site could be attained, but never with the proper number of trees to produce the right combination of biomass, cubic-meter volume or board-foot volume. No combination of parameters could be found to improve the projections of the ZELIG model to the level attained by the NE-TWIGS model.

8. Conclusion

The NE-TWIGS model performed better than the ZELIG model at predicting future volumes on both sites. The parameters used to configure ZELIG were altered in attempts to improve its predictions. No suitable combination of maximum diameter, maximum age, soil fertility, and growth factor allowed ZELIG to provide a better fit for this limited validation set than the unmodified NE-TWIGS simulation.

The inability of the ZELIG model to accurately or precisely predict 30 years of tree growth and development for two specific points in space and time calls into question the proper use of any forest succession simulator. Many reviewers of this manuscript stated that the gap models were not designed to work at such a short time frame. However, the appropriate time frame for the use of gap models is not limited by Botkin (1993). The algorithms developed here to simulate forest dynamics, and which are used in gap models such as ZELIG, work on a yearly time step. If the projections are unreliable after 30 iterations, one would not expect the projections to improve after 300 or 3000 iterations. At what spatial and time scales do gap model predictions become acceptable?

Of the two models tested in this study, NE-TWIGS is preferred for short-term (30–50 year) projections of stand structure, species composition, and volume estimation. Neither model is appropriate for projecting the effects of a doubling of atmospheric CO^2 within the next 50 years.

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