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Validation of a multispecies forest dynamics model using 50-year growth from *Eucalyptus* forests in eastern Australia

Michael R. Ngugi[a,*], Daniel B. Botkin[b,1]

[a] Biodiversity and Ecosystem Sciences, Environment and Resource Sciences, Department of Environment and Resource Management, Queensland Herbarium, Mt Coot-tha Road, Toowong, Qld 4066, Australia
[b] Dept. of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, United States

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ABSTRACT

One of the key problems confronting ecological forecasting is the validation of computer models. Here we report successful validation of a forest dynamics model Ecosystem Dynamics Simulator (EDS), adapted from the JABOWA-II forest succession model. This model and many variants derived from it have successfully simulated growth dynamics of uneven-aged mixed forests under changing environment with a moderate amount of input data. But rarely are adequate time-series data available for quantitative model validation. This study tested the performance of EDS in projecting the tree density, tree diameter at breast height (*dbh*), tree height, basal area and aboveground biomass of uneven-aged, mixed species sclerophyll forests in St. Mary state forests of eastern Australia. The test data were collected between 1951 and 2005. Every tree was uniquely numbered, tagged and measured in consecutive re-measurements. Projected growth attributes were compared with those observed in an independent validation dataset. The model produced satisfactory projections of tree density (91.7%), *dbh* (92.3%), total tree height (82.8%), basal area (89.3%) and aboveground biomass (87.6%) compared to the observed attributes. These results suggest that the EDS model can provide reasonable capability in projecting growth dynamics of uneven-aged, mixed species sclerophyll forests.

1. Introduction

The goal of this study is to validate an ecological model of forest dynamics for the purpose of supporting management and ecological restoration of disturbed forests. Few ecological models of any kind have been tested against long-term data (Botkin, 2011). We demonstrate one form of such validation using the Ecosystem Dynamics Simulator (EDS), a gap-phase forest dynamics model based on the JABOWA model first published in 1972 (Botkin et al., 1972). This class of models has been applied to a wide range of ecological issues including examining potential impacts of climate change on forest structure and vegetation patterns, and impacts of resource management and disturbances on fauna habitat values (Shugart, 1984, 2002; Botkin, 1993; Porte and Bartelink, 2002; Kimmins, 2003). Gap-phase forest dynamics model have been tested to a relatively greater degree compared to most ecological models (Shugart, 2002). But no validation attempt for a model of this type have been reported using long-term dataset in which every tree was uniquely numbered and consecutively measured enabling unequivocal test of model simulations (Botkin, 1993; Lindner et al., 1997; Yaussy, 2000; Risch et al., 2005; Wehrli et al., 2005; Larocque et al., 2006; Pabst et al., 2008). We have such a data set, which is used in this study. In this paper we take advantage of such a data set.

Clearly, model validation is becoming increasing important, because of the widespread use of computer simulations to forecast ecological effects of global warming and other rapid climate change, to aid in climate change mitigation and carbon sequestration options. Such model validation is also important for forest conservation including protecting biodiversity of flora and fauna, sustainable use of forest, restoration plantings and establishment of forest plantations.

Validation of ecological models is a difficult, complex, and still contentious topic, as it is for all forecasting models of complex systems. Perhaps the most thorough analysis of forecasting model validation is in J. Scott Armstrong's *Principles of Forecasting* (Armstrong, 2001). Armstrong (2001) lists more than 100 characteristics that lead to a complete validation, but states that a specific model does not have to meet every one of the criteria. Other aspects of model validation can be found in Nisbet et al. (2009) and in scientific and scholarly literature devoted to this topic.

* Corresponding author. Tel.: +61 7 3406 6049; fax: +61 7 3896 9624.
E-mail addresses: michael.ngugi@derm.qld.gov.au (M.R. Ngugi), danielbotkin@rcn.com (D.B. Botkin).
[1] Tel.: +1 917 747 3068.

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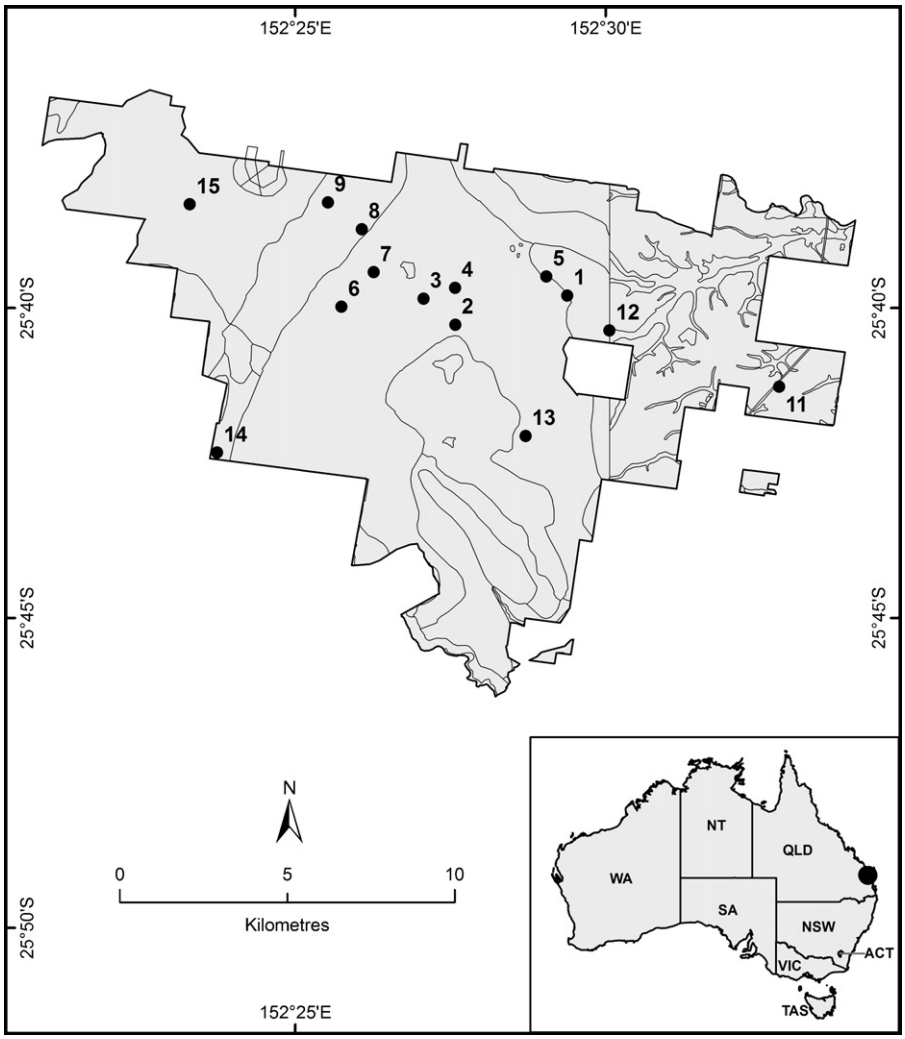

Fig. 1. Location of St. Mary State forest in eastern Australia. Numbering indicate the location of the long-term plots used for testing performance of Ecosystem Dynamics Simulator (EDS). The plots were established between 1951 and 1952. The States are: QLD, Queensland; NSW, New South Wales; SA, South Australia; NT, Northern Territory; WA, Western Australia; TAS, Tasmania and ACT, Australian Capital Territory.

Ironically, the validation of models of complex systems is often limited by adequate empirical observations, especially for systems whose dynamics take place of years, decades, and centuries. Also ironically, ecology has a long history of the use of models that have never been adequately validated and some that continue to be used even though available data contradicts their forecasts, including the logistic and Lotka Volterra models, which continue to provide the basis for much management of fisheries and conservation policies for marine mammals (Botkin, 1990).

2. Materials and methods

2.1. Study area

The study was conducted at the St. Mary state forests (25° 31′S, 152° 41′E) in southeast Queensland, Australia which covers and area of 172,000 ha (Fig. 1). The climate of the location is subtropical, characterised by hot humid summers and cool, dry winters. The mean annual rainfall is about 1100 mm (Fig. 2). December and January are the hottest months, while July is the coldest month.

In the Australian landscape, mixed species forests (native forests) cover 147 million hectares (99% of Australia's forests) while plantations cover about 1.9 million hectares (1% of Australia's forests) (Department of Agriculture Fisheries and Forestry, 2008).

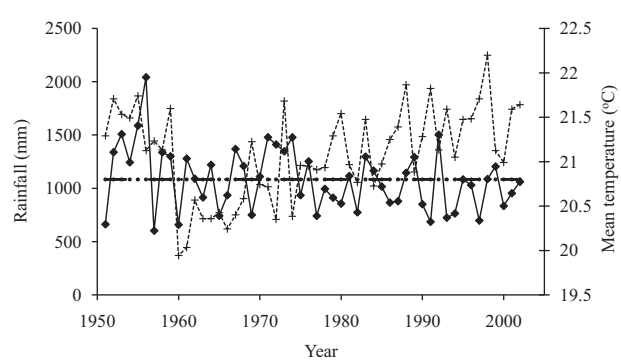

Fig. 2. Total annual rainfall (diamond symbol and solid line, mm), mean rainfall (dashed line) and mean annual temperature (cross symbol and dotted line, °C) between 1950 and 2005 at the St. Mary state forest, Queensland.

Since some of these mixed species forests have in the past been disturbed by land clearing, timber harvesting, and wild fires, restoration and long-term management are paramount in the protection of biodiversity, water catchments and for long-term climate change mitigation purposes. Although *Eucalyptus* forests dominate most forest landscapes in Australia (78% of Australia's native forests) (Department of Agriculture Fisheries and Forestry, 2008),

studies aimed at modelling long-term growth dynamics in these forests are very few (Shugart et al., 1981; Shugart and Noble, 1981; Pausas et al., 1997; Ranatunga et al., 2008).

The St. Mary state forest consists of dry, mixed species eucalypt forests typical to coastal lowlands of eastern Australia. Although these forests are in the process of being preserved for biodiversity, they have in the past been managed to improve timber productivity and selectively logged on 20–30-years cycles. The dominant tree species are *Corymbia citriodora* subsp. *variegata* (spotted gum) mixed with *Eucalyptus siderophloia* (grey ironbark), or mixed with *Eucalyptus fibrosa* subsp. *fibrosa* (broad-leaved ironbark), or with *Eucalyptus crebra* (narrow-leaved ironbark). On other sites the dominant species *Eucalyptus acmenoides* (white mahogany) is mixed with *Corymbia intermedia* (red bloodwood) or with *Corymbia trachyphloia* subsp. *trachyphloia* (brown bloodwood). Other less dominant tree species in the forest include *Eucalyptus tereticornis* (forest red gum), *Eucalyptus moluccana* (gum-topped box) and *Angophora leiocarpa* (smooth-barked apple). The understorey is mainly composed of grasses, *Acacia leiocalyx* (black wattle) and *Allocasuarina torulosa* (baker's oak).

2.2. Long-term forest data

Data used in this study were collected from 15 permanent sample plots distributed across St. Mary state forest (Fig. 1). The plots were established between 1951 and 1952, managed in similar manner to the adjacent forest stand and remeasured at 5–10-year intervals until 2005 when routine measurement of the plots ceased. These plots are about 0.4 ha (100.6 m × 40.2 m) in size and are rectangular in shape. Each plot is subdivided into four equal sections of about 0.1 ha (25.15 m × 40.2 m). In each plot, all individual trees ≥10 cm in *dbh* over-bark were uniquely identified, tagged and regularly measured for diameter (Beetson, 1992). Trees and saplings, <10 cm in *dbh* were not included in the routine data collection until in the mid-1990 when the re-measurement protocol was amended to include all tree stems >2 m in height. These data were therefore not included in this analysis because most plots had only a single instance measure. Height measurements were recorded on selected intervals only and most plots had at least one height measurement done on most trees on the plot or on dominant and co-dominant trees only. During the life history of the plots, silvicultural treatments that included thinning from below and selective logging were recorded. Consequently, the affected plot was measured before and after the treatment or logging operation was completed. A list of plots, initial statistics and statistics obtained from the last data collection are presented in Table 1.

2.3. Overview of EDS model

The EDS model is a derivative of JABOWA-II forest dynamics model (Botkin, 1993; Ngugi et al., 2007), which in turn is an improvement of the predecessor JABOWA model (Botkin et al., 1972), the progenitor of computer based gap models (Kimmins, 2003; Monserud, 2003). The EDS model differs from other forest growth and biomass models currently being applied in Australia (Landsberg and Waring, 1997; Battaglia et al., 2004; Waterworth et al., 2007; Nightingale et al., 2008; Miehle et al., 2009) in that it simulates the growth of individual tree stems in uneven-aged, mixed species forests based on local growth conditions. These elements allow analyses of changes in species composition, tree age and tree size structure and aboveground tree biomass, which are essential for monitoring biodiversity values and carbon sequestration, and for assessing impacts of different disturbance options such as fire, grazing, timber harvesting and silvicultural thinning on sustainable ecosystem management.

The JABOWA-II model was selected to be adapted to model forest dynamics in Australia using similar criteria to that described by Robinson and Monserud (2003): (1) the model can be localized using site specific variables; (2) it has a generic structure that can be applied to different geographic locations with exactly the same model structure; (3) the model has been broadly and successively adapted, calibrated and tested in mixed species forests (Shugart et al., 1981; Shugart and Noble, 1981; Shugart, 1984; Botkin, 1993; Pausas et al., 1997; Bugmann, 2001; Kimmins, 2003; Pabst et al., 2008); (4) the model is well documented (data requirements, assumptions, calibration, sensitivity analysis, validation tests and examples of potential applications) (Botkin, 1993) and; (5) computer code for the model is available and initial technical support was available.

The EDS is a non-spatial forest dynamics model that predicts long term dynamics of a forest by simulating tree growth, tree regeneration and tree mortality on an annual time step in a changing environment. Realised tree growth and regeneration are modelled by constraining maximum potential growth by limiting

Table 1
Characteristics of long-term monitoring plots from sclerophyll forests used for testing the EDS model. All the plots are located in St. Mary state forests, Queensland. Data were collected between 1951 and 2005.

Site	Initial conditions				Measure times	No. of years monitored	Conditions at last measure date		
	Established date	SPH	Basal area ($m^2\,ha^{-1}$)	Biomass ($t\,ha^{-1}$)			Date	Basal area ($m^2\,ha^{-1}$)	Biomass ($t\,ha^{-1}$)
1	11/26/1951	288	6.32	52.08	7	43	8/4/1997	24.48	206.31
2	11/26/1951	63	7.04	65.08	7	51	6/27/2002	22.59	195.60
3	11/26/1951	38	4.50	43.89	9	51	6/26/2002	16.90	146.44
4	1/1/1952	150	10.29	98.30	10	53	7/5/2005	14.08	131.23
5	8/20/1951	125	9.79	95.30	9	51	5/10/2002	20.95	196.47
6	11/26/1951	40	4.62	46.15	8	45	2/7/1996	11.59	103.42
7	11/26/1951	110	8.68	85.70	10	52	2/10/2003	15.32	146.13
8	10/20/1951	100	5.59	53.30	9	51	6/27/2002	14.27	124.38
9	2/7/1952	310	15.66	134.63	7	50	10/10/2002	22.84	200.65
10	1/1/1952	118	15.82	144.20	2	2	7/3/1954	16.16	147.59
11	8/20/1951	253	9.89	92.90	12	51	1/14/2002	16.57	163.75
12	10/20/1951	113	7.20	73.30	10	51	6/20/2002	10.10	95.37
13	11/26/1951	193	7.36	65.66	6	51	6/25/2002	18.50	163.42
14	11/26/1951	53	5.98	59.80	10	51	6/26/2002	10.89	92.43
15	11/26/1951	235	9.11	83.90	10	51	6/26/2002	13.80	136.66
Averages		146	8.52	79.61	8			16.60	149.99

SPH is stem density ha^{-1}, Measure times indicates the number of remeasurements on the plot.

soil moisture, fertility, temperature and light (Botkin, 1993). The details of this class of models is well documented (e.g. Shugart, 1984; Botkin, 1993, and many papers in the scientific literature), and it is therefore not necessary to explain the model in detail here. For those readers not familiar with these models, we provide the following brief overview. Growth of each tree is calculated by decreasing the maximum potential diameter growth rate by growth multipliers for each of the environmental factors that are below optimum. Hence the growth of an individual stem of a particular species in a plot is modelled relative to the growth of a tree in optimal conditions using (Botkin, 1993):

$$\delta D_{i,j} = \frac{\{G_j D_{i,j}[1 - [D_{i,j}(130 + b_{2j}D_{i,j} - b_{3j}D_{i,j}^2)/D_{\max,j}H_{\max j}]]\} * f(\text{environment})}{260 + 3b_2 D_{i,j} - 4b_3 D_{i,j}^2}$$

$\delta D_{i,j}$ is diameter (D) at breast height (dbh) increment (cm) of tree i of species j. G is a derived parameter determining how rapidly a tree of species j growing under optimum conditions reaches one-half its maximum diameter ($D_{\max}$, cm) and height ($H_{\max}$, cm). Parameters b_2 and b_3 relate tree diameter and height of species j. f is a function of environmental conditions that affect tree growth and includes light, soil moisture, temperature and soil fertility.

Tree recruitment in any year is determined by a combination of factors that relate to availability of light at the forest floor and site quality (the product of soil moisture, fertility and thermal conditions of the environment). The requirements for each tree species are species specific and the number of saplings recruited annually is a stochastic function of the number of saplings for each species (with a minimum height of 130 cm) that can recruit annually under optimal conditions. Tree mortality in the EDS model occurs as a combination of age-related and stress-induced death rates. Each tree has an inherent risk of natural death likely to occur to any healthy tree from lightning strikes, storms, fire and other random causes. Small trees are subject to high mortality due to strong competition for resources and old trees to high mortality due to diminishing growth vigour. Trees growing poorly due to adverse environmental conditions are subjected to stress-induced mortality (Shugart, 1984; Urban et al., 1991; Botkin, 1993). Output from the models consists of individual tree species, diameter and total tree height. These tree dimensions are analysed to provide charts for *dbh* distribution, species abundance and biomass accumulation.

2.4. Model parameters

EDS requires data input that define optimal growth attributes of each species and the local characteristics of a subject site that include soil description, local weather records and individual tree measurements (species and *dbh*). Parameter estimates for each of the 21 tree species observed in St. Mary state forests were determined using the detailed procedure contained in Botkin (1993). The model requires species specific data that include maximum *dbh*, height and age, minimum and maximum growing degree-days for the southern and northern limits of a species' geographical distribution, relative tolerance to shade, waterlogging, and drought, and estimates of annual diameter increment and annual recruitment rates (Botkin, 1993).

Initial information on growth attributes of individual species was derived from reported observations in forest and ecology publications of Australian forests (Beadle, 1981; Boland et al., 1984; Milson, 1995; Stanley and Ross, 2002). Species geographical distribution maps generated using Australian Virtual Herbarium, an on-online species collections database for State and Territories Herbaria of Australia were used to determine the southern and northern limits of a species (Australian National Botanic Gardens, 2004). Temperature records of the closest weather station to the southern and northern limit were used for estimating growing degree days. One of the greatest challenges in applying forest dynamics models to the tropics is in estimating maximum age of tree species in the absence of reliable annual growth rings. In this study, the maximum age for each species was estimated by dividing the maximum recorded diameter of the species by the mean annual diameter growth increments of trees in the dominant crown class (Baker, 2003).

Some 5240 tree observations from eight plots (#1, #2, #3, #4, #6, #9, #10, #13) were used to refine estimates of leaf weight, age (where no sufficient diameter increment data were available), relative tolerance to waterlogging and drought and available nitrogen that were more difficult to obtain. These plots were selected because they contained good representation of the list of species observed in the different sites, and plots #2, #3 and #4 had been used in a preliminary adaptation trial of JABOWA-II (Ngugi et al., 2005). The parameters were adjusted using standard calibration procedure used for process-based models, and bounded by the range of parameters values reported in literature for species with comparable growth habits (Ngugi et al., 2011). A list of the species parameter values is presented in Table 2.

2.5. Soil and weather data

Soil characteristics for each plot were obtained from field measurements. Four soil samples were obtained in each permanent sample plot, with each soil core dug at the centre of each quarter section of the plot. Soil texture of the top 30 cm of the soil profile, soil depth (depth to a rock or hard pan) and the minimum depth of the soil subject to water saturation (as shown by signs of mottling) were determined from the soil cores (Botkin, 1993). Estimates of soil water holding capacity of the various soil textures observed on the plots were obtained from the Queensland Department of Primary Industries (Harris, 2006). Soil parameters for each plot are shown in Table 3. Soil nitrogen content of 80 kg ha^{-1} obtained during calibration was used for all plots. The maximum basal area (*SOILQ*) for a dry eucalypt forest was estimated at 30 m^2 ha^{-1} based on pre-harvest inventory data for dry sclerophyll forests in Queensland. Monthly rainfall data for 1952–1979 were obtained from a weather station within St. Mary state forest that was closed in 1980. Hence weather records for 1980–2005 were obtained from Maryborough weather station, which is 20 km from St. Mary state forest. Time series data on monthly rainfall and monthly mean temperatures for consecutive years between 1951 and 2005 were used for the study (Fig. 2). During each simulation, the weather records were matched with the corresponding time period of the projections.

3. Approach to validation

As we discussed earlier, there are many possible approaches to model validation. We have chosen one approach, which is to refine some species parameters by calibrating a model against observations for one set of tree observations and test the model by having it make forecasts for another analogous set. We do not claim that this is a definite, universal validation of the model, merely a useful step forward, both for this class of models in general and for forecasting for this type of Australian forest.

3.1. Model validation

The validation dataset comprised 5350 growth observations taken from seven permanent sample plots (#5, #7, #8, #11, #12, #14, #15). These data were independent from the eight plots used for parameterisation and calibration of the model (Table 1). All measurements were recorded between 1951 and 2005 at St. Mary state forests (Table 3). These plots provided data records for species,

Table 2
List of trees species recorded in the St. Mary State forest and their estimated parameters. These parameters were estimated using the detailed methods described for the JABOWA-II model (Botkin, 1993) and age of trees was determined using method described by Baker (2003).

Species name	D_{max}	H_{max}	Age_{max}	G	b_2	b_3	DD_{min}	DD_{max}
Acacia aulacocarpa	80	30	70	225	71.75	0.45	5237	9851
Acacia flavescens	40	20	40	300	93.50	1.17	4251	7782
Acacia leiocalyx	40	15	30	225	68.50	0.86	3444	8017
Allocasuarina littoralis	30	12	80	70	71.33	1.19	2379	9360
Allocasuarina torulosa	90	30	200	200	63.78	0.35	3224	7368
Alphitonia excelsa	50	18	100	216	66.80	0.67	3275	9956
Angophora leiocarpa	90	28	450	187	44.50	0.19	1791	4509
Corymbia citriodora[a]	116	44	1142	135	73.62	0.32	3310	6942
Corymbia intermedia	159	45	1140	156	54.97	0.17	3226	8560
Corymbia tessellaris	160	30	836	84	35.88	0.11	4903	7749
Corymbia trachyphloia[b]	86	33	836	169	73.72	0.43	3903	7295
Eucalyptus acmenoides	170	50	799	169	57.29	0.17	3580	7368
Eucalyptus exserta	72	30	427	77	79.72	0.55	4216	7028
Eucalyptus fibrosa[c]	109	41	600	131	72.84	0.33	3134	8117
Eucalyptus moluccana	137	41	689	84	57.96	0.21	3399	5747
Eucalyptus siderophloia	94	42	838	169	86.60	0.46	3328	7166
Eucalyptus tereticornis	127	37	730	121	56.22	0.22	3134	8828
Lophostemon confertus	165	50	1335	74	59.03	0.18	3403	8017
Lophostemon suaveolens	80	25	864	188	67.71	0.48	4903	7749
Melaleuca linariifolia	50	10	80	120	24.86	0.18	2996	7404
Melaleuca quinquenervia	50	25	80	300	79.00	0.66	3852	9802

D_{max}, maximum diameter at breast height (cm) and H_{max}, maximum height (cm); Age_{max}, maximum age (years); G, growth rate scaling coefficient determining how rapidly a tree growing under optimum conditions reaches one-half its maximum size or inflection point ($G = 5H_{max}(\delta D_{max}/D_{max})$; b_2 and b_3, derived parameters relating height to dbh; DD_{min}, minimum growing degree-days (°C); DD_{max}, maximum growing degree-days (°C).
[a] subsp. *variegata*.
[b] subsp. *trachyphloia*.
[c] subsp. *fibrosa*.

dbh and height spanning more than 50 years. The performance of EDS was evaluated by comparing the projected outputs from the simulator against the observed individual tree attributes (diameter and height), and species and plot attributes (density, basal area and aboveground biomass), and presented as charts and a regression line relative to 1:1 line to provide a visual examination of bias. The comparison was also done by computing the relative model bias as the percent difference between the simulated and observed attributes for each plot (Vanclay, 1994; Landsberg et al., 2003; Wehrli et al., 2005; Pabst et al., 2008):

$\text{Bias} = \left[\frac{\text{projected}-\text{observed}}{\text{observed}} \times 100\right]$ The relative bias was averaged among plots at the point of comparison to provide an overall indication of the correspondence of the simulation and empirical data. A low bias value indicates a high agreement, a negative value indicates a tendency to underestimate and positive values a tendency to overestimate. The proportion of the observation that was explained by the model was determined by computing the average of absolute percent difference (projected %) between projections and observations for each plot (Larocque et al., 2006), and subtracting that from 100%:

$\text{Projected}\,\% = 100 - \text{absolute}\left[\frac{\text{projected}-\text{observed}}{\text{observed}} \times 100\right]$

Root mean square error (RMSE) was used to estimate the error in the projected *dbh* and total tree height based on number of observations (n).

$$\text{RMSE} = \sqrt{\frac{\sum_i^n (\text{projected} - \text{observed})^2}{n}}$$

3.2. Aboveground biomass

Live aboveground biomass was determined using a generalised allometric equation for tropical dry forest stands (below 1500 mm/year, over 5 months dry season) (Chave et al.,

Table 3
List of long-term field plots used for validation of the EDS model including soil conditions and dominant species at each site. All the plots are located in St. Mary state forests.

Plot[a]	Simulation period	Soil depth (m)	Soil texture	Dominant species
5a 5b	1951–19641964–2002	1.0	Clay loam	*Eucalyptus acmenoides*, *Corymbia citriodora* subsp. *variegata*, *Eucalyptus fibrosa* subsp. *fibrosa*
7	1951–2002	1.0	Sandy clay loam	*Eucalyptus acmenoides*, *Corymbia citriodora* subsp. *variegata*, *Eucalyptus siderophloia*, *Eucalyptus fibrosa* subsp. *fibrosa*
8a 8b	1951–19641981–2003	1.0	Silty clay loam	*Eucalyptus acmenoides*, *Corymbia citriodora* subsp. *variegata*, *Eucalyptus siderophloia*, *Eucalyptus fibrosa* subsp. *fibrosa*
11a 11b	1951–19641964–1980	1.0	Sandy clay loam	*Eucalyptus acmenoides*, *Angophora leiocarpa*, *Corymbia citriodora* subsp. *variegata*, *Eucalyptus siderophloia*, *Eucalyptus fibrosa* subsp. *fibrosa*
12	1951–1997	1.5	Silty clay loam	*Eucalyptus tereticornis*, *Corymbia citriodora* subsp. *variegata*, *Eucalyptus siderophloia*
14a 14b	1951–19641964–1987	0.8	Silty clay loam	*Corymbia citriodora* subsp. *variegata*, *Eucalyptus siderophloia*, *Eucalyptus tereticornis*
15a 15b	1951–19751978–2002	1.2	Sandy clay loam	*Corymbia intermedia*, *Eucalyptus acmenoides*, *Eucalyptus moluccana*, *Corymbia citriodora* subsp. *variegata*, *Eucalyptus siderophloia*, *Eucalyptus fibrosa* subsp. *fibrosa*

[a] Plots with same number but different letter represent plots that were initialized twice by using data at the beginning of the simulation period. Simulations were reinitialized after a silvicultural treatment that resulted in removal of multiple trees occurred.

2005). The dbh-based equation used, include correction for log-transformation and has been tested for trees with $dbh \geq 5$ cm.

$$\text{Aboveground biomass (tonnes)} = \frac{\rho \times \exp(-0.667 + 1.784)\ln(dbh) + 0.207(\ln(dbh))^2 - 0.0281(\ln(dbh))^3}{1000}$$

where ρ is wood density (g/cm^3) and *dbh* is the diameter at breast height (cm) measured at 1.3 m. Wood density values were extracted from a dataset for Australian species (Ilic et al., 2000). Where density values for a species were not available, mean values at genus and then family taxonomic level were used.

3.3. Simulation of plots

Each plot was initialised using tree data (species and *dbh*) recorded from first measurements at the time the plots were established in 1951 or 1952 (Table 1). The species list for each 0.1 ha plot included tree species recorded in the 0.4 ha plot. Recruitment option of the model was switched off because the available data were only for trees with $dbh > 10$ cm. Each plot was simulated 200 times (>50 iterations provided reproducible results) for the period of years between thinning treatments or logging disturbances to enable comparisons with field data collected before these operations. Model outputs of a corresponding year to that of observed data were used to compare diameter and height projections of individual trees. At the end of each simulation period, the results from the 200 iterations were averaged to provide projected plot attributes (density, species list, basal area and aboveground biomass). Basal area and aboveground biomass were derived from projected diameter data of individual species and the 95% confidence interval of the mean was computed for the whole plot. All trees measured immediately after a silvicultural treatment or a logging operation was completed were used to re-initialise the simulation (Table 3).

4. Results

4.1. Height and diameter

Height estimation in most gap models is based on a relationship between *dbh* and total tree height that uses species specific parameters b_1 and b_2 (Shugart, 1984; Botkin, 1993):

$$H(\text{height}) = \text{datum} + b_1 dbh - b_2(dbh)^2$$

where datum is the height (cm) at which tree diameter (*dbh*, cm) is measured. The universal suitability of this generic equation form (second order quadratic equation) has in some cases been found inadequate and alternative equation forms proposed (Lindner et al., 1997; Risch et al., 2005). In this study, the adequacy of the generic equation form was first examined by fitting *dbh* and height measurements for 479 trees recorded in the calibration dataset. The recorded tree heights in the dataset ranged from 5 to 42 m, and showed a wide range of height values (20–42 m) for trees with diameter greater than 40 cm (Fig. 3a). An r^2 of 0.83 was obtained for the height-diameter relationship (Fig. 3a), indicating a satisfactory fit for the purpose of estimating tree heights in this study.

Height and diameter measurements of 121 uniquely numbered trees that were recorded in the validation dataset were compared to corresponding projected height and *dbh* values from EDS model. The average bias in height projection based on the 121 trees was −1.0% which indicated a slight underestimation of projected height, and the model explained 82.8 (±1.2)% of the observed height values in the plots. A comparison between observed and projected total tree height had an r^2 of 0.59 (Fig. 3b) and the average error in projected tree height as shown by RMSE was 5.7 (±1.9) m. The observed

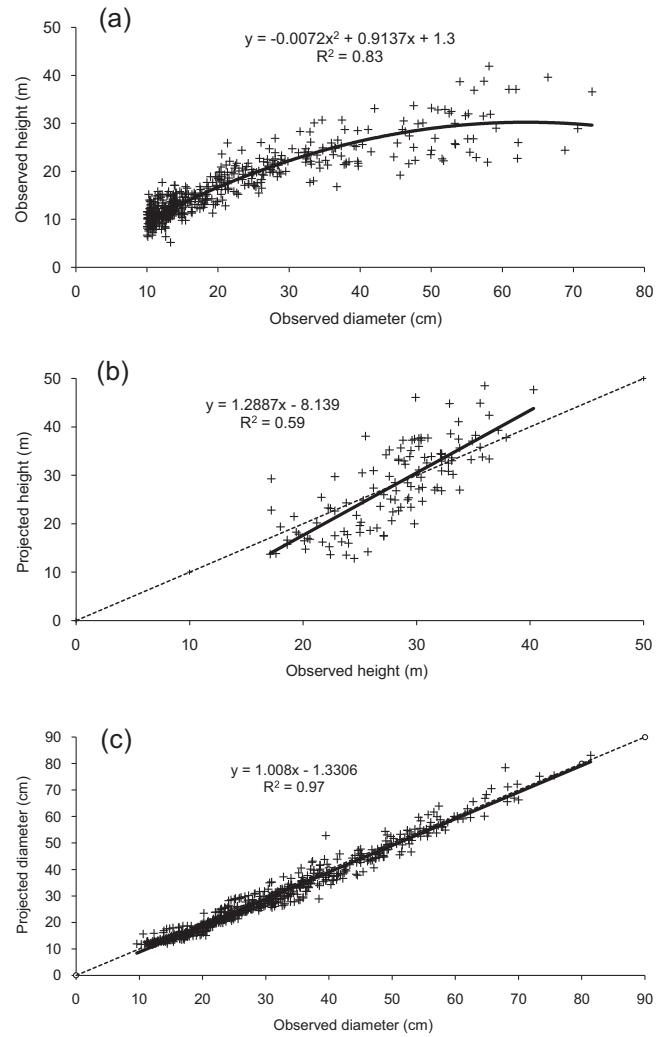

Fig. 3. Height and diameter relationships showing (a) relationship between observed tree diameter and observed total tree height based on 479 trees from the calibration dataset that had heights measured, (b) comparisons between projected and observed total tree height in the validation dataset ($n = 121$) and (c) comparisons between projected and observed tree diameter in the validation dataset ($n = 621$).

tree diameters in the validation dataset ranged from 10 and 81 cm. Projected and observed tree diameters were compared at the end of each simulation period. The average bias in diameter projection was −4.2% indicating a tendency to underestimate tree *dbh*, and the relative percentage of the observed diameter that was explained by the model was 92.3 (±0.2)%. The RMSE of projected diameter values was 2.6 (±0.7) cm. A satisfactory relationship between projected and observed diameter with an r^2 of 0.97 was obtained (Fig. 3c).

4.2. Tree density and species composition

Recorded initial stem density in all plots in 1951 and 1952 ranged from 38 to 310 stems ha^{-1} (Table 1). The initial diameter distribution in the validation plots displayed a wide range of stand structure (Fig. 4). Plots #11 and #15 were the densest plots and were dominated by small sized trees within the 10–20 cm diameter class. All other plots had a relatively similar diameter distribution structure characterised fewer small stems but a gradual decrease in stem density with increase in diameter except Plot #14 that had the lowest density and contained a few large trees (Fig. 4). Species composition varied among the plots but the number of species ranged from three to six.

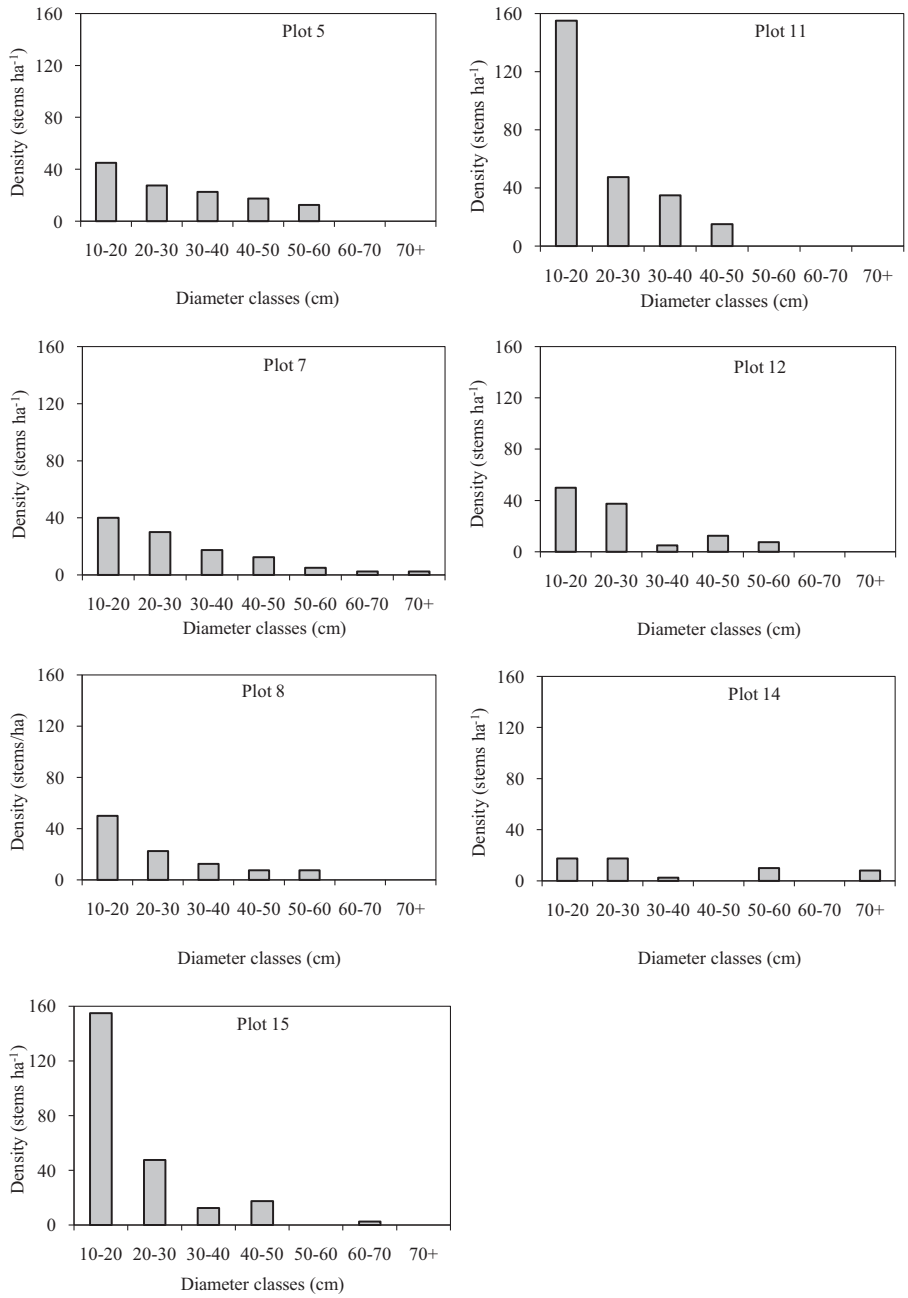

Fig. 4. Diameter size class distribution in each validation plot at the time the plots were established (1951 and 1952).

Projections of stem density for the plots compared favourably with observed density as shown in Fig. 5a. A mean bias of −2.4% was obtained for the plots indicating a slight underestimation of density. On average, the model projected 91.7 (±1.6)% of the observed tree density. For all plots, changes in species composition during simulation period were minor because most of the trees in the plots were large and well represented in various diameter classes.

4.3. Basal area and aboveground biomass

The recorded basal area in the plots ranged from 4.2 to 24.5 m^2 ha^{-1} throughout the 55-years monitoring period (Table 1). A comparison between projected and observed basal area (Fig. 5b) had a mean bias of −4.7% indicating a tendency for the model to slightly underestimate basal area. However, the model projections explained 89.3 (±1.8) % of the observed basal area for the plots. Observed biomass in all plots ranged from 43.9 to 206.3 t ha^{-1} (Table 1). Diameter values simulated by EDS and those observed at the corresponding time period were used to estimate aboveground biomass. A comparison between simulated and observed aboveground biomass presented in Fig. 5c, showed that the projected biomass closely approximated the observed biomass in each plot. The mean bias between projected and observed biomass among the plots of −3.5% indicated a slight underestimation of observed biomass. EDS projections described 87.6 (±1.7)% of the observed live aboveground biomass.

5. Discussion

Gap-based forest dynamics models provide a reasonable compromise in data requirements, ability to simulate growth dynamics

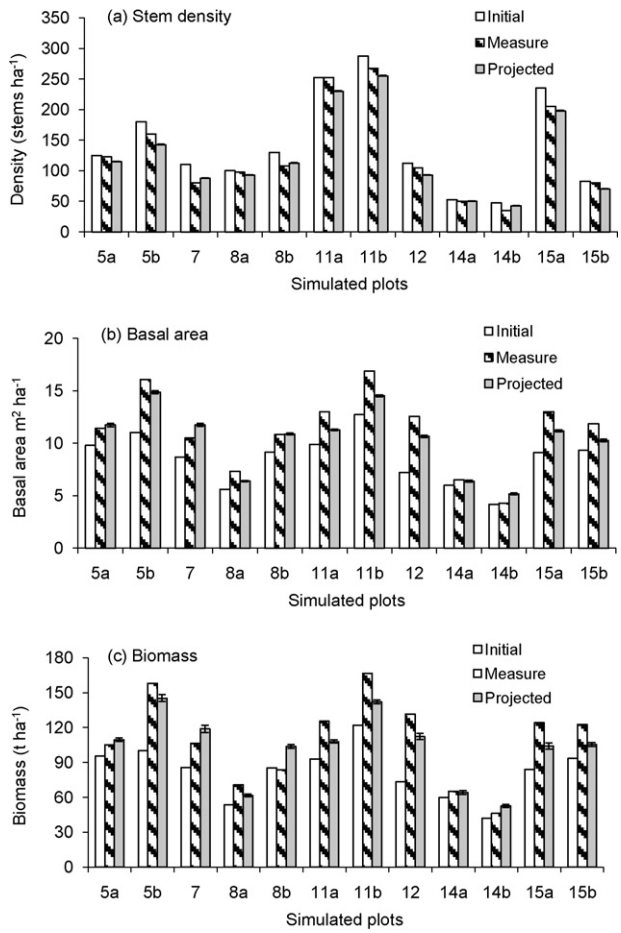

Fig. 5. Validation results showing comparison among initial (open), observed (hatched) and projected (grey) of (a) stem density in stems ha^{-1}, (b) basal area in m^2 ha^{-1}, and (c) live aboveground biomass in t ha^{-1}. Error bars represent the 95% confidence interval of simulations and plots with same number but with *a* and *b* indicate that they were reinitialised after a silvicultural treatment or harvest.

of uneven-aged mixed forests under changing environment and in producing practical outputs for supporting decisions on sustainable forest ecosystem management compared to process-based models or empirical growth and yield models (Shugart, 2002; Larocque et al., 2006; Pabst et al., 2008). This study examined parameterisation, calibration and validation of EDS, a forest dynamics simulation model that is a variant of JABOWA-II model (Botkin, 1993). Parameters for 21 tree species commonly found in sclerophyll forests in eastern Australia were determined. The model was calibrated and validated using tree records collected between 1951 and 2005. Projected growth attributes were compared with those observed in the independent validation dataset. Good agreement between projected and observed tree height (82.8%), *dbh* (92.3%), stem density (91.7%), basal area (89.3%) and aboveground biomass (87.6%) was obtained. However, the agreement between projected and observed tree height though reasonable was less satisfactory (r^2 = 0.59) compared to diameter which had an r^2 of 0.97 (Fig. 3b and c).

Model accuracy is important in providing confidence with regard to practical applications. The long-term data used for this study provided detailed individual tree growth data for model parameterisation and calibration enabling reliable estimates of individual species maximum diameter, age and diameter increment. These parameters determine many aspects of growth and mortality within gap models (Yaussy, 2000). The independent data used for validation of the EDS model, provided unequivocal comparisons of model projections against observations of the same attributes. The high agreement obtained between EDS projections and observations of tree diameter growth and stem density suggest that both growth and mortality were well predicted. The average error in *dbh* projection of ±2.6 cm (RMSE) suggests satisfactory diameter projections.

Height growth function in the EDS model as with most gap models is based on second order quadratic function of tree diameter (Botkin, 1993). This relationship has been criticized in that it is density independent (Lindner et al., 1997) and may not be accurate in dense forests. Similarly is the assumption of the tree growth function that a tree grows minimally in diameter as it approaches its maximum height (Risch et al., 2005). However, the results obtained in this study from fitting the second order equation to observations of tree diameter and height (r^2 = 0.83, Fig. 3) compared well with the best fitting equation (r^2 of 0.53–0.82) of the alternative relationships proposed for several species in Swiss mountain forests (Risch et al., 2005). In Lindner et al. (1997), dense stands (>2440 stems ha^{-1}) were used compared to <300 stems ha^{-1} characteristic of open eucalypts woodland in Australia (Table 1). Hence although Lindner et al. (1997) and Risch et al. (2005) have suggested replacement of the generic height estimation equation used in most gap models, such a need was not necessary for the range of data observed in this study (Fig. 3). Moreover, based on the high r^2 and low bias obtained from EDS for projections of individual tree diameter growth and survival, there was no indication that slow diameter growth of large trees (related to the use of a generic growth function) predisposed them to excessive growth-related mortality rate (Risch et al., 2005). However, the biological plausibility of an asymptotic function proposed by Lindner et al. (1997) is acknowledged.

In this study, the low r^2 value obtained for the comparison between projected and observed height is likely to be the result from errors in model itself, empirical data source or complex growth habits of sclerophyll forests. The greater error in height projection compared to diameter projection is consistent with results reported for the TRIPLEX forest model (Peng et al., 2002). Unlike tree diameter data that are directly measured, the use of trigonometric methods for measuring tree heights is subject to greater errors. As shown by the spread of height data (Fig. 3a), a tree with the largest diameter is not always the tallest. This is often the case, partly because emergent old eucalypt trees are subject to wind damage and hence are characterised by broken limbs that form hollows (Harper et al., 2005). The RMSE value obtained for height projection by using the EDS model (±5.7 m) is higher than that reported using an empirical growth model for *Eucalyptus globulus* forests (RMSE = 2.8 m) in Spain, but the r^2 value obtained using EDS is within the range of r^2 values reported in that study (Crecente-Campo et al., 2010).

The percentage bias of growth projections obtained from the EDS model tended to underestimate density, *dbh*, height, basal area and aboveground biomass. Relative to other studies, the range of the mean bias (%) values obtained for the growth attributes using the EDS model (−4.7 to −1.0%) indicated better agreement between observations and projections compared to the range of −53.4 to 22.8% obtained for application of 3-PG model in Loblolly pine plantations in USA (Landsberg et al., 2003). The mean bias obtained for aboveground biomass projections using the EDS model was comparatively smaller than that reported in the application of 3-PG and 3-PG$^+$ in predicting aboveground biomass of *E. globulus* plantations in Southern Australia (Miehle et al., 2009). Bias in biomass projections using the EDS model were however more comparable to those obtained for the CABALA model in the same study in Southern Australia. Unlike the EDS model which is a forest succession model, 3-PG, 3-PG$^+$ and CABALA models are hybrid process-based forest growth models and have comparatively more onerous input data

requirements and especially in regards to applications involving native mixed species forests.

Although regenerating trees with <10 cm *dbh* were not included in this simulation, they were still present in all plots. This would imply that a source of competition for growth resources from small trees was present in the plots. The potential impact of this competition on the simulated tree growth was reduced by calibrating the model using data with *dbh* > 10 cm. Moreover, reinitializing a plot with data measured in the same plot at a later date also ensured that any trees that had attained 10 cm *dbh* after the first initialization of the plot were then included in the simulation. The high agreement obtained for comparison between projections and observations of tree diameter and the low basal area occupancy observed in plots used in this study (Table 1) relative to potential basal area of the plots (30 m^2 ha^{-1}) suggests that growth of trees with *dbh* > 10 cm in the validation plots was not constrained by presence of small trees in the plots.

The acceptable accuracy from a model should be a compromise between developing a model that is as simple as possible and complex as necessary for the intended use (Kimmins et al., 2008). Generally, forests are highly variable and complex, and seemingly identical forests can vary considerably in any attribute. For example, results of a study conducted to estimate biomass of large areas in North American Borea forests showed that 95% confidence interval was about 20% of the observed mean biomass (Botkin and Simpson, 1990). Similarly, such large differences in biomass estimates have been reported for inland and coastal tropical dry evergreen forests in India (Mani and Parthasarathy, 2007). The relative percentages of the observed density, *dbh*, height, basal area and aboveground biomass that were projected by the EDS model were between 82 and 92%. These results are comparable to those obtained in validation tests of the JABOWA model in north America using short-term dataset (10 years) and medium-term dataset (50–60 years) that projected 80–90% of the observed attributes (Botkin, 1993).

Is this a complete validation of the model? No, but it is a useful step forward in determining that this class of models can forecast the dynamics of tree species in a complex forest ecosystem. Some criticize the approach we have taken by suggesting that similar results might be obtained from a simple linear extrapolation. This misses the point. Obviously, linear extrapolation cannot work over the long term for forest ecosystems. We want to know if a model designed to make forecasts for such systems for both short and long time periods is validated for any data set, especially such thoroughly monitored forests as those of the St. Mary state forest. To this question we can provide one more yes.

6. Conclusion

This study tested the performance of the EDS model, a forest dynamics model adapted from the JABOWA-II forest succession model (Botkin, 1993) in projecting attributes of growth dynamics of uneven-aged, mixed species sclerophyll forests in eastern Australia. The JABOWA-II model was selected for adaptation because it has been widely calibrated and tested in succession studies of uneven-aged mixed species forests, can be applied in different geographical locations with little change in model structure, has reasonable input data requirements, is well documented and computer code for the model is readily available. Long-term forest measurement data collected between 1951 and 2005 were available for calibration and validation of the model. Individual trees in this dataset were uniquely numbered enabling unambiguous comparisons between projections and observations.

The model was parameterised for 21 tree species commonly found in sclerophyll forests in eastern Australia. Calibrated model produced satisfactory projections of tree density, tree diameter, basal area, aboveground biomass and tree height that were between 82 and 93% of the observed attributes. This study did not include sapling recruitment because regular plot measurements only recorded trees with *dbh* > 10 cm. However this limitation of the dataset was partly counteracted by reinitializing the plot simulation with data recorded at different points in the life history of the plot. Recruitment is a significant phase in the rejuvenation of a forest and performance test of the EDS model in projecting attributes of stand dynamics of sclerophyll forests that include trees with *dbh* < 10 cm preferably using long-term monitored data is required. Further testings of the EDS model in other forest types and multiple locations in Australia are suggested.

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