

Assessing the carbon sequestration potential of managed forests: a case study from temperate Australia

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Summary

1. The concept of assessing forests for carbon sequestration is well established. Operationally, estimating a forests' potential to sequester carbon requires comparing its current carbon state with a prediction of its carbon carrying capacity (CCC). Assessment of CCC is, however, problematic. Mathematical models can be used, although traditional modelling techniques, where parameters are estimated from empirical measurements, are usually limited by a lack of field data. For example, estimates of carbon residency times in vegetation and soil are not generally available, nor are they easily measured. Alternative methods are required.

2. Current carbon stocks in 17 previously logged field sites were measured by field survey. CCC for those sites was then predicted using a terrestrial carbon model, calibrated with measurements from mature, unlogged vegetation of a comparable forest type. Model parameters were estimated using 'model–data fusion' methods, where the model is inverted and field measurements of the carbon stocks (the model outputs) are used to calibrate the model parameters. Spatial variation was included through functions defining landscape-scale effects on plant growth relating to topographic influences on light and soil water availability.

3. Current above-ground carbon stocks (living plus litter) varied with management history, averaging $273 \pm 30 \text{ tC ha}^{-1}$ (mean \pm SE). Model-predicted CCC was $445 \pm 13 \text{ tC ha}^{-1}$, yielding a carbon sequestration potential of $172 \pm 31 \text{ tC ha}^{-1}$. Model simulations predicted the recovery of an average site to take 53 years to reach 75% carrying capacity, and 152 years to reach 90% carrying capacity. Extrapolation of these results to 7 Mha of comparable managed forests in the same region suggested a potential carbon sink of 680–895 Mt C.

4. *Synthesis and applications.* In this study we have demonstrated that forests recovering from prior logging have the potential to store significant amounts of carbon, with current biomass stocks estimated to be approximately 60% of their predicted carrying capacity, a value similar to those reported for northern temperate forests. Although sequestration activities often focus on the afforestation and reforestation of previously cleared land, our results suggest that, where appropriate, native forest management should also be considered when developing terrestrial carbon management options, and for terrestrial carbon accounting more generally.

Key-words: carbon carrying capacity, coarse woody debris, forest biomass, inverse modelling, net primary productivity

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Introduction

Given the potential impacts of rising atmospheric CO₂ concentrations on global climate (IPCC 2001) and government commitments to climate change initiatives through the United Nations Framework Convention on Climate Change, there is an increasing demand for countries to assess their contributions to sources and sinks of CO₂ and to evaluate processes that control CO₂ accumulation in the atmosphere. Imperative to such assessments is the development of techniques for measuring stocks and fluxes of carbon in terrestrial ecosystems. Forest ecosystems have been a particular focus of carbon accounting research because they represent the largest stock of terrestrial ecosystem carbon (Saugier, Roy & Mooney 2001).

Carbon carrying capacity (CCC) is defined as the mass of carbon able to be stored in a forest ecosystem under prevailing environmental conditions and natural disturbance regimes, but excluding anthropogenic disturbance (Gupta & Rao 1994). CCC provides a useful baseline against which current carbon stocks (CCS), which include anthropogenic disturbance, can be compared. The difference between CCC and CCS, defined here as carbon sequestration potential (CSP), is one way of quantifying the carbon impact of human land-use activity (Gupta & Rao 1994; Falloon *et al.* 1998; Lal & Singh 2000; Zhang & Justice 2001; Leinonen & Kramer 2002; Laclau 2003).

We tested a method for estimating CSP within a forested landscape based on a comparison of field observations of CCS with modelled estimates of CCC. Model–data fusion techniques were used to integrate the field observations within the modelling framework to provide an optimal fit between data and model, to provide optimal estimates for model parameters, and to allow uncertainties on model parameters and model outputs to be quantified (Raupach & Lu 2004; Raupach *et al.* 2005).

Methods

The overall strategy was to (i) select a network of forested field sites within the study area representative of a range of environmental domains and logging histories, and at each site quantify, by field survey, above-ground carbon stock in living, litter and coarse woody debris (CWD); (ii) use field survey data of carbon stocks in mature forests of a comparable vegetation type to calibrate the carbon accounting model and generate estimates of CCC across the study area; and (iii) compare the CCC estimates from (ii) against the measured carbon stocks from (i) to quantify the CSP. Soil carbon was measured in a subset of the mature forest sites only, thus estimates of CSP were restricted to a comparison of above-ground carbon stocks only.

STUDY AREA

The Kioloa study area is located within the southern forest zone region of New South Wales, Australia (Regional Forest Agreement 2000), and includes Murrumbidgee National Park and South Brooman State Forest (see Fig. S1 in the supplementary material, location D). The study area is located within a coastal lowland belt, characterized by rolling and undulating terrain (Galloway 1978). Landscape-scale vegetation patterns follow a gradient from rainforest, through tall open *Eucalyptus* forest, to heath on the poorer drained, higher acidity soils (Davey 1989). Rainforests prevail as patches embedded within a *Eucalyptus* matrix, dominated by *Corymbia maculata* (Hook.) K. D. Hill & L. A. S. Johnson (formerly known as *Eucalyptus maculata* Hook.), *Eucalyptus pilularis* Sm., *Eucalyptus sieberi* L. A. S. Johnson, *Eucalyptus botryoides* Sm. and *Corymbia gummifera* (Gaertn.) K. D. Hill & L. A. S. Johnson [formerly known as *Eucalyptus gummifera* (Gaertn.) Hochr.]. The area has also been periodically subject to unplanned fires, controlled hazard reduction burning and post-harvest burns. A large tract of the study area has recently changed land tenure from state forest to national park.

FIELD MEASUREMENT OF CCS

Seventeen field sites (the Kioloa sites) were surveyed for CCS (see Fig. S1 in the supplementary material, location D). The sites were a stratified random subsample of 180 sites in the Kioloa study area, assembled and surveyed by Davey (1989). Stratification was based on ensuring a representative sample of topographic position, slope and aspect. A digital elevation model (DEM) with a resolution of 25 m (Lees 1997) was used to estimate site slope and aspect, and relative topographic position was derived from a topographic wetness index (TWI) surface (Wilson & Gallant 2000), calculated from the DEM. The TWI quantifies landscape position relative to up-slope catchment area and slope angle. The slope, aspect and topographic position of the 17 sites are provided in Table S1 (see the supplementary material).

A 60 × 60-m square plot was randomly located within each site, orientated parallel to the slope. The taxonomy and stem diameter at breast height over bark (d.b.h.; 130 cm) were recorded for all trees greater than 30 cm d.b.h. The plot was further divided into five subplots: four 10 × 10-m plots in each corner and a 20 × 20-m plot in the centre. Within these subplots, identical measurements to those for trees greater than 30 cm d.b.h. were carried out additionally on all trees with a d.b.h. between 20 cm and 30 cm, and the number of stems between 2 cm d.b.h and 20 cm d.b.h. was counted.

Tree biomass was calculated using the regression equations developed by Ash & Helman (1990). These equations were based on extensive measurements of

foliage, branches, roots and stems of felled trees within the Kioloa study area (Ash & Helman 1990). The Ash & Helman (1990) study is one of only three studies of allometric relationships in south-eastern Australian forests that include trees greater than 100 cm d.b.h. (Keith, Barrett & Keenan 2000). Because these equations predict total tree biomass, it was necessary to subtract root biomass (as calculated from the root volume equation in table 2 of Ash & Helman 1990) to derive above-ground tree biomass. Carbon content in above-ground vegetation was assumed to be 50% of dry weight biomass (Grierson, Adams & Attiwill 1992).

The Ash & Helman (1990) equations do not include adjustments for internal tree decomposition and tree hollows, which can be significant for larger trees. Recent data collected by State Forests of New South Wales (F. Ximines, personal communication) showed that in a sample of 527 trees destructively harvested from within the study area, those with a d.b.h. above approximately 50 cm begin to show signs of internal decomposition, and at approximately 120 cm d.b.h. actual tree mass is approximately 50% of that predicted by the allometric equations. The following adjustment to the predicted biomass from the Ash & Helman (1990) allometric equations was therefore made:

$$Y' = Y \quad \text{for trees } \leq 50 \text{ cm d.b.h.}$$

$$Y' = Y \times (-0.00714 \text{ d.b.h.} + 1.35714)$$

for trees > 50 cm d.b.h and ≤ 120 cm d.b.h.

$$Y' = Y \times 0.5 \quad \text{for trees } > 120 \text{ cm d.b.h.}$$

where Y is the biomass predicted from Ash & Helman (1990) and Y' is the modified biomass adjusted for internal tree decomposition. The resulting growth allometric of Ash & Helman (1990), adjusted for internal decomposition and tree hollows, is shown in Fig. 1 (method a).

CWD was defined as all forest floor debris > 2.5 cm in diameter, standing dead trees > 20 cm d.b.h., and stumps > 20 cm in diameter and 1.3 m in height. The line intersect method of van Wagner (1968) was used to measure forest floor CWD. The transect comprised the perimeter of two opposing 10 × 10-m subplots and the

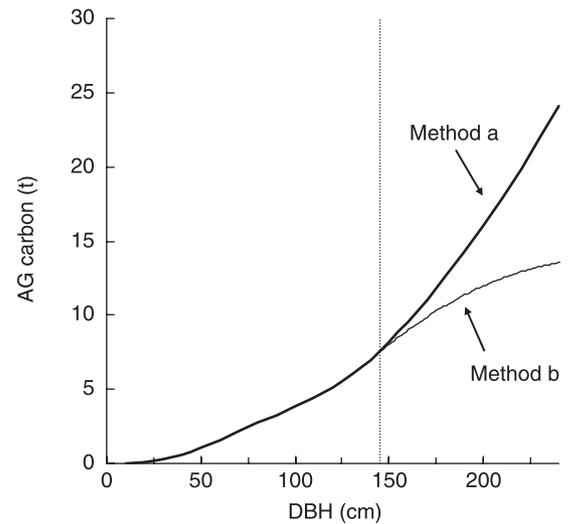


Fig. 1. Above-ground biomass relationship of Ash & Helman (1990) modified for tree hollows. Two curves are shown. Method a (heavy line) predicts an exponential biomass increase for trees greater than 145 cm d.b.h. Method b (fine line) shows the alternative allometric that asymptotes for d.b.h. values greater than 145 cm d.b.h. The equation of the curve from 145 cm to 240 cm d.b.h. for method b is $y = -0.0004x^2 + 0.234x - 17.077$. The dashed vertical line is the upper size limit of trees used by Ash & Helman (1990) to develop their allometrics.

central 20 × 20-m subplot, to give a total length of 160 m. The diameter, species (where possible) and density class were recorded for each CWD piece > 25 mm intersected by the transect line. The d.b.h., height and species (where possible) were recorded for stumps and standing dead trees in the 60 × 60-m plot. Mean CWD densities and carbon concentrations for each density class were obtained from Woldendorp, Keenan & Ryan (2002) (Table 1).

Four 0.25-m² quadrats were located randomly within each plot, from which all dead leaves, twigs and branches less than 2.5 cm diameter, charcoal and other comminuted litter were collected down to the mineral soil layer. The litter samples were oven dried at 70 °C for 48 h. Samples were cooled for 1 h then weighed to provide a bulk estimate of litter mass for each site. The percentage of carbon in litter was assumed to be 45% of biomass (Woldendorp, Keenan & Ryan 2002).

Table 1. Mean wood densities and carbon concentration for each coarse woody debris density class (SE shown in parentheses)

Wood density class*	Mean density (g cm ⁻³)		Mean carbon concentration (%)
	Eucalyptus species	Rainforest species	
1	0.78 (0.064)	0.512	47.81 (0.14)
2	0.70 (0.038)	0.384	48.08 (0.25)
3	0.41 (0.035)	0.192	48.00 (0.27)

*1, sound; 2, outer layers and sapwood showing signs of decomposition; 3, signs of decomposition extend to heartwood.

FIELD MEASUREMENT OF CARBON IN MATURE FORESTS

Three data sets were used as a basis for estimating CCC. In the first, 12 sites within the southern forest zone of New South Wales were located that were considered representative of mature, unlogged forest and in which there was a visual absence of anthropogenic disturbance, such as sawn tree stumps (see Fig. S1 in the supplementary material, location A). All sites were situated in small areal patches of forest, and typically contained many large living trees, often some senescing large trees and significant CWD. To estimate carbon in

the living, litter and CWD pools, the methodology was based on that used to determine CCS, with the following differences. The plot dimensions were 40 × 20 m, randomly located. Within this plot, all trees greater than 30 cm d.b.h. were identified and measured. Within a 20 × 20-m subplot all trees 20–30 cm d.b.h. were additionally measured, and within a 10 × 20-m subplot all stems between 2 cm d.b.h and 20 cm d.b.h. were counted.

Across the 12 sites described above the total area sampled was 0.96 ha, with each plot 0.08 ha. These were relatively small areas considering the large size and low stocking rate of individual trees in mature forests, and were susceptible to random sampling error. To overcome this potential problem, the data for above-ground vegetation carbon were augmented with two additional data sets collected from tall open *Eucalyptus* forests within the same region of south-eastern Australia. The Monga data set (see Fig. S1 in the supplementary material, location B) included d.b.h. measurements of all trees 20–100 cm d.b.h. within four randomly located 0.08-ha plots, and d.b.h. measurement of all trees greater than 100 cm d.b.h. within a surrounding 4.5-ha area. The East Gippsland data set (see Fig. S1 in the supplementary material, location C) comprised d.b.h. measurements of all trees greater than 20 cm d.b.h. within 45 × 0.2-ha plots, yielding a total sampling area of 9 ha. Data from all three locations were combined to yield a single set of values representative of carbon stocks in mature forests. The mean long-term climate across the managed sites (see Fig. S1 in the supplementary material, location D) was 1235 mm precipitation, with a mean annual temperature of 15.5 °C. For the three mature locations (see Fig. S1 in the supplementary material, locations A, B and C) the mean annual precipitation was, respectively, 1173, 1250 and 1168 mm, and the temperature 14.1, 13.0 and 12.1 °C.

There were a number of trees within the mature forest sites that exceeded the maximum tree size of 145 cm d.b.h. measured by Ash & Helman (1990) to develop their equations. Because these equations are exponential, extrapolating outside the range of data used to construct the relationships must be treated with caution (Brown, Schroeder & Birdsey 1997). We addressed this concern by using two variations to provide upper and lower bounds of the estimated tree biomass. In the first version (method a), the unmodified equations were used to estimate biomass (Fig. 1, dark line). In the second (method b) the curve was forced to asymptote after 145 cm d.b.h., with a maximum tree biomass of approximately 15 tC (Fig. 1, fine line). Although the difference between the two curves in Fig. 1 increases dramatically for trees greater than 150 cm d.b.h., suggesting a potentially important source of error, when applied to our field data the difference between the two methods was an approximately 8% greater biomass estimate using method a. Because of the relatively small overall difference between the two methods, and for clarity of presentation, we have chosen only to present the results using the more conservative estimates of method b.

MODEL PREDICTION OF CCC

While it is possible to use the mean values of measured carbon stock across the mature forest sites as a crude estimate of CCC, a modelling approach was adopted to investigate more specifically the CCC of the 17 Kioloa sites surveyed for CCS. The model allowed between-site variation in this variable to be quantified, and allowed estimates of the rate of recovery of the existing vegetation to be made.

The terrestrial carbon model is driven by net primary productivity (NPP) and the partitioning of that productivity into living, litter and soil components (Fig. 2; see Appendix S1 in the supplementary material). Carbon is partitioned into seven compartments; living leaf, living stem, living root, leaf litter, stem litter, root litter and soil.

For the purposes of terrestrial carbon modelling the available empirical information was limited primarily to estimates of the stocks of carbon in the various pools, yet the model contains a range of unknown parameters that define the carbon fluxes. These include allocation fractions of NPP to the leaf, stem and root living pools, turnover times of carbon in the living, litter and soil pools, and a humification fraction (see Appendix S1 in the supplementary material). The one flux for which estimates were available was NPP. This

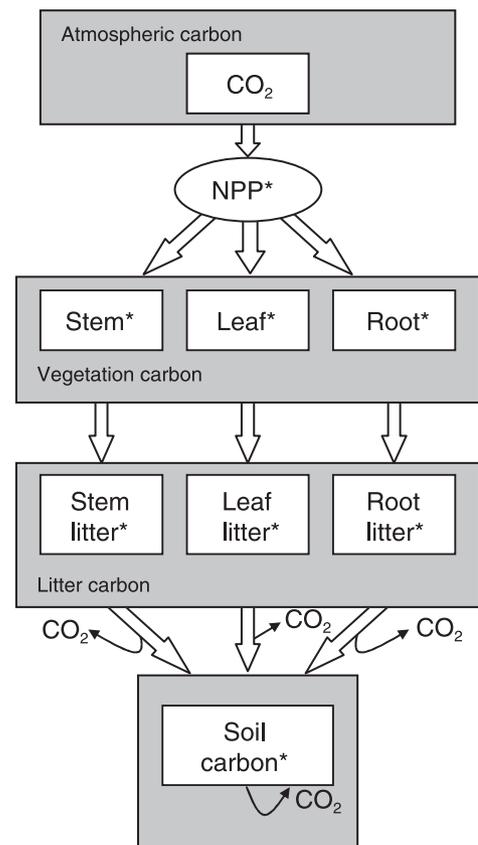


Fig. 2. Major pools and fluxes in the carbon model. The components marked with * indicate the input data collected from mature forests that were used in the model calibration.

Table 2. Summary of observed carbon stock estimates for the three sets of mature and minimally managed forest sites used to estimate carbon carrying capacity (CCC) and for net primary productivity (NPP) across those sites

	Mean	SD	Reference
Stock (tC ha ⁻¹)			
Leaf	1.80	0.45	Ash & Helman (1990), calculated from $n = 31$ branch samples
Stem	372.9	81.41	Mean and SD across $n = 61$ field plots (see Appendix S2 in the supplementary material, data sets A–C)
Root	65.83	16.83	Root carbon was calculated as 14% of total 'tree' carbon (Ash & Helman 1990).
Leaf litter	10.83	3.73	Mean and SD across $n = 12$ field plots (see Appendix S2 in the supplementary material, data sets A)
Stem litter	76.6	63.7	Mean and SD across $n = 12$ field plots (see Appendix S2 in the supplementary material, data sets A)
Root litter	10	3	Estimated as approximately 10–20% of root biomass
Soil	231.23	60.57	Mean and SD across $n = 12$ field plots (see Appendix S2 in the supplementary material, data sets A)
Flux (tC ha ⁻¹ year ⁻¹)			
NPP	7.09	0.55	Mean site NPP and SD extracted from a composite of five spatially explicit NPP maps covering the study area ($n = 61$ locations). The five NPP maps were 3PG, VAST, Aussie-Grass, Miami-Oz and BiosEquil (Roxburgh <i>et al.</i> 2004)

Table 3. Optimal model parameter estimates derived from function minimization ($n = 1000$ parameter sets). The mean and SD reflect the variability in the observed data on which the analysis was based (Table 2). The constraints are the ranges the parameters were allowed to vary within during the minimization procedure

Parameter	a_{leaf}	a_{stem}	a_{root}	L_{leaf} (year)	L_{stem} (year)	L_{root} (year)	L_{leaflit} (year)	L_{stemlit} (year)	L_{rootlit} (year)	hf	L_{soil} (year)
Mean (SD)	0.39 (0.05)	0.49 (0.05)	0.12 (0.05)	0.67 (0.20)	118.0 (34.7)	86.1 (36.7)	4.0 (1.5)	21.6 (16.0)	26.1 (9.9)	0.43 (0.08)	78.6 (26.7)
Constraints	0.3–0.6	0.3–0.6	–	0.1–3.0	20–350	20–200	0.1–10	5–100	1–50	0.3–0.6	20–550

a_i , allocation fraction of NPP to plant component i ; L_i , residency time of plant component i ; hf, humification fraction.

quantity was estimated as the average of five published spatial estimates of NPP that covered the entire study area (Table 2). The five spatially explicit NPP estimates comprised a mixture of empirical and process-based models (Roxburgh *et al.* 2004).

Calibration of the model was achieved by model inversion. This method requires specifying the model outputs (the carbon pools in the mature forests, as determined by field survey; Table 2) and also the estimates of NPP. Function minimization was then used to vary the unknown flux parameters, under constraints (Table 3), until the model predictions matched the observations (Michalewicz 1992). The calibration procedure was performed as follows. 'Pseudo-observed' values for each carbon pool and NPP were selected at random from a normal distribution with a mean and standard deviation (Table 2). The exception was stem litter, for which a log-normal distribution was required because of the skewed nature of the observations. No correlation structure was imposed on the random deviates. Model parameters were then fitted by minimizing the function:

$$\Phi = \sqrt{\sum_{i=1}^7 \left(\frac{C_{i,\text{pred}}}{C_{i,\text{obs}}} - 1 \right)^2} / 7 \quad \text{eqn 1}$$

where i is [leaf, stem, root, leaf litter, stem litter, root litter, soil], $C_{i,\text{pred}}$ is the model-predicted size of carbon pool i , and $C_{i,\text{obs}}$ is the pseudo-observed carbon pool size. Function Φ can be interpreted as the average deviation of all model-predicted pools relative to their

corresponding observations. A single iteration of this method selects a set of observations for each carbon pool within the field-estimated range of variability, and then generates a set of model parameters that minimizes the difference between the model predictions and the observations. This process is then repeated 999 times, resulting in 1000 sets of pseudo-observed carbon stocks, each of these being associated with 1000 sets of model parameters. Full details of the model calibration are given in Appendix S1 in the supplementary material. To apply the model, 1000 replicate runs are performed (one per parameter set), generating a total set of 1000 model predictions for each output variable. These final model results are then summarized as a mean and standard deviation across the 1000 runs. One of the major advantages of model calibration by inversion and function minimization, as opposed to the more traditional manual 'tuning' methods, is that variability in field observations (Table 2) is explicitly included within the model as the 1000 sets of parameters, resulting in appropriately calculated uncertainties around the model predictions.

MODELLING SPATIAL VARIABILITY IN NPP

Extending the model spatially to predict CCC, for each site where CCS had been estimated from field survey, required first modelling the spatial distribution of NPP at a resolution of 25 m, using topographic variability as the major source of landscape heterogeneity. No attempt was made to make other model parameters spatially

variable. Variability in forest growth as a function of landscape-scale topographic heterogeneity has been implemented in a range of forest modelling studies (Tickle *et al.* 2001; Mackey *et al.* 2002; Dean, Roxburgh & Mackey 2004).

In this study the radiation use-efficiency model of Roderick *et al.* (2001), incorporating the effects of diffuse irradiance on canopy photosynthesis (Sinclair, Murphy & Knoerr 1976; dePury & Farquhar 1997), was combined with a modifier function that adjusted growth according to an index of soil water availability. The required spatial input data included monthly mean daily solar radiation at the top of the canopy, monthly mean daily solar radiation at the top of the atmosphere, and an index of potential soil water availability. The fraction of photosynthetically active radiation absorbed by the canopy (fPAR) for mature *Eucalyptus* forest, also required in the calculation of Roderick *et al.* (2001), was estimated to be 0.78, using the methods described in Berry & Roderick (2002). The program SRAD (Wilson & Gallant 2000) was used to produce spatial estimates of topographically corrected potential solar radiation at the top of the canopy as a function of latitude, slope, aspect and topographic shading, using the 25-m resolution DEM.

The soil water modifier was created using simple linear relationships involving the TWI and radiation (see Appendix S2 in the supplementary material). The modifier assumes that soil moisture is predominantly determined by topographic controls on hydrological flows and evaporative demand. The modifier (S) takes the form of an index ranging from 0 to 1, and was applied as follows:

$$\text{NPP} = \text{NPP}_R \times S$$

where NPP_R is the NPP predicted by the calculation of Roderick *et al.* (2001) and S the soil water modifier. This formulation is similar to that employed by a number of other radiation use-efficiency models (Landsberg & Waring 1997; Medlyn *et al.* 2003). NPP was calculated on a monthly time step and then summed to produce an estimate of annual NPP ($\text{tC ha}^{-1} \text{ year}^{-1}$). The NPP of the 25×25 -m grid cell coinciding with the centre of each of the 17 Kioloa field sites was combined with the set of model parameters from the calibration procedure described in the previous section. Modelled estimates of CCC at each site were obtained by substitution into equations S9–S15 in Appendix S1 (see the supplementary material).

Results

CURRENT CARBON STOCKS

Mean carbon stock and SE ($n = 17$) in above-ground vegetation, CWD and litter were $210.6 \pm 19.5 \text{ tC ha}^{-1}$, $52.2 \pm 15.6 \text{ tC ha}^{-1}$ and $10.4 \pm 1.5 \text{ tC ha}^{-1}$, respectively (Fig. 3a–c). There was marked variation in carbon

stock among sites for each of the forest components, with carbon in above-ground vegetation ranging from 26.6 tC ha^{-1} to 337.7 tC ha^{-1} . The highest above-ground carbon stocks tended to be in sites with an abundance of large trees and minimal evidence of disturbance. The lowest above-ground carbon stocks were typically sites that had been disturbed in the recent past (see Tables S1 and S2 in the supplementary material). The percentage of mean total carbon allocated to the components of above-ground vegetation, CWD and litter was approximately 77%, 19% and 4%, respectively (Fig. 3d).

Relative to mature forests, the impact of the logging regime on the distribution of tree d.b.h. indicated a significant increase in the smaller size classes and a decline in the larger size classes (Fig. 4).

CARBON CARRYING CAPACITY

The predicted CCC across the 17 field sites for above-ground vegetation was (mean and SE) $363.7 \pm 11.2 \text{ tC ha}^{-1}$ (Fig. 3a). For CWD and fine litter, CCC was estimated to be $70.8 \pm 15.2 \text{ tC ha}^{-1}$ and $10.6 \pm 1.1 \text{ tC ha}^{-1}$, respectively (Fig. 3b,c). The percentage of mean total carbon allocated to the components of above-ground vegetation, CWD and litter was approximately 82%, 16% and 2%, respectively. The model parameters used to calculate CCC are summarized in Table 3.

CARBON SEQUESTRATION POTENTIAL

Current carbon stocks in above-ground vegetation were consistently below the estimated CCC (Fig. 3). Over all 17 field sites, the difference between these two quantities, the CSP, averaged $153.2 \pm 21.5 \text{ tC ha}^{-1}$ (mean and SE) for above-ground vegetation, with a range 47 – 353 tC ha^{-1} . The CSP of CWD was $18.6 \pm 15.3 \text{ tC ha}^{-1}$, and the CSP for fine litter was $0.2 \pm 1.5 \text{ tC ha}^{-1}$. The CSP of individual plots was related to the occurrence of large trees greater than 100 cm d.b.h., with plots closest to CCC tending to have more large trees and a higher percentage of total plot biomass residing in those trees (Fig. 5).

LANDSCAPE VARIABILITY IN NPP

The spatial distribution of NPP over the Kioloa study is shown in Fig. 6. NPP over the landscape ranged from 4.6 to $9.6 \text{ tC ha}^{-1} \text{ year}^{-1}$, with a mean of $7.1 \text{ tC ha}^{-1} \text{ year}^{-1}$. The spatial variation in NPP reflected the effects of topographically modified surface radiation and TWI, where higher NPP is predicted to occur in gullies and lower NPP on south-facing slopes. Estimated NPP across the 17 sites ranged from 6.2 to $7.5 \text{ tC ha}^{-1} \text{ year}^{-1}$, with a mean of $6.9 \text{ tC ha}^{-1} \text{ year}^{-1}$. Variation in NPP between sites was largely attributable to variations in modelled surface solar radiation. A significant relationship was found between model-predicted NPP and CCS for the nine Kioloa plots closest to predicted CCC, and with a CSP for above-ground vegetation of less than 100 tC ha^{-1} (Fig. 7).

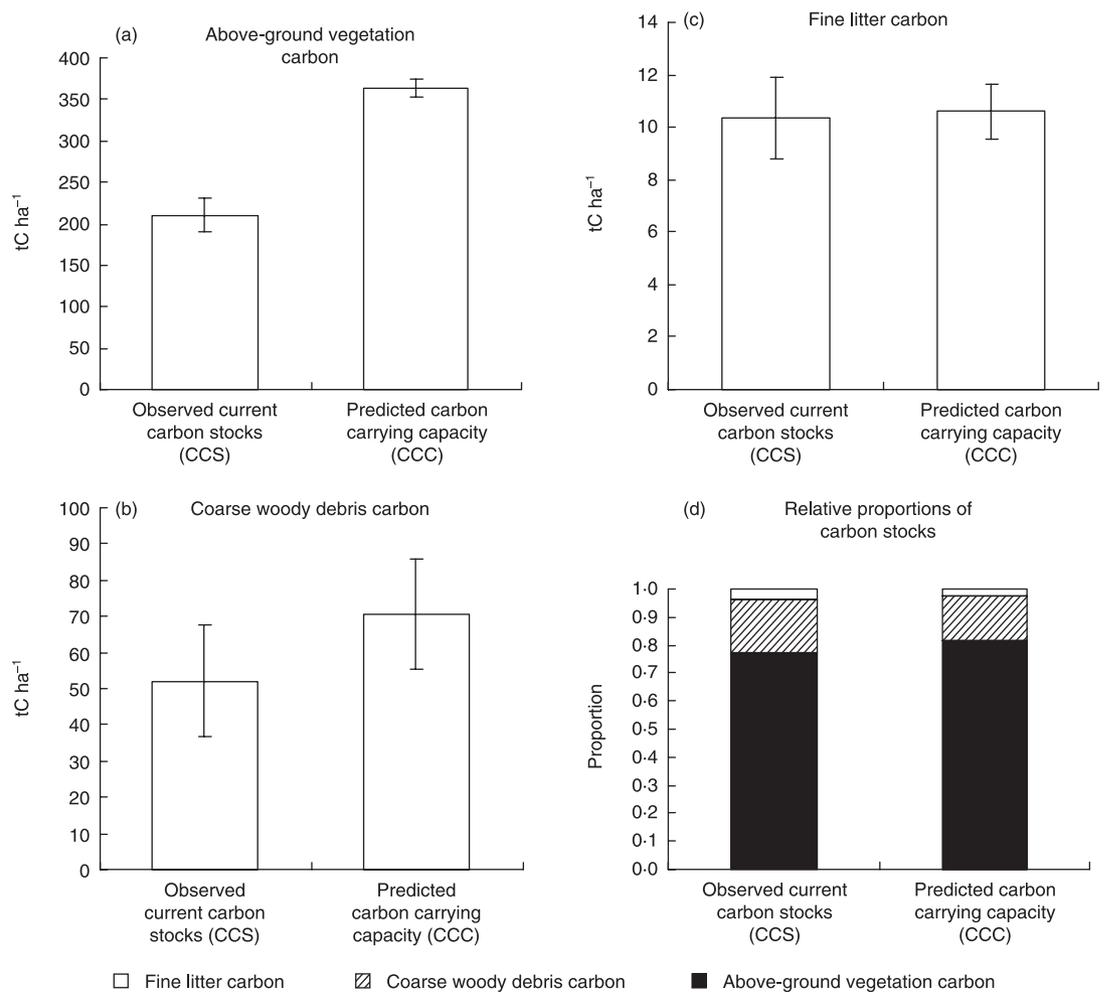


Fig. 3. Comparison of current carbon stocks (CCS) and predicted carbon carrying capacity (CCC). Error bars are standard errors and reflect between-site variability in carbon stock as determined by field survey (Table 2). (a) Above-ground vegetation carbon (*t*-test for difference in means, $P < 0.001$). (b) Coarse woody debris carbon (*t*-test for difference in means, $P = 0.234$). (c) Fine litter carbon (*t*-test for difference in means, $P = 0.854$). (d) Relative proportions of each carbon component.

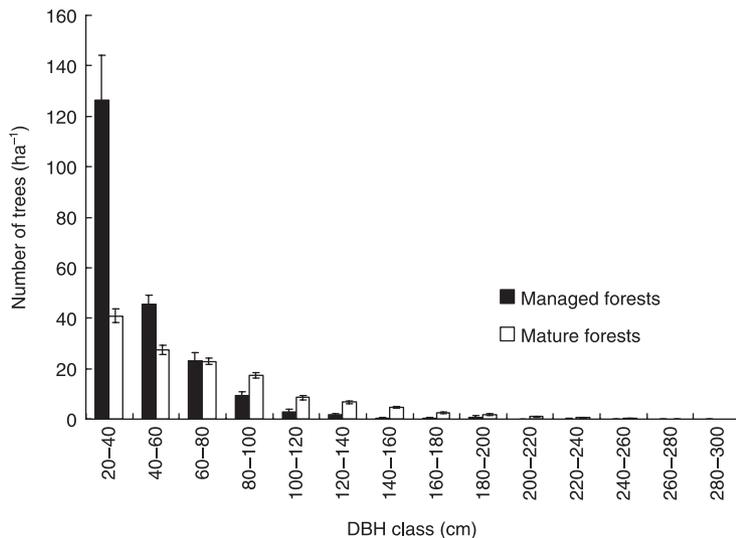


Fig. 4. Frequency histograms comparing the distributions of d.b.h. between managed and mature forests. Managed forests are depauperate in large trees greater than 100 cm d.b.h. but have relatively more smaller trees less than 60 cm d.b.h.

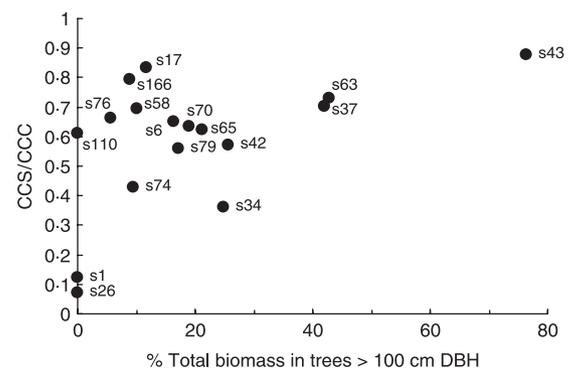


Fig. 5. Relationship between the proportion of biomass within each plot that is contained within trees greater than 100 cm d.b.h. and the ratio of current total plot biomass to predicted carbon carrying capacity (CCS/CCC). Plots with the largest proportion of biomass residing in large trees also tended to be plots closest to their predicted CCC ($r = 0.50$, $n = 17$, $P = 0.04$). The identification numbers adjacent to the symbols correspond to the Kioloa plot database codes (Davey 1989).

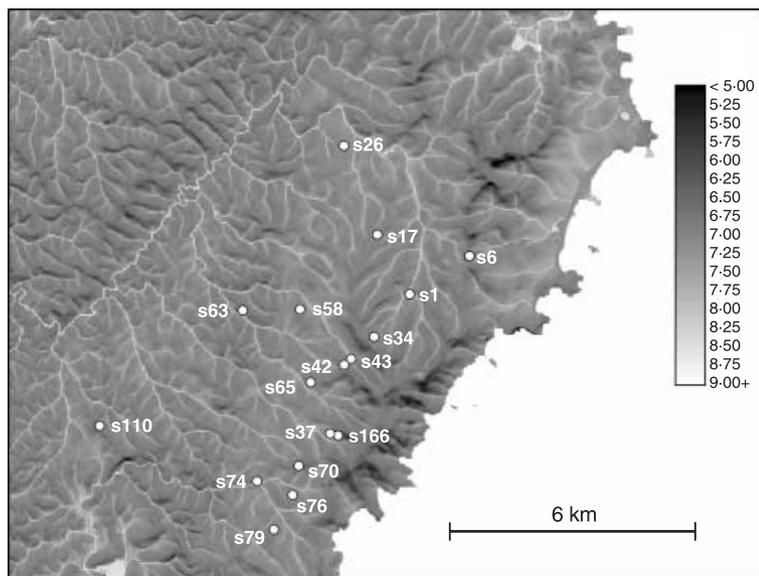


Fig. 6. The spatial distribution of model-predicted net primary productivity (NPP, tC ha⁻¹ year⁻¹) across the Kioloa study area (see Fig. S1 in the supplementary material, area D) and locations of the 17 Kioloa study sites.

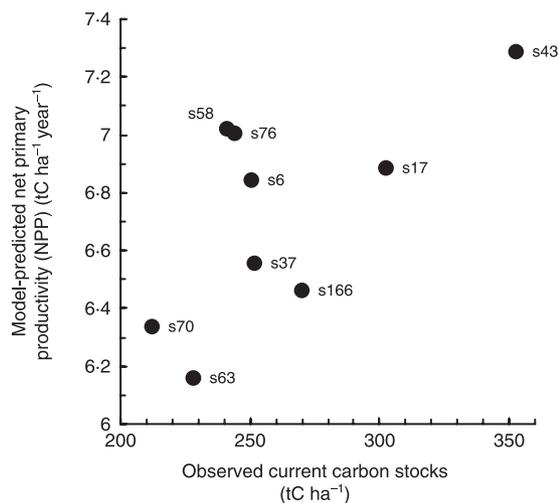


Fig. 7. Relationship between current total plot biomass and model-predicted net primary productivity (NPP) for the nine plots closest to carbon carrying capacity, with carbon sequestration potentials of less than 100 tC ha⁻¹. The figure shows a significant relationship between predicted NPP and independently measured observed carbon stocks from field survey ($r^2 = 0.44$, $n = 9$, $P = 0.05$).

SIMULATED RATES OF FOREST RECOVERY

Given the high potential for carbon sequestration, the timeframe over which these forests would be expected to recover is of interest and can be estimated through initializing the model with the average estimates of current above-ground living biomass (211 tC ha⁻¹) and running the model forward through time with the parameters derived from the model calibration (Table 3). Such an analysis predicted an average forest plot would take approximately 53 years to exceed 75% CCC and 152 years to exceed 90% CCC.

Discussion

CURRENT CARBON STOCKS

The range of above-ground vegetation, CWD and litter carbon estimates for the Kioloa study area spans published carbon stock estimates for managed *Eucalyptus* forests, of approximately 50–500 tC ha⁻¹ (Attiwill 1979; Stewart, Flinn & Aeberli 1979; Feller 1980; Adams & Attiwill 1986; Applegate 1989; O'Connell 1989; Grierson, Adams & Attiwill 1992). The wide range of biomass values reported across the 17 Kioloa sites (see Table S1 in the supplementary material) can be attributed, in part, to differences in past logging activity and time since last disturbance (see Table S2 in the supplementary material). The average of 211 tC ha⁻¹ reported in this study for above-ground vegetation is similar to the range of 223–255 tC ha⁻¹ reported in other biomass studies within the Kioloa region (Furrer 1971; Neave 1987; Ash & Helman 1990).

CWD is a commonly neglected forest component in ecological studies (Harmon *et al.* 1986) and assessments of carbon stock and sequestration (Harmon & Hua 1991; Woldendorp, Keenan & Ryan 2002). However, CWD comprises an important store of carbon, particularly in old-growth forests (Harmon & Hua 1991). In this study, CWD accounted for 19% of total above-ground carbon, which supports the need to include this pool in carbon budgets.

CARBON CARRYING CAPACITY

The three mature forest data sets used to estimate CCC in this study yielded an above-ground biomass carbon estimate with a 95% confidence interval of 341–386 tC ha⁻¹. Although estimates of biomass carbon in mature tall *Eucalyptus* forests are rare, our estimate is consistent with the information that is available. Reported values for forest stands older than approximately 40 years are typically in the range 200–400 tC ha⁻¹ (Feller 1980; Adams & Attiwill 1986) and in old-growth forests the values can be even higher; Dean, Roxburgh & Mackey (2003) reported values of 700–800 tC ha⁻¹ in mature *E. regnans* forests and Applegate (1989) reported a value of 892 tC ha⁻¹ for an old-growth stand of *E. pihularis*.

CARBON SEQUESTRATION POTENTIAL

Generally, the current carbon stock in above-ground vegetation in the Kioloa study area (the managed sites) was well below the estimated CCC (the mature sites), with an average CSP of 153.2 tC ha⁻¹. For the CWD and litter pools, the CSP was generally much lower, at 18.6 and 0.2 tC ha⁻¹, respectively. The results suggest above-ground carbon stocks in managed forests are approximately 60% of their potential CCC.

In a study with similar objectives, Brown, Schroeder & Birdsey (1997) assessed the sequestration potential for two eastern USA hardwood forests recovering from past disturbance by estimating their above-ground

biomass density and comparing the results with undisturbed forests considered to be at maximum potential carbon stock capacity. Brown, Schroeder & Birdsey (1997) demonstrated that the managed eastern hardwood forests had much lower above-ground biomass density than the old-growth forests, and generally less than 50% of the predicted CCC of approximately 250 tC ha⁻¹, suggesting that through recovery and regrowth these forests have the potential to accumulate significant quantities of additional biomass, and thus sequester atmospheric carbon into the future. Although maximum CCC in the eastern USA forests is less than that reported here, the relative difference between managed and mature forests is approximately the same, at 50–60% of predicted CCC.

The number and importance of large trees in contributing to the total carbon budget in the 17 Kioloa sites can be contrasted with the size class distribution in the mature forest sites (Fig. 4). In mature forests, large diameter trees greater than 100 cm d.b.h. comprised 18% of all trees greater than 20 cm d.b.h. and contained 54% of the total above-ground carbon in living vegetation. The stocking rate of large trees (> 100 cm d.b.h.) in mature forests was approximately 23 trees ha⁻¹, compared with approximately 6 large trees ha⁻¹ in the managed forests. Across the 17 study sites the size and abundance of large trees (greater than 100 cm d.b.h.) was also highly influential on the magnitude of CSP, with sites closest to CCC tending to have a greater proportion of biomass in large trees (Fig. 5). Large diameter trees were recorded in 14 sites, and although they comprised less than 5% of trees greater than 20 cm d.b.h. across all sites, large diameter trees contained 25% of the carbon.

The influence of large trees on carbon stock therefore increases with their increasing size and abundance. Several studies have shown that mature tropical moist forests have a high proportion of biomass in large trees (Brown & Lugo 1992; Brown *et al.* 1995; Clark & Clark 1996). Those forests had 30–50% of the biomass in a few large trees with diameters greater than 70 cm (Brown 1996). Similarly, in old-growth deciduous hardwood forests in eastern USA, the proportion of biomass distributed in large trees with a diameter greater than 70 cm was up to 30% (Brown, Schroeder & Birdsey 1997). Brown, Schroeder & Birdsey (1997) further noted that in those forests that had been subject to historical clearing and harvesting the percentage of biomass in large trees was reduced to approximately 8–10%.

LANDSCAPE VARIABILITY IN NPP

The impacts on NPP of spatial variability in radiation and soil water across the landscape were included in the analysis in order to estimate between-site variation in CCC. A comparable application using the 3PG model in south-eastern New South Wales *Eucalyptus* forests was conducted by Tickle *et al.* (2001). However, in that study the spatial variability in NPP was not reported.

The model estimate of NPP averaged across the Kioloa landscape (7.1 tC ha⁻¹ year⁻¹; Fig. 6) agreed approximately with the only empirically based estimate of NPP for the Kioloa study area of 6.4 tC ha⁻¹ year⁻¹ (Ash & Helman 1990), which was based only on stem increment measurements and hence did not include canopy or root productivity. No other data were available for validation of the NPP predictions. NPP over most of the landscape falls within the range of 2–8 tC ha⁻¹ year⁻¹ estimated for other *Eucalyptus* forests (cited by Ash & Helman 1990) and is comparable with the estimate of approximately 7 tC ha⁻¹ year⁻¹ from a regional-scale 3PG application in the Kioloa study area by Coops, Waring & Landsberg (1998).

The soil water modifier developed for use in the NPP calculation simulated topographic-scale processes known to affect NPP. Neave (1987) noted that the volume of soil available for soil moisture storage was less on upper slopes, consistent with our interpretation of the TWI in developing the soil moisture index. The spatial variability in model-predicted NPP also showed a significant positive relationship with the independently derived CCS, as measured by field survey (Fig. 7). Thus we infer there is a residual signal in current biomass of the influence of environmental gradients on NPP. This in turn suggests that the soil water modifier included in the NPP function has some physical basis that warrants further testing. Significant relationships between productivity and carbon stock have been observed across a wide range of Australian forested ecosystems, and have been used as a basis for modelling forest growth at a continental scale (Richards & Brack 2004).

The spatial modelling of NPP included topographically controlled variation in light environment and water regime. While water is undoubtedly a major limiting factor in most Australian ecosystems, it is not the only one. At a continental scale it has been shown that explicitly including nutrient cycling within NPP models tends to produce lower NPP estimates (Roxburgh *et al.* 2004). Spatial variability in soil nutrient status, and in the processes controlling litter and soil decomposition and accumulation, are also likely to be important in the Kioloa region. However, the analysis presented here assumes that growth limitations as a result of fertility are constant across all managed sites. Additional fieldwork quantifying the topographic variability in soil fertility and litter decomposition rates, and incorporation of this information into the modelling framework, would allow refinement of the carbon sequestration estimates presented here.

CONCLUSIONS

CSP was evaluated by comparing CCS derived from field survey to CCC predicted by a spatially distributed landscape-scale model of terrestrial carbon dynamics. Across the Kioloa study area, current carbon stock in above-ground vegetation was well below the estimated CCC, largely because of the removal of biomass in

large trees through prior logging. These results imply that through regrowth and recovery from past disturbance, previously managed temperate *Eucalyptus* forests may be currently functioning as significant sinks for atmospheric carbon. Although Kyoto-related terrestrial carbon accounting is focused primarily on afforestation, reforestation and deforestation since 1990 (Watson *et al.* 2000), our results suggest that native forests should also be a consideration when developing terrestrial carbon management options, and for terrestrial carbon accounting more generally.

In comparing the model predictions with the field data collected from the Kioloa sites there was evidence to suggest that, despite the long land-use history, the influence of local environmental gradients on NPP and biomass could still be detected. These relationships warrant further study.

If our results are accepted as characteristic, then it is possible to estimate the CSP of the surrounding region. Temperate forests in south-east Australia cover a total area of about 70 940 km², with 32% classified as unlogged in 1992 (Resource Assessment Commission 1992). Based on our calculations, a 95% confidence interval for above-ground living biomass CCC in these forests was 341–386 tC ha⁻¹, with CCS in logged forests of approximately 200 tC ha⁻¹ and hence a CSP in logged forests of 141–186 tC ha⁻¹ (Fig. 3). Thus the CSP of temperate forests in south-east Australia (which comprise approximately 76% of these forest types Australia-wide) is in the order of 680–895 MtC.

The methods developed by this study provide a general framework for determining the CSP across a range of forested ecosystems where current biomass is below its potential because of historical management practices. Quantifying the impact of anthropogenic activity on the terrestrial carbon sink is an important component of the global carbon budget. For example, Hurtt *et al.* (2002) suggested that the currently observed carbon sink across the co-terminous USA forests is caused largely by ecosystem recovery from prior land use. The methods developed here provide one approach to quantifying the historical human impact on forested ecosystems, and for quantifying their future CSP.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>.

Appendix S1. Description of the carbon accounting model and its calibration.

Appendix S2. Description of the soil water modifier used in the NPP calculation.

Figure S1. Location map of the study sites where field survey was undertaken.

Table S1. Summary of plot-level results for the measurement of current carbon stocks.

Table S2. Management histories, locations and year sampled for each of the 17 Kioloa sites.