

Changing Australian vegetation from 1788 to 1988: effects of CO₂ and land-use change

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Abstract. We present a tractable and transparent approach (the TMSC model) to estimating the total stock of carbon (roots, stems and leaves) in living vegetation (C_{living}), from gross primary productivity (GPP) estimates. The TMSC model utilises the TMS scheme of canopy functional types and a generic allometric scheme to derive these estimates. Model estimates are presented for the Australian continent under the following three vegetation–[CO₂] scenarios: the present (1988) vegetation and a hypothetical natural (1988) vegetation cover with atmospheric CO₂ concentration ([CO₂]) of 350 $\mu\text{mol mol}^{-1}$ (pveg350 and nveg350), and the natural vegetation (1788) having [CO₂] of 280 $\mu\text{mol mol}^{-1}$ (nveg280). The change between the nveg280 and pveg350 scenarios represents the combined effects of changes in land use and CO₂. The change resulting from CO₂ alone is the difference between the nveg280 and nveg350 scenarios. The estimated C_{living} for the continent is 21 Gt for pveg350, 23 Gt for nveg350 and 10 Gt for nveg280. This translates to an averaged rate of increase in C_{living} (CSI) of about 50 Tg C year^{−1} over the last 200 years for the continent. Where wooded areas have been extensively cleared for agriculture, the CSI is negative (down to $-4 \text{ g C m}^{-2} \text{ year}^{-1}$). Elsewhere, the CSI over the last 200 years ranges from $\sim 55 \text{ g C m}^{-2} \text{ year}^{-1}$ in the tropical and subtropical forests to $\sim 0 \text{ g C m}^{-2} \text{ year}^{-1}$ in the most arid regions.

Introduction

How has the Australian vegetation changed since European settlement in 1788? We will never know for certain as there was no systematic ecological survey of the continent at that time. However, we can explore the past by using models. This is made possible in Australia because we have an invaluable resource—Carnahan's vegetation maps (AUSLIG 1990). There are two maps and they are usually described as the 1788 'natural' vegetation and the 1988 'present' vegetation. The 1788 natural vegetation map was made by starting with the 1988 present vegetation map, and using remnants, and various other information sources to estimate what the vegetation distribution would have been like without clearing. Hence, the so-called 1788 natural vegetation map would be better described as an estimate of the vegetation that would have existed in 1988 if there had been no clearing. This is not the same thing as the vegetation in 1788 because clearing is not the only factor that causes vegetation change. For example, observed changes in the Australian vegetation that have occurred during the last 50 years have also been attributed to changes in the fire regime (Bowman 1998; Bowman *et al.* 2001), rainfall

(Fensham *et al.* 2005) and grazing (in rangelands, Archer *et al.* 2001; Burrows *et al.* 2002).

The commencement of European settlement coincided with the commencement of the 'industrial period' and an upward trend, to the present day, in the concentration of carbon dioxide ([CO₂]) in the atmosphere, as evidenced from analyses of air bubbles trapped in glacial ice, and more recently, direct atmospheric measurement (Fig. 1). In recent years there have been many studies (globally) into the effects of increasing [CO₂] on the vegetation and its components. However, few studies have looked the other way—at the effect of decreasing [CO₂] on the vegetation. Despite that, there is clear evidence from experiments (e.g. Polley *et al.* 1992, 1993, 2002; Phillips *et al.* 1998; Körner 2003) and theoretical reasons (Berry and Roderick 2002a, 2004) to expect that the greatest response of the vegetation to increasing [CO₂] should occur at [CO₂] < 500 $\mu\text{mol mol}^{-1}$. Consequently, the vegetation that would have existed in 1988 if there had been no change in land use, would not be the same as the natural vegetation in 1788 because in 1988 the [CO₂] was $\sim 350 \mu\text{mol mol}^{-1}$, whereas in 1788 the [CO₂] was $\sim 280 \mu\text{mol mol}^{-1}$. Hence,

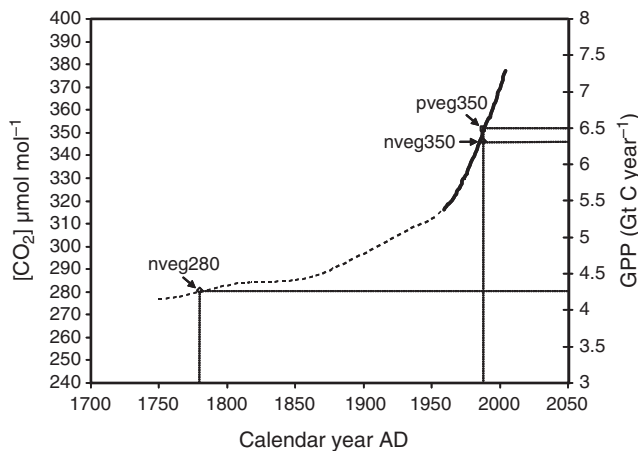


Fig. 1. Relationship between the concentration of CO_2 in the atmosphere ($[\text{CO}_2]$), calendar year and estimates of gross primary productivity (GPP) over the Australian continent. CO_2 data are from the Law Dome, Antarctica glacier (dashed line; 1750–1974 AD; Etheridge *et al.* 1996) and the Mauna Loa, Hawaii, instrument record (solid line; 1959–2004 AD; (Keeling and Whorf 2005)). GPP estimates (dotted, right-hand axis) for the existing vegetation in 1988 (pveg350), the hypothetical natural vegetation in 1988 (nveg350) and the vegetation in 1788 (nveg280) are from Berry and Roderick (2004).

the question remains: what was the Australian vegetation like in 1788?

The response of the vegetation to the increase in $[\text{CO}_2]$ between 1788 and 1988 may be manifested as an increase in the canopy cover over space/time and a corresponding increase in the mean amount of photosynthetically active radiation intercepted by the vegetation over a year (\bar{F}_V , Berry and Roderick 2002a), an increase in the gross uptake of CO_2 (i.e. GPP), and an increase in the mass of carbon in the stems, roots and foliage of living plants. Recently, estimates of GPP in 1988 and 1788 have been published for the Australian continent (Berry and Roderick 2004; Fig. 1). That study was based on continental-wide satellite imagery at $\sim 5\text{-km}$ resolution to estimate the GPP of the present vegetation in 1988, and the flux estimates for a hypothetical ‘natural’ vegetation cover in 1988 and for the vegetation cover 1788 are also at the same spatial resolution. The next challenge is to use the existing estimates of \bar{F}_V and GPP to estimate the change in the mass of carbon in the living vegetation at $\sim 5\text{-km}$ resolution for the continent.

One possible approach for estimating gross features of the vegetation, such as the mass of carbon, is to use simple functional models. By this approach, the carbon in the vegetation is estimated as a function of the input flux and turnover time. Hence, if a way could be found for estimating the turnover time in 1788 and in 1988, then it might be possible to estimate the carbon in living vegetation in those two periods.

The most common approach to estimating the turnover time is to use (often biome-specific) parameters that describe the allocation and turnover of carbon in various pools. Recently, a generic allometric scheme for vascular plants was proposed (Niklas and Enquist 2002). This is a useful advance for the purposes of carbon modelling because the allometric scheme implicitly summarises how both the standing stock, and the flux of newly assimilated carbon, are distributed between the various pools (leaves, stems, roots). Importantly, the generic allometric scheme also implicitly defines the turnover time of each pool because the total mass of carbon in an individual plant, which is also a function of time, is used as the basis for the allometric equations. Hence, the generic allocation scheme offers an approach that might be very useful for vegetation modelling.

In this paper, we describe a simple model (the TMSC model) that combines the flux estimates we reported previously (Berry and Roderick 2004) with the generic allometric scheme of Niklas and Enquist (2002) to estimate the total mass of carbon in the living vegetation in 1788 and 1988. The basic idea is to make continental-wide estimates of the carbon in living vegetation for the following three different scenarios: (1) the vegetation in 1988 (denoted pveg350), (2) a hypothetical ‘natural’ vegetation in 1988 (denoted nveg350), and (3) the vegetation in 1788 (denoted nveg280). The differences between the nveg350 and nveg280 scenarios, and the nveg350 and pveg350 scenarios, are estimates of the effects of the change in $[\text{CO}_2]$ and land-use change on the storage of carbon in living vegetation in Australia, whereas the difference between the nveg280 and pveg350 scenarios is an estimate of the total change.

Table 1 gives a list of symbols used throughout.

Materials and methods

Data sources

The climate and vegetation data sources that were used to calculate the GPP of the T, M and S components of the canopy (see below) are described in Berry and Roderick (2004). In that paper mean monthly estimates of global solar radiation, maximum and minimum air temperature, and estimates of the fraction of photosynthetically active radiation absorbed by the vegetation (F_V) were used to estimate the mean monthly net radiation and transpiration fluxes. The annual sum of GPP of the T, M and S components of the canopy was then estimated from the transpiration flux. The resolution of pixels for all of the spatial analyses was $0.05^\circ \times 0.05^\circ$. Because the surface area of these pixels varies with latitude, the images were reprojected to a Lambert equal area projection prior to summation of fluxes and stocks for the entire continent.

TMSC model formulation

TMS scheme

The TMSC model is built on the TMS scheme. The TMS (turgor, mesic, sclerophyll) scheme is a framework that links canopy leaf properties, vegetation structure and cover with resource availability. It is based on a quantitative synthesis of numerous ecophysiological studies and links leaf longevity, photosynthetic capacity and composition with

Table 1. Synonyms and acronyms

Symbol or acronym	Meaning	Unit
pveg350	The existing 1988 vegetation [CO ₂] 350 µmol mol ⁻¹	
nveg350	The 'natural' 1988 vegetation [CO ₂] 350 µmol mol ⁻¹ (The vegetation in the absence of land use change)	
nveg280	The vegetation estimated to exist in 1788 [CO ₂] 280 µmol mol ⁻¹	
\bar{F}_V	Average fraction of photosynthetically active radiation (PAR) intercepted by the canopy over a year	
T	Turgor leaf form	
M	Mesic leaf form	
S	Sclerophyll leaf form	
$\bar{F}_T, \bar{F}_M, \bar{F}_S$	Average PAR absorbed by T, M and S leaf forms over a year	
X_T, X_M, X_S	$\bar{X}_T = \bar{F}_T / \bar{F}_V, \bar{X}_M = \bar{F}_M / \bar{F}_V, \bar{X}_S = \bar{F}_S / \bar{F}_V$	
WUE_{ph}	Water use efficiency of photosynthesis	
GPP	Gross primary productivity	kg C m ⁻² year ⁻¹
NPP	Net primary productivity	kg C m ⁻² year ⁻¹
NPP*	The component of NPP that is usually measured	kg C m ⁻² year ⁻¹
R_a	Proportion of GPP expended on autotrophic respiration	
F	Proportion of GPP expended on various fluxes away from the living vegetation other than autotrophic respiration	
NNCI	Net new carbon increment	kg C m ⁻² year ⁻¹
NNCI _{leaf}	Net new carbon increment partitioned to canopy	kg C m ⁻² year ⁻¹
L_1	Leaf longevity in canopy	year
C_{leaf}	Carbon stock in canopy	kg C m ⁻²
$C_{stemroot}$	Carbon stock in roots and stems	kg C m ⁻²
C_{living}	Carbon stock in living vegetation	kg C m ⁻²
CSI	Increment C_{living} over a period of time ($t_2 - t_1$)	kg C m ⁻² year ⁻¹

changes in resource availability (Roderick *et al.* 2000). The TMS scheme recognises that vegetation canopies are composed of mixtures of leaves that have different properties. A brief summary of the TMS scheme is given below and detailed descriptions are available in earlier publications (Berry and Roderick 2002a, 2002b, 2004).

In the TMS scheme, canopies are described in terms of three functional leaf types, i.e. T, M and S leaves. Turgor (T) leaves rely on the turgor pressure of the protoplasm for structural support. They are short-lived (e.g. leaves of deciduous trees and shrubs, and soft-leaved herbaceous species), have high photosynthetic rates per unit volume and low C : N ratios. Mesic (M) and sclerophyll (S) leaves are longer-lived and may occur on trees, shrubs and herbaceous plants. The structural support for M and S leaves is provided by cell walls. S leaves have a smaller surface : volume ratio than M leaves, and are longer-lived. M leaves have lower rates of photosynthesis per unit volume and higher C : N ratios than T leaves. S leaves have the lowest photosynthetic rates and the highest C : N ratios.

The currency for the TMS scheme is the fraction of photosynthetically active radiation (PAR) absorbed by the canopy (F_V), as well as the fractions absorbed by T (F_T), M (F_M) and S (F_S) leaves:

$$F_V = F_T + F_M + F_S.$$

In applications, F_V is estimated from satellite-derived NDVI data. The contributions from T, M and S leaves are estimated by time series analysis of the same satellite data. The basic idea is that, if a time series for a pixel has large month-to-month variations in F_V , the vegetation in the pixel must have a substantial component of short-lived leaves, i.e. T leaves. Conversely, if there is little month-to-month variation in F_V , the leaves are longer-lived, i.e. M and/or S leaves. The partitioning of this 'evergreen' component of F_V into F_M and F_S is determined by resource availability. As resources required for photosynthesis and growth (CO₂, O₂, water, mineral nutrients and sunlight) become more readily available

throughout the annual period, the mean F_V (\bar{F}_V) increases. When $\bar{F}_V \geq 0.75$, all of the evergreen component is deemed to be mesic (i.e. $\bar{F}_V - \bar{F}_T = \bar{F}_M$). In contrast, when $\bar{F}_V \leq 0.20$ all of the evergreen component is deemed to be sclerophyll (i.e. $\bar{F}_V - \bar{F}_T = \bar{F}_S$). A mixture analysis is used to calculate \bar{F}_M and \bar{F}_S when \bar{F}_V is greater than 0.2 and less than 0.75. See Berry and Roderick (2002a, 2002b) for more details.

The proportional contribution (X) of the T, M and S leaves to the absorbed PAR over a specified period is calculated by the following equation:

$$X_T = \frac{\bar{F}_T}{\bar{F}_V}; X_M = \frac{\bar{F}_M}{\bar{F}_V}; X_S = \frac{\bar{F}_S}{\bar{F}_V},$$

where the overbar indicates the mean value over a specified period. From the above equation it follows that

$$X_T + X_M + X_S = 1.$$

The T, M and S proportions can be related to the vegetation structure, resource availability (CO₂, H₂O, mineral nutrients, energy) and disturbance by using a ternary diagram (Berry and Roderick 2002a, 2002b, 2004). The ternary diagram allows changes in X_T , X_M and X_S , arising from changes in resource availability and land use, to be tracked through time. For example, we have previously shown (Berry and Roderick 2002a) that when $X_T \rightarrow 1$, the Australian vegetation largely comprises turgor (i.e. short-lived) leaves forming, for example, cereal crops, ephemeral herbfields and annual herbfields. When $X_M \rightarrow 1$, the natural vegetation is closed forest, such as a complex mesophyll rainforest or a tall eucalypt forest having an understorey of lower trees. When $X_S \rightarrow 1$, the vegetation comprises sclerophyllous shrubs, having an understorey of lower sclerophyllous shrubs or sclerophyllous hummock grassland, or no understorey.

Overall concept for estimating C stocks

The modelling approach is summarised in Fig. 2. Briefly, the purpose of Steps 1–4 is to estimate the stock of carbon in the leaf tissues that form the canopy. Following that, an allometric relationship is used to estimate the carbon stock in the stems and roots from the carbon stock of the canopy (Step 5).

The TMS description of the canopy is used as the starting point for all the calculations used to estimate the fluxes and stocks of carbon (Fig. 2). The calculation steps used are conventional, i.e. first estimate (1) *GPP*, then (2) *NNCI* (net new carbon increment to the vegetation; *NNCI* is explained below), then (3) *NNCI*_{leaf}, then (4) *C*_{leaf}, then (5) *C*_{stemroot}. Step 1 involves the estimation of *GPP* by a transpiration–water use efficiency approach and has been described in detail in a companion paper (Berry and Roderick 2004). Generic allometric equations (Niklas and Enquist 2002) are used in Steps 3 and 5. The other main calculation Steps (2, 4) are novel implementations of conventional concepts. In Step 2, we assess evidence for, and then assume that, the *NNCI*:*GPP* ratio scales linearly with the annual mean fraction of the incident PAR absorbed by the canopy (\bar{F}_v). In Step 4, leaf longevity is assigned from the original definitions in the TMS scheme (Berry and Roderick 2002a, 2002b).

One key feature of the scheme is that very few additional data, beyond the estimates of TMS composition of the canopy, are necessary. For the implementation described here, changes in land use and [CO₂] (and any other possibility) are handled by starting with different estimates of TMS composition (see Berry and Roderick 2004). The calculations (Fig. 2) are done separately for each set of TMS estimates.

In the following sections, the model formulation for each step is described in more detail.

Estimating GPP via transpiration (Step 1, Fig. 2)

The method for estimating *GPP* from the transpiration flux is described in detail elsewhere (Berry and Roderick 2004). The basic steps are as follows. First, the net radiation flux is calculated by using global solar radiation, mean monthly maximum and minimum air temperatures, and vegetation cover (TMS). The transpiration flux is then estimated from the net radiation and vegetation cover (TMS). The *GPP* is then calculated from the transpiration flux, assuming that the water use efficiency of photosynthesis (*WUE*_{ph}) for the canopy is optimal, such that over periods of days to years, the amount of carbon assimilated

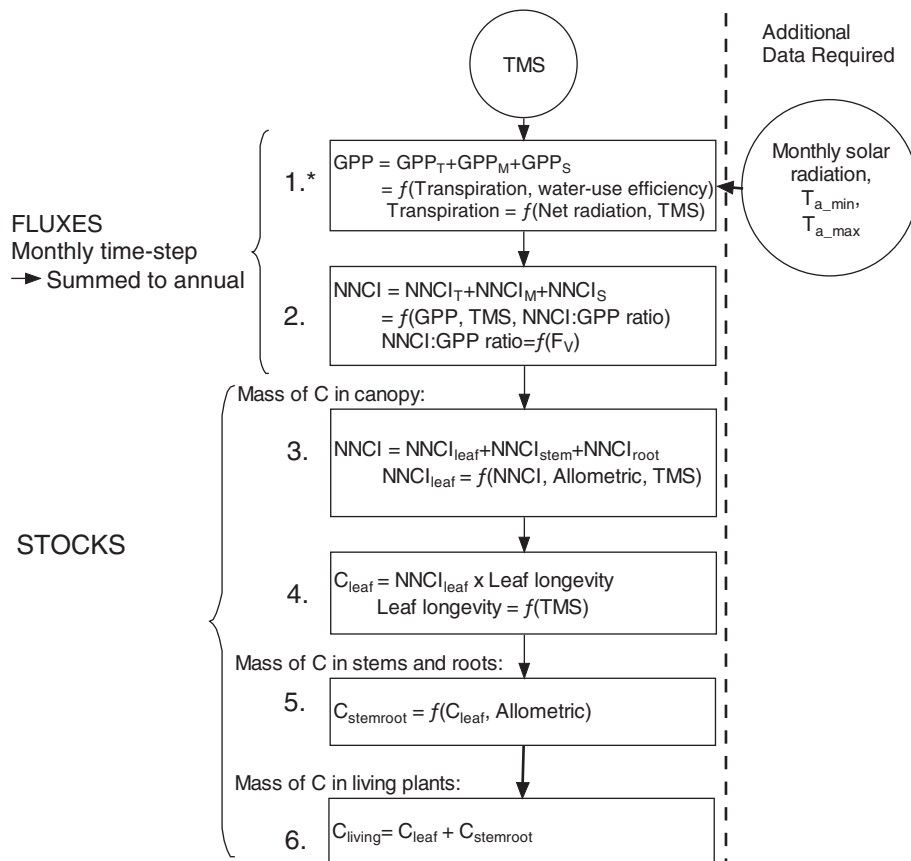


Fig. 2. Flow diagram summarising the TMSC model for estimating carbon fluxes and stocks. The input data required are estimates of the fractions of photosynthetically active radiation intercepted by T, M and S leaf functional types (input into Steps 1–4). The monthly solar radiation received at the surface and the monthly mean daily maximum and minimum air temperatures are input into Step 1 only. *GPP* is the gross primary productivity over the annual period, of T, M and S type leaves. *NNCI* is the net new carbon increment to the vegetation over the annual period; *C*_{leaf} is the carbon stock in the canopy; *C*_{stemroot} is the carbon stock in the stems and roots of the living vegetation; *C*_{living} is the carbon stock in the living vegetation. Asterisk indicates that the method for calculating this step is described elsewhere (Berry and Roderick 2004).

is maximised for a fixed amount of transpiration. Berry and Roderick (2004) estimated GPP as follows:

$$GPP \approx \frac{[CO_2]}{360} 3.79 E_{trans, yr} \text{ g C m}^{-2} \text{ year}^{-1},$$

where $E_{trans, yr}$ is the mass of transpired water ($\text{kg m}^{-2} \text{ year}^{-1}$) and $[CO_2]$ is the appropriate atmospheric concentration ($\mu\text{mol mol}^{-1}$).

Estimating $NNCI$: GPP ratio (Step 2, Fig. 2)

The net new carbon increment ($NNCI$) is that part of the GPP (integrated over the annual period) that is retained by the vegetation as new growth. The $NNCI$ is used to estimate the carbon stock in the canopy (Steps 3 and 4, Fig. 2). It is defined as follows:

$$NNCI = GPP - \left(R_a + \sum_i F_i \right) GPP, \quad (1)$$

where R_a is the proportion of GPP that is expended on autotrophic respiration, and F_i are proportions of GPP that are expended on various non-respiratory fluxes (away from the living vegetation), e.g. herbivory, root exudations, short-lived fine roots and root hairs, emission of volatile organic compounds, leaching and carbohydrate export to symbionts, which are summed to obtain the total over 1 year.

It is apparent from a review of the literature (see Appendix 1, available as an accessory publication on the web) that the ratio of $NNCI$: GPP varies with environmental conditions. To incorporate this variability we assume that this ratio is linearly related to \bar{F}_V , such that

$$\frac{NNCI}{GPP} = \frac{(0.70 - 0)}{(0.95 - 0)} \bar{F}_V = 0.737 \bar{F}_V. \quad (2)$$

In this equation, the ratio $NNCI$: GPP has a range from 0 (for an unvegetated surface having $\bar{F}_V = 0$) to 0.70 in environments most favourable to plant growth (having $\bar{F}_V = 0.95$). By using subscripts to denote the GPP for the three functional types (T, M, S), we have

$$NNCI_T = GPP_T(0.737 \bar{F}_V),$$

$$NNCI_M = GPP_M(0.737 \bar{F}_V) \quad \text{and}$$

$$NNCI_S = GPP_S(0.737 \bar{F}_V).$$

To evaluate this approach we compared our estimates of $NNCI$ with published estimates for a range of vegetation types. The ratio of $NNCI$: GPP (calculated with Equation 2) for six vegetation types representative of the continental vegetation cover is shown in Fig. 3. This ratio ranges from 0.58 in complex mesophyll closed forest to ~ 0 in regions having sparse, low chenopod shrubland and sparse, tall *Acacia* shrubland. For eucalypt forests (Fig. 3, eT3 and eM3) having foliage projective cover (FPC) of the upper canopy layer ranging from 30 to 70%, the calculated $NNCI$: GPP is mostly between 0.33 and 0.5, and similar to the values obtained independently for a variety of forest types (see Appendix 1).

Estimating the mass of carbon in the living vegetation (Steps 3–6, Fig. 2)

In this section we describe the method used to estimate the mass of carbon in the leaves, roots and stems of the living vegetation. The equations and input values required for this estimation are provided in Table 2. Partitioning the seasonally green canopy into woody deciduous and herbaceous components is shown in Table 2, Steps 1 and 2.

The canopy has an evergreen (M and S) component, and a seasonally green (T) component. The T component may be associated with herbaceous or woody stems and roots. Consequently, it must be apportioned between these two forms. These are identified in

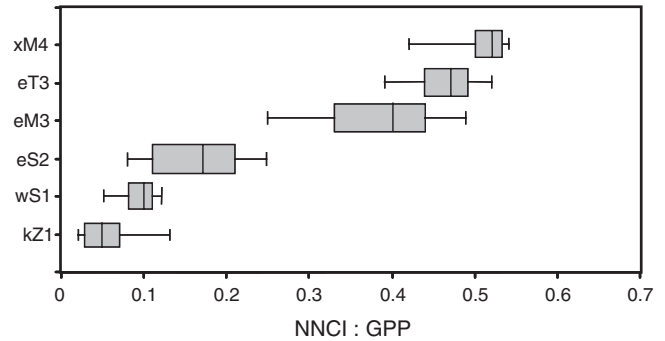


Fig. 3. Box plots showing the ratio of $NNCI$: GPP (Equation 2) for major Australian vegetation types as depicted by the present vegetation map (AUSLIG 1990); xM4, closed mesophyll forest (height of upper canopy layer, height 10–30 m; projective foliage cover (pfc) >70%); eT3, tall eucalypt forest (height >30 m; pfc 30–70%); eM3, medium eucalypt forest (height 10–30 m; pfc 30–70%); eS2, open eucalypt shrubland or mallee (height 3–10 m; pfc 10–30%); wS1, sparse open acacia shrubland (height 3–10 m; pfc <10%); kZ1, sparse open low chenopod shrubland (h <3 m; pfc <10%). The vertical line within a box indicates the median value and the box boundaries indicate the upper and lower quartile about the mean. Ninety-five per cent of data points occur within the range delimited by the whiskers.

Table 2 by the subscripts ‘T woody’ and ‘T herb’. To do this it is necessary to partition \bar{F}_T into woody ($\bar{F}_{T \text{ woody}}$) and herbaceous ($\bar{F}_{T \text{ herb}}$) components. For agricultural (herbaceous crop) land the value of $\bar{F}_{T \text{ woody}}$ is prescribed as zero. For non-agricultural land we assume that the proportion of \bar{F}_T that is woody will increase as the proportion of evergreen vegetation increases. The rationale for this assumption is that as the amount of evergreen cover increases, competition for light will increase and the T component will increasingly require woody stems to access light in the canopy.

Partitioning the $NNCI$ between the canopy and the stems and roots (Table 2, Step 3)

The flux of new carbon into the canopy ($NNCI_{\text{leaf}}$) is subsequently required, along with an estimate of leaf longevity (L_1), for the estimation of the mass of carbon in the canopy. We use allometric relationships, based on the work of Niklas and Enquist (2002) to partition the whole plant $NNCI$ into a leaf and a stem and root component. By using a large database (for trees) Niklas and Enquist (2002) estimated proportions of $NNCI$ forming new leaf, stem and root tissues for angiosperms (which we equate with mesic vegetation, i.e. M) and conifers (which we equate with sclerophyll vegetation, i.e. S). We assume that the partitioning of $NNCI$ between leaves and stems and roots of T vegetation is similar to that of sclerophyll vegetation. The rationale for this assumption is that (a) for the herbaceous T vegetation, most of the $NNCI$ is allocated to leaves and roots, as the stems are generally short and have little secondary cell-wall development and (b) for the woody T vegetation, the whole canopy must be renewed annually (compared with the partial canopy replacement in evergreens) (Kozlowski 1991), and the vascular system of deciduous trees is less extensive than that of evergreens (Waring 1991).

According to Niklas and Enquist (2002), the proportion of $NNCI$ ‘allocated’ to the leaves of angiosperm forest trees is 0.32, the remainder being allocated to the stems and roots. For coniferous forest trees, Niklas and Enquist (2002) recommend 0.44. Hence, the proportions of $NNCI_T$, $NNCI_M$ and $NNCI_S$ allocated to leaves in the TMSC model are 0.44, 0.32 and 0.44, respectively.

Table 2. Equations and input values used to estimate the C stock in the living vegetation for T, M and S leaf types (Steps 3–5, Fig. 2)

Step	Variable (unit)	Equation
1.	\bar{F}_T woody; \bar{F}_T herb	\bar{F}_T woody = $\bar{F}_T(1 - X_T)$; \bar{F}_T herb = $\bar{F}_T - \bar{F}_T$ woody
2.	X_T woody; X_T herb	X_T woody = $\frac{\bar{F}_T \text{ woody}}{\bar{F}_V}$; X_T herb = $\frac{\bar{F}_T \text{ herb}}{\bar{F}_V}$
3.	$NNCI_{\text{leaf}}$ (g C m ⁻² year ⁻¹)	$NNCI_{\text{leaf T woody}} = 0.48 NNCI_T \frac{X_T \text{ woody}}{X_T}$; $NNCI_{\text{leaf T herb}} = 0.48 NNCI_T \frac{X_T \text{ herb}}{X_T}$; $NNCI_{\text{leaf M}} = 0.32 NNCI_M$; $NNCI_{\text{leaf S}} = 0.48 NNCI_S$
4.	L_1 (year)	$L_{1T} = 1$; $L_{1M} = 1.5$; $L_{1S} = 6$
5.	C_{leaf} (g C m ⁻²)	$C_{\text{leaf T woody}} = L_{1T} NNCI_{\text{leaf T woody}}$; $C_{\text{leaf T herb}} = L_{1T} NNCI_{\text{leaf T herb}}$; $C_{\text{leaf M}} = L_{1M} NNCI_{\text{leaf M}}$; $C_{\text{leaf S}} = L_{1S} NNCI_{\text{leaf S}}$
6.	C_{stemroot} (g C m ⁻²)	$C_{\text{stemroot T woody}} = C_{\text{leaf T woody}} \left(19 \frac{X_M}{X_M + X_S} + 5 \right)$; $C_{\text{stemroot T herb}} = NNCI_T \frac{X_{\text{Therb}}}{X_T} L_{1T} - C_{\text{leaf T herb}}$; $C_{\text{stemroot M}} = 24 C_{\text{leaf M}}$; $C_{\text{stemroot S}} = 5 C_{\text{leaf S}}$
7.	C_{living} (g C m ⁻²)	$C_{\text{living}} = C_{\text{leaf}} + C_{\text{stemroot}} = C_{\text{leaf T woody}} + C_{\text{leaf T herb}} + C_{\text{leaf M}} + C_{\text{leaf S}}$ $+ C_{\text{stemroot T woody}} + C_{\text{stemroot T herb}} + C_{\text{stemroot M}} + C_{\text{stemroot S}}$
8.	CSI (g C m ⁻² year ⁻¹)	$CSI = \frac{C_{\text{living } t_2} - C_{\text{living } t_1}}{t_2 - t_1}$

Estimating the mass of carbon in the canopy (Table 2, Steps 4 and 5)

For each leaf type, the mass of carbon in the canopy is calculated as the product of the $NNCI_{\text{leaf}}$ and leaf longevity (L_1). L_1 is defined within the TMS scheme (Berry and Roderick 2002b). The longevity of T leaves is ≤ 1 year. In the TMS model L_{1T} is set at 1 year. The longevity of M leaves is between 1 and 2 years, and L_{1M} is set at 1.5 years in the TMS model. S leaves may have a longevity of ~ 3 to >40 years and Wright and Cannon (2001) estimated leaf longevities of up to 6 years for sclerophyll vegetation near Sydney, Australia. In the TMS model L_{1S} is set to 6 years.

Estimating the mass of carbon in the stems and roots (Table 2, Step 6)

According to Niklas and Enquist (2002) for every 1.0 unit mass of carbon in the canopy of angiosperm trees (which we equate with a typical eucalypt forest, 10–40 m tall, that intercepts $\sim 60\%$ of the incoming PAR and has a canopy mix of M : S leaf types in the ratio of $\sim 3 : 1$), there is, on average, 19 units mass of carbon in stem and root tissues. For conifers (which we equate with sclerophyll (S) vegetation), for every 1.0 unit mass of carbon in the canopy, there is, on average, 5 units mass of carbon in stem and root tissues. On the basis of these values, if the canopy comprises solely M type leaves and intercepts 75% or more of the incoming PAR, we would predict that there would be 24 units mass of carbon in the stem and root tissues for every 1.0 unit mass in the canopy. For deciduous woody vegetation we would expect the mass of carbon in the stems to decline with a decline in the fraction of PAR (\bar{F}_V) intercepted by woody vegetation, and decreasing canopy height as a consequence of decreasing competition for light, and limitations of resource availability that have resulted in the decline in \bar{F}_V . We assume that the ratio of canopy carbon mass : stem and root carbon mass of the deciduous woody vegetation is identical to the pixel average for the evergreen (M plus S) vegetation.

For herbaceous raingreen vegetation the maximum amount of carbon stored in the living tissues of stems and roots is the $NNCI_{\text{leaf T herb}}$ minus $NNCI_{\text{leaf T woody}}$ (as $L_{1T} = 1$ year).

Estimating the mass of carbon in the living vegetation (Table 2, Step 7)

The mass of carbon in the living vegetation (C_{living} , kg C m⁻²) is the sum of carbon in leaves, stems and roots of the T, M and S components.

Estimating the average annual increment to the carbon stock (Table 2, Step 8)

The carbon stock increment (CSI) is the average rate of change per annum of the mass of carbon in the living vegetation between two dates (t_1 and t_2).

TMS model scenarios

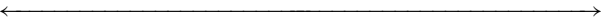
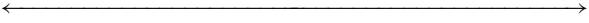

The $NNCI$ and C_{living} were estimated for the following three vegetation-[CO₂] scenarios: the present vegetation in 1988 with [CO₂] 350 $\mu\text{mol mol}^{-1}$ (pveg350), the hypothetical natural vegetation in 1988 (nveg350), and the natural vegetation in 1788 with [CO₂] 280 $\mu\text{mol mol}^{-1}$ (nveg280). Further details are provided in Table 3. The overall change in C_{living} from 1788 to 1988 is given by the difference between the pveg350 and nveg280 scenarios. Of that overall change, some is due to CO₂ and some to land use. The CO₂ effect was estimated as the difference between the nveg350 and nveg280 scenarios. The land use effect was calculated as the remainder.

Validation data

To validate estimates of the C stock in living forest vegetation we extracted model estimates from pixels identified as closed forest, tall open eucalypt forest and medium open eucalypt forest in the present vegetation map (AUSLIG 1990). We compare these estimates with values derived from the literature that are summarised in Tables A1–A3. To convert published values of above-ground drymass to C_{living} we assumed that carbon comprises 50% of the dry mass, and the shoot : root ratio of dry mass is 3 : 1 (based on Niklas and Enquist 2002).

Model estimates of C stocks in woodland vegetation were also compared with estimates from the TRAPS field study of Burrows *et al.* (2002). For that comparison we extracted model estimates for pixels

Table 3. Description of model scenarios and data sources
The nveg350 scenario represents a 'hypothetical' state of the vegetation in 1988 assuming no land clearing

Scenario	pveg350	nveg350	nveg280
Year	1988	1988	1788
Vegetation	Present	Hypothetical natural	Natural
[CO ₂] $\mu\text{mol mol}^{-1}$	350	350	280
Data source	10-year monthly time series of satellite-derived NDVI. Present vegetation map of Australia (AUSLIG 1990)	Natural vegetation map of Australia (AUSLIG 1990)	Derived from Nveg350 by using the TMS model to estimate the effect of reduced water use efficiency and nutrient use efficiency owing to the low [CO ₂], as described by Berry and Roderick (2002a)
Model variables	F_V, F_T, F_M, F_S derived directly from the NDVI data as described by Berry and Roderick (2002b)	F_V, F_T, F_M, F_S derived by converting existing vegetation maps into TMS maps in a GIS, as described by Berry and Roderick (2002a)	F_V, F_T, F_M, F_S derived from Nveg350 as described by Berry and Roderick (2002a, 2004)
Land-use change			
[CO ₂] change			
Land-use change + [CO ₂] change			

mapped (present vegetation map, AUSLIG 1990) as open eucalypt woodland (eM1) and eucalypt woodland (eM2) in the region bounded by 143.375°E–151.675°E and 18.225°S–27.675°S, corresponding to the TRAPS study region. In making those comparisons, the model was used to estimate $NNCI$ and C_{living} for pveg with [CO₂] 344 $\mu\text{mol mol}^{-1}$ and [CO₂] 366 $\mu\text{mol mol}^{-1}$ which corresponded to the [CO₂] during the period of data collection by the TRAPS program (see Appendix 2, available as an accessory publication on the web).

Results

Overall summary

Estimates of carbon fluxes and stocks for the continent under the three vegetation–[CO₂] scenarios are summarised

in Table 4, and Figs 4 and 5. To confirm the veracity of these estimates we compare them with published estimates and measurements from other studies. These comparisons are presented in Appendix 2. Although $\bar{F}_{V_{\text{nveg280}}}$ was 80% of $\bar{F}_{V_{\text{pveg350}}}$ (Berry and Roderick 2004), the $NNCI$ and the total carbon stock in living vegetation (C_{living}) for the nveg280 scenario were 52% and 49% of the pveg350 values, respectively. These correspond to $NNCI$ estimates of 0.85 and 1.62 Gt year^{-1} , and C_{living} estimates of 10.3 and 20.5 Gt , respectively, for nveg280 and pveg350. Hence, the doubling of C_{living} over the last 200 years for the Australian continent means an average rate of increase in C_{living} (carbon stock

Table 4. Estimated carbon fluxes and stocks in Australia for the present vegetation at [CO₂] 350 $\mu\text{mol mol}^{-1}$ and the natural vegetation at 350 $\mu\text{mol mol}^{-1}$ and 280 $\mu\text{mol mol}^{-1}$

Vegetation (CO ₂ $\mu\text{mol mol}^{-1}$)	Seasonality	GPP (Gt C year ⁻¹)	NNCI (Gt C year ⁻¹)	C in canopy (Gt)	C in stems and roots of living vegetation (Gt)	Total C in living vegetation (Gt)
350, present vegetation	Raingreen (T)	2.90	0.31 herbaceous 0.35 woody	0.15 herbaceous 0.17 woody	0.16 herbaceous 1.29 woody	0.31 1.46
	Evergreen (M+S)	3.59	0.96	1.56	17.19	18.75
	Total (T+M+S)	6.49	1.62	1.88	18.64	20.52
350, natural vegetation	Raingreen (T)	2.44	0.16 herbaceous 0.36 woody	0.08 herbaceous 0.17 woody	0.08 herbaceous 2.06 woody	0.16 2.23
	Evergreen (M+S)	3.88	1.05	1.71	19.75	21.46
	Total (T+M+S)	6.32	1.57	1.95	21.89	23.85
280, natural vegetation	Raingreen (T)	2.35	0.18 herbaceous 0.26 woody	0.09 herbaceous 0.12 woody	0.10 herbaceous 1.57 woody	0.19 1.69
	Evergreen (M+S)	1.92	0.41	0.68	7.77	8.45
	Total (T+M+S)	4.27	0.85	0.89	9.44	10.33

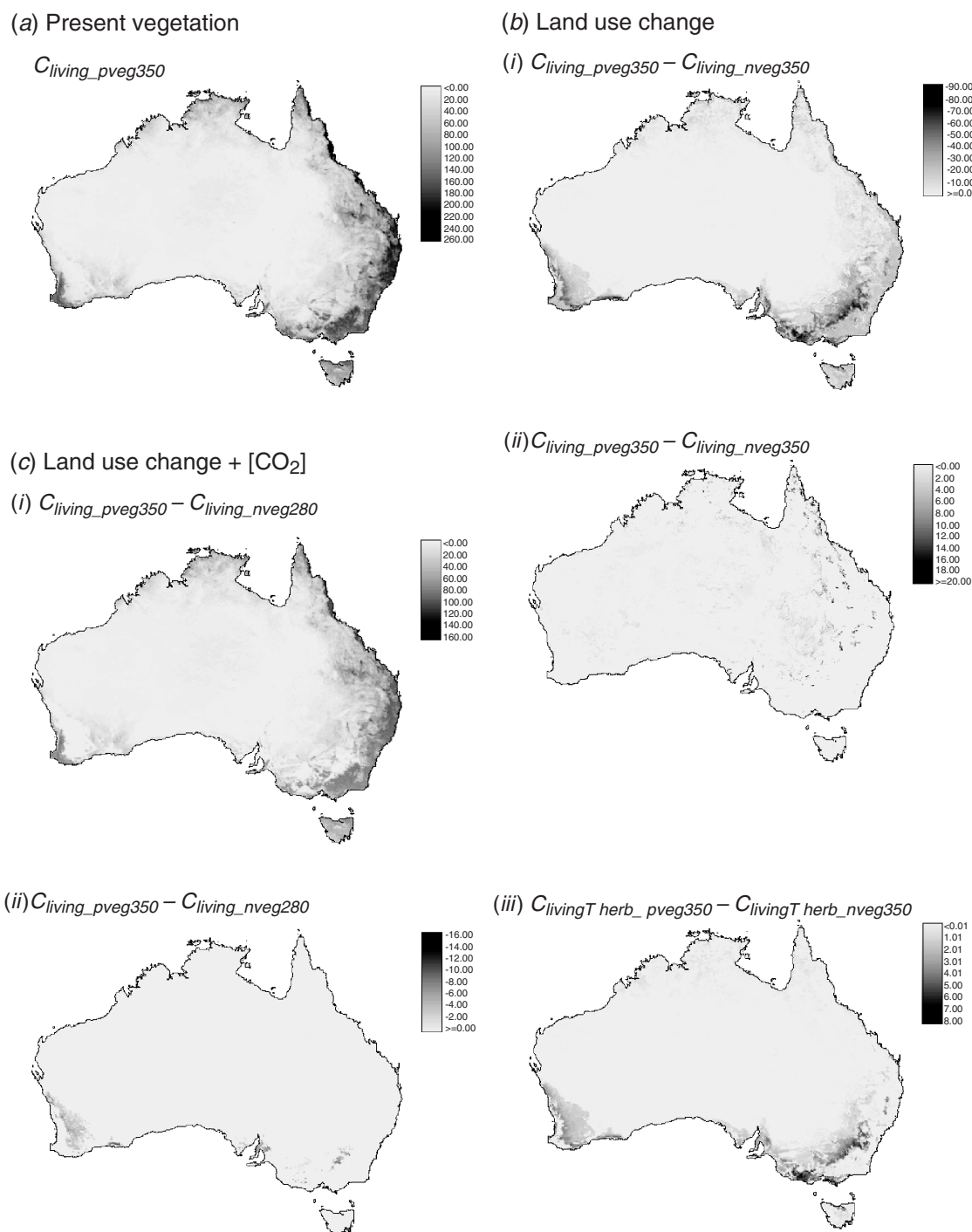


Fig. 4. (a) TMSC model estimates of the mass of carbon in living vegetation (tC ha^{-1}) with present vegetation at $[\text{CO}_2]$ $350 \mu\text{mol mol}^{-1}$ ($C_{\text{living_pveg350}}$). (b) TMSC model estimates of the effect of land-use change on C_{living} shown as the difference ($C_{\text{living_pveg350}} - C_{\text{living_nveg350}}$). (i) The negative values indicate a reduction in C_{living} (tC ha^{-1}) resulting from land-use change. Positive values indicate an increase in C_{living} (tC ha^{-1}) resulting from land-use change for (ii) all components and (iii) the herbaceous T component ($C_{\text{livingT herb_pveg350}} - C_{\text{livingT herb_nveg350}}$). (c) TMSC model estimates of the net effect of land-use change and the increase in $[\text{CO}_2]$ since 1788 on C_{living} ($C_{\text{living_pveg350}} - C_{\text{living_nveg280}}$): (i) increased C_{living} and (ii) decreased C_{living} (tC ha^{-1}).

increment, denoted CSI) of 51 MtC year^{-1} . In comparison, the $NNCI$ and C_{living} for the nveg350 were $1.57 \text{ Gt year}^{-1}$ and 23.9 Gt . Thus, the $[\text{CO}_2]$ effect over the last 200 years

was estimated to be much larger than the reduction owing to land use. In the following sections we discuss the results in more detail.

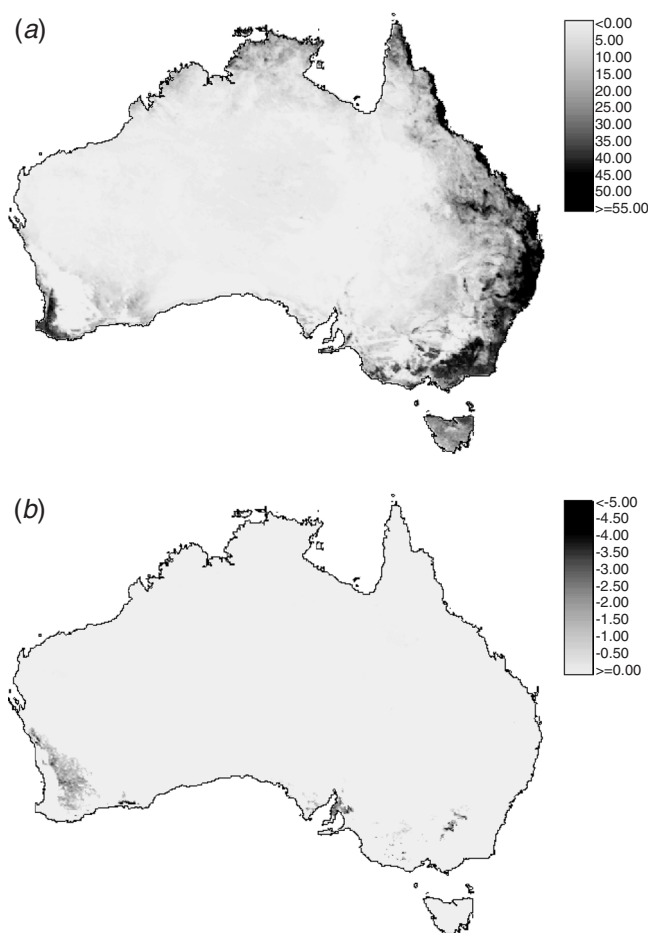


Fig. 5. Map showing estimated CSI ($\text{g C m}^{-2} \text{ year}^{-1}$) over Australia across 200 years (from 1788 to 1988, i.e. $C_{\text{living_nveg280}}$ to $C_{\text{living_pveg350}}$). (a) Pixels showing a positive CSI across 200 years. (b) Pixels showing a negative CSI across 200 years. Living and dead trees for 57 sites.

Effect of increasing $[CO_2]$ since 1788

The effect of increasing $[CO_2]$ from 1788 to 1988 is represented by the difference between the nveg280 and the nveg350 scenarios (Table 4). C_{living} for the nveg280 scenario is 43% of that estimated for nveg350. This smaller C_{living} in 1788 is entirely attributable to a smaller store of carbon in woody vegetation. Although C_{living} of the total woody (M + S + woody T) component was reduced in the nveg280 scenario, a greater amount of it (17%) is due to the presence of deciduous trees and/or shrubs (woody T), in contrast to nveg350 (9%). The herbaceous T component of C_{living} for the nveg280 scenario is 19% larger than that for nveg350.

The relative reduction in the flux components and the carbon stock resulting from a reduction in $[CO_2]$ (i.e. differences between nveg scenarios) from 350 to $280 \mu\text{mol mol}^{-1}$ show a sequential increase from \bar{F}_V (reduced by 20%) > GPP (33%) > $NNCI$ (46%) > C_{living} (57%) (Table 4). This is a consequence of flow-on effects

of allocation, reflecting interactions between the vegetation, the climate, the soil and the atmosphere. In the TMSC model, \bar{F}_V is prescribed, decreasing linearly with decreasing $[CO_2]$ as discussed by Berry and Roderick (2002a). As \bar{F}_V decreases (with decreasing $[CO_2]$) its seasonal variability increases. This is manifested as an increase in X_T and a decrease in X_M and X_S . The reduction in overall greenness (i.e. \bar{F}_V), and the total amount of light intercepted by the canopy, combined with the reduced WUE_{ph} at reduced $[CO_2]$ result in the proportionately lower GPP for the nveg280 scenario. Because the reduced $[CO_2]$ environment is less favourable for plant growth, a larger proportion of the GPP is expended on respiration and fluxes of carbon away from the plant (see Equation 1) thus the ratio of $NNCI : GPP$ is reduced. Finally, the reduced $NNCI$, and canopy cover lead to a concomitant reduction in stem and root carbon stock. These outcomes would be manifested in the woody vegetation by a reduced basal area of stems, and shorter stems comprising wood having a lower mass of dry matter per unit fresh volume (Roderick and Berry 2001; Atwell *et al.* 2003). Associated with the change in conditions there would be a change in the competition dynamics and hence the relative abundance of species within a study site or pixel.

Effect of land-use change

The effect of land-use change on $NNCI$ and C_{living} , quantified as the difference between pveg350 and nveg350 scenarios, is summarised in Table 4 and Fig. 4b. It is estimated that C_{living} for pveg350, summed over the continent is 20.5 Gt, approximately 3.3 Gt less than the value for the nveg350 scenario. This difference, shown in Fig. 4b, is to be expected because of the conversion of native vegetation (mostly M and S leaves) to agricultural crops (herbaceous T leaves), with the concomitant application of fertiliser and/or irrigation. The estimated GPP and $NNCI$ of pveg350 and nveg350 (Table 4, 'Total T+M+S') are more or less identical. However, $C_{\text{living_nveg350}}$ is greater than $C_{\text{living_pveg350}}$ for most pixels as the hypothetical 'natural' vegetation has a larger evergreen component, and hence the longevity of the carbon is greater.

Net effect of increasing $[CO_2]$ and land-use change

The predicted change in the vegetation from 1788 to 1988 is represented by the difference between the pveg350 and nveg280 scenarios (Table 4, Fig. 4c). According to the TMSC model the continental carbon stock in living vegetation, C_{living} , has increased from $\sim 10 \text{ Gt C}$ in 1788 to $\sim 20 \text{ Gt C}$ in 1988. Thus, the carbon stock increment, CSI , averaged over this period is about $51 \text{ Mt C year}^{-1}$ for the continent. At smaller spatial scales, this increment is negative (about $-4 \text{ g C m}^{-2} \text{ year}^{-1}$) in regions where woody vegetation has been extensively cleared for agriculture. Elsewhere, the CSI ranges from $\sim 55 \text{ g C m}^{-2} \text{ year}^{-1}$ in tropical and subtropical forests, to ~ 0 in the most arid parts of Australia (Fig. 5). However, as $[CO_2]$ has increased more rapidly in the last

50 years than in the previous 150 years, the *CSI* averaged over the last five decades would presumably be greater than the mean value for the last 200 years.

Discussion

According to the TMS model the Australian vegetation has changed a great deal since European settlement in 1788. Two opposing forces have been at work. The increasing $[\text{CO}_2]$ has acted to increase the water-use efficiency of photosynthesis and, consequently, increase C_{living} in woody vegetation over the entire continent, while humans have acted to reduce C_{living} in woody vegetation and increase the productivity of the herbaceous annual vegetation over parts of the continent. The net effect is an estimated doubling of C_{living} over the continent since 1788. Hence, the TMS model generally predicts a more open and grassy vegetation cover in 1788. That the vegetation was more open and grassy in 1788 is widely accepted, and the current paradigm is that it was maintained in that state through the frequent application of fire by humans, and that a change in the fire regime has resulted in the increase in C_{living} . However, according to the TMS model, the increasing $[\text{CO}_2]$ would be a very important factor contributing to the increase in C_{living} over the last 200 years.

The utility of models, such as the TMS model, comes from their capacity to provide insights into complex systems through simplification, and the capacity to explore change over large spatial and temporal scales. This simplification necessitates the utilisation of suitable input data to meet the spatial and temporal data requirements of the model,

along with a number of assumptions about the system being modelled. The TMS-model approach to estimating carbon stocks and fluxes uses readily available satellite and climate data. The agreement with estimates from other independent sources (see Appendix 2) is encouraging, as we made no attempt to tune the model. The assumptions made in the model are summarised in Table 5.

The most sensitive part of the model is the allometric relationship linking the leaf to stem and root carbon (Table 2, Step 6). Fundamental to the use of the allometric approach is the assumption that the mass of carbon in the wood accumulates in proportion to the mass of carbon in the canopy. This places a limitation on the maximum mass of carbon that can be predicted for a pixel. In the most mesic forests, according to the allometric, the canopy will contain 4.2% of the carbon. As the mass of carbon in the canopy decreases, the proportion of the carbon that is in the canopy increases. This generalisation appears to be reasonable when considering large patches of the landscape, but does not hold at the site scale for forest types with very large trees, e.g. *Eucalyptus regnans* forests in Australia. The trees in these forests typically attain a height of 55–75 m and the diameter at breast height of mature trees is ~2.5 m. The crown, which comprises the upper third of the stem is open and relatively small (Boland *et al.* 1984). In these open forests the canopy may comprise only 1% or less of the carbon stock in the trees. Consequently, the allometric will underestimate the stock in these forests.

According to the TMS model there has been a large effect of increasing $[\text{CO}_2]$ on the vegetation over the past 200 years.

Table 5. Overview of assumptions of the model

Formulation of model/assumptions made to implement the model	Relationship	Comment
<i>NNCI/GPP</i> increases with increasing resource availability	Equation 3	This recognises that as resource availability decreases, a larger proportion of assimilated C will be required to maintain the vegetation and the animals that feed on it
The proportion of the T component of the canopy in non-agricultural pixels that belongs to deciduous woody plants increases as the evergreen vegetation cover increases	Table 2, Step 1	As the amount of evergreen cover increases, competition for light will increase and the T component will increasingly require woody stems to access light in the canopy
The relationship between the proportions of evergreen leaves that are M or S, and the proportion of <i>NNCI</i> that is allocated to the canopy is linear	Table 2, Step 3	A fundamental assumption of this approach is that the vegetation becomes more mesic, and taller, as resource availability increases. Thus, more C will be allocated to connecting the water supply (in the soil) to the light supply in the canopy
The proportion of <i>NNCI</i> that is allocated to the canopy of T leaves is the same as for S leaves	Table 2, Step 3	Herbaceous T vegetation comprises mostly canopy and roots
Leaf longevity of evergreen leaves increases linearly with the proportion of evergreen leaves that are S	Table 2, Step 5	Fundamental assumption of the TMS scheme
The relationship between C_{stemroot} and C_{leaf} is linear	Table 2, Step 6	According to the allometric used in the TMS model, the ratio of $C_{\text{leaf}} : C_{\text{stemroot}}$ has a minimum value of 4 : 96. This will result in an underestimation of C_{living} for very large trees (e.g. mature stands of <i>Eucalyptus regnans</i>)

This is manifested as an increase in gross photosynthesis (Berry and Roderick 2004), and a proportionally larger increase in the stock of carbon in the living vegetation. Field data also show increases in woody vegetation cover, and a change in the carbon stock in living vegetation over recent decades has been reported for several woodland environments in Australia and elsewhere (e.g. Bowman *et al.* 2001; Burrows *et al.* 2002; Asner *et al.* 2003; Sharp and Whittaker 2003; Fensham *et al.* 2005). However, this increase has generally been attributed solely to changes in land use, such as release from extreme overgrazing by cattle and consequent land degradation, resulting in the replacement of grass with shrubs (Sharp and Whittaker 2003), or changes in the fire regime (e.g. Burrows *et al.* 2002), or to changes in rainfall (Fensham *et al.* 2005). Nonetheless, just because these changes in land use and rainfall are happening does not mean that the increase in [CO₂] has no effect on the vegetation.

Prior to attributing causal factors for vegetation thickening at a site, all possibilities need to be considered. In the context of the TMSC model, the carbon stock in living vegetation is a function of both the net flux (*NNCI*) and the longevity, and the stock may change because of changes in the flux and/or longevity. For example, *NNCI* for the vegetation may remain constant, but the longevity could increase because a greater portion of the carbon may accumulate in long-lived, woody plant tissues, so that there is less *NNCI* contributing to the high-turnover, short-lived tissues on which livestock graze. This requires a shift in utilisation of available resources (i.e. water, mineral nutrients, CO₂) from herbaceous to woody vegetation (i.e. reduced disturbance, see Berry and Roderick 2002a). Alternatively, the *NNCI* for the vegetation may decline, while the longevity of the woody plant tissues increases proportionally more. This implies a shift from turgor and mesic to sclerophyllous foliage, and an associated increase in the C : N ratio of the vegetation, associated with land degradation and nutrient loss from the soil. A third possibility is that there is an increase in *NNCI*, while longevity remains near constant, which would result in more foliage and more woody tissues. This would be associated with increased availability of resources for plant growth. In grazing lands all of these possibilities may affect the vegetation at a site, and it is difficult to separate these effects. Nevertheless, the net effect according to the TMSC model is an increase in the carbon stock in the living vegetation. In terms of carbon accounting, this does not mean that Australia is a 'carbon sink'. That also depends on the dynamics of the carbon stock in the soil, and this is presently an unknown quantity at the continental scale.

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Appendix 1. The relationship between the *NNCI* and *NPP***Appendix 2. Validation of model estimates**

These Appendices, and associated tables and figures, are available as accessory publications on the web. Please go to the issue contents page www.publish.csiro/nid/66/issue/1416.htm, and click on the Appendix links.