Agricultural legacy, climate, and soil influence the restoration and carbon potential of woody regrowth in Australia

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Abstract. Opportunities for dual restoration and carbon benefits from naturally regenerating woody ecosystems in agricultural landscapes have been highlighted recently. The restoration capacity of woody ecosystems depends on the magnitude and duration of ecosystem modification, i.e., the "agricultural legacy." However, this legacy may not influence carbon sequestration in the same way as restoration because carbon potential depends primarily on biomass accumulation, with little consideration of other attributes and functions of the ecosystem. Our present study simultaneously assesses the restoration and carbon potential of *Acacia harpophylla* regrowth, an extensive regrowth ecosystem in northeastern Australia. We used a landscape-scale survey of *A. harpophylla* regrowth to test the following hypotheses: (1) management history, in combination with climatic and edaphic factors, has long-term effects on stem densities, and (2) higher-density stands have lower restoration and carbon potential, which is also influenced by climatic and edaphic factors. We focused on the restoration of forest structure, which was characterized using stem density, aboveground biomass, stem heights, and stem diameters. Data were analyzed using multilevel models within the hierarchical Bayesian model (HBM) framework. We found strong support for both hypotheses. Repeated attempts at clearing Brigalow (*A. harpophylla* ecosystem) regrowth increases stem densities, and these densities remain high over the long term, particularly in high-rainfall areas and on gilgaied, high-clay soils (hypothesis 1). In models testing hypothesis 2, interactions between stem density and stand age indicate that higher-density stands have slower biomass accumulation and structural development in the long term. After accounting for stem density and stand age, annual rainfall had a positive effect on biomass accumulation and structural development. Other climate and soil variables were retained in the various models but had weaker effects. Spatial extrapolations of the HBMs indicated that the central and eastern parts of the study region are most suitable for biomass accumulation; however, these may not correspond to the areas that historically supported the highest biomass Brigalow forests. We conclude that carbon and restoration goals are largely congruent within areas of similar climate. At the regional scale, however, spatial prioritization of restoration and carbon projects may only be aligned where carbon benefits will be high.

Key words: Acacia harpophylla; *Brigalow regrowth; carbon sequestration potential; hierarchical Bayesian models; landscape restoration; multilevel models; pastoralism; Queensland, Australia.*

Introduction

The world's agricultural landscapes are highly fragmented and the integrity of remaining forest fragments is jeopardized by ongoing direct (e.g., over-grazing, Augustine and Frelich 1998) and indirect (e.g., altered fire regimes, D'Antonio and Vitousek 1992) threats. However, the area of abandoned agricultural land is increasing globally (Ramankutty and Foley 1999) and woody vegetation is recolonizing many formerly forest-ed areas (Aide and Grau 2004, Lugo and Helmer 2004). Naturally regenerating woody vegetation, or woody regrowth, can provide important habitat for native fauna in fragmented landscapes (Castellon and Sieving 2006, Bowen et al. 2007, 2009) and represents an efficient means to reinstate habitat connectivity and increase forest area (Stouffer et al. 2006). Many regrowth ecosystems also sequester substantial amounts of atmospheric CO_2 and thus have considerable potential as land-based carbon sinks (Silver et al. 2000, Feldpausch et al. 2004).

However, in terms of restoration and carbon potential not all regrowth is equal, even within the same ecosystem. Often a gradient of potential exists that is strongly related to climatic and environmental conditions as well as the duration and intensity of previous

land uses, i.e., the biotic and abiotic legacy (Hobbs and Harris 2001, Cramer et al. 2008). Also, carbon and restoration goals may not be congruent. The main goal of land-based carbon sinks is to maximize the total amount of carbon that can be sequestered by a system over a specified period. The species composition, forest structure, and habitat values of the system may be irrelevant. So, if we want to seize opportunities to restore regrowth via carbon investment (Fensham and Guymer 2009) it is important to choose regrowth ecosystems for which carbon and restoration goals can be aligned.

Despite recent comment papers on the need to reconcile restoration and carbon sequestration goals (Bekessy and Wintle 2008, Dwyer et al. 2009), broad-scale case-studies have not yet been conducted. Prioritization of restoration and carbon sequestration projects requires that the goals be statistically or mechanistically correlated with site- and landscape-scale predictors. Multilevel modeling techniques have been recently applied in ecology (Buckley et al. 2003, McMahon and Diez 2007) and are ideal for exploring relationships between responses and predictors at multiple scales. The resulting models can be used to predict where, in a spatially heterogeneous landscape, activities are most likely to meet management goals. Here we present an empirical study assessing restoration and carbon sequestration goals of woody regrowth at a landscape scale. We use the case study of *Acacia harpophylla* F. Muell regrowth in northeastern Australia to assess its potential to sequester carbon and provide biodiversity benefits in a heavily fragmented agricultural landscape.

"Brigalow" is the term applied to both *A. harpophylla* and to the forests and woodlands in which it is dominant or codominant. Prior to European settlement these forests and woodlands covered ~7.5 million ha, but 90% have since been cleared (Accad 2001) and converted to agricultural land uses. Despite the fervor of agricultural development, Brigalow regrowth persists due mainly to *A. harpophylla*'s capacity to resprout from root suckers (Johnson 1964). It is estimated to cover at least 280 000 ha throughout its former range (Butler 2009).

A conflict may exist between carbon and restoration goals for Brigalow regrowth that relates to stem density (Dwyer et al. 2009). Following clearing, *A. harpophylla* suckers can emerge at a range of densities, but are often many times denser than the original mature forest (e.g., 25 000 stems/ha compared to 3000 stems/ha). Due to the larger number of growing stems in dense stands they produce more biomass than lower density regrowth, at least in the medium term (0–30 years, limit of available empirical data). However, the restoration of structural attributes (e.g., diameter size-class distribution, stem density) and floristic composition tends to be far slower in dense stands (Chandler et al. 2007). This apparent conflict may, however, diminish over longer time periods.

In order to examine carbon and restoration potential, it is first necessary to adopt suitable goals. Given the large geographic range of Brigalow ecosystems and the variation in floristic assemblages throughout, we chose to focus only on the restoration of structure, which we characterized using multiple structural variables. Regrowth structure influences the diversity and abundance of woodland-dependent birds (Bowen et al. 2009) and is also likely to influence rates of plant species' recruitment (Dwyer et al. 2010). We adopted the following restoration goal: *To develop structure and biomass comparable to mature reference ecosystems in the fastest possible time*. Setting the carbon goal was not so straightforward. The potential conflict between carbon and restoration goals mentioned above underscores the need to clarify the temporal scale, which for carbon will correspond to the crediting lifetime used to calculate credits (OECD 2007). In Australia, carbon permits from accredited reforestation projects will be calculated based on the "total projected net greenhouse gas removals over the long term" (see Carbon Pollution Reduction Scheme White Paper, pages 6–56; Australian Government Department of Climate Change 2008). Therefore, we adopted the following carbon goal: *To maximize the amount of living aboveground biomass accumulated over the next 100 years*. This 100-year period is somewhat arbitrary, but it is likely that living aboveground biomass accumulation in regrowth stands will become asymptotic within this period. Because the upper age limit of regrowth in the present study was 53 years, we considered both the amount of biomass accumulated within 53 years and also the relative rates of accumulation to provide evidence of carbon potential over 100 years.

Based on these restoration and carbon goals, our two hypotheses were (1) management history, in combination with climatic and edaphic factors, has long-term effects on stem densities and (2) higher-density stands have lower restoration and carbon potential, which are also influenced by climatic and edaphic factors. We sampled regrowth across different management histories and climatic and edaphic conditions. Multilevel models within a hierarchical Bayesian framework are used in a two-step process to test the two hypotheses. These models are also used to identify regions that have the most suitable climate and geomorphology for structural development and biomass accumulation. Finally, we synthesize the results from all models to provide recommendations for assessing the carbon and restoration potential of Brigalow regrowth.

METHODS

Study ecosystem

Brigalow ecosystems occur mainly on fertile deep clay soils that commonly exhibit pronounced mounds and depressions (termed "gilgais"). Mature Brigalow forests were mainly cleared after World War II using the "pulling" method whereby an oversized chain was dragged between two bulldozers to clear large areas of
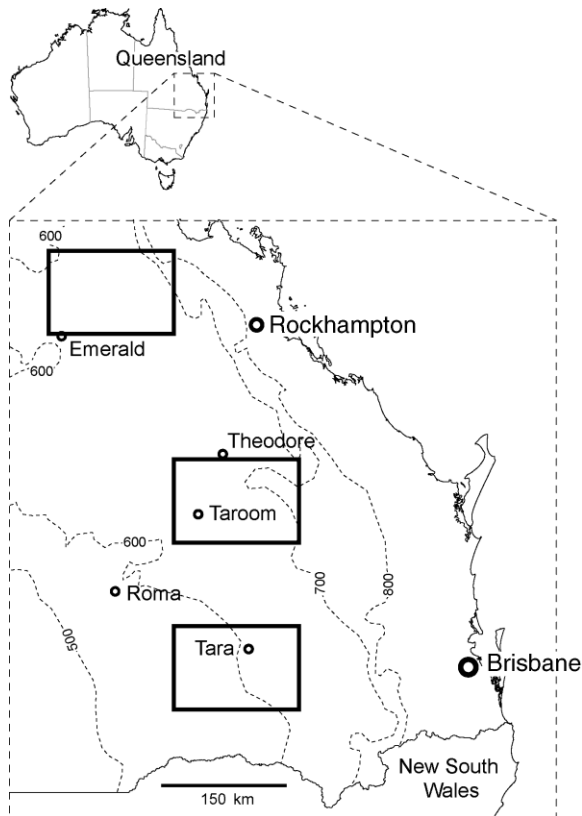
Fig. 1. National and regional context of the three 100×150 km study blocks (black rectangles) for Brigalow regrowth sampling in Queensland, Australia. Dotted lines are annual rainfall isohyets (in millimeters per year). "Brigalow" is the term applied to both *Acacia harpophylla* and to the forests and woodlands in which it is dominant or co-dominant.

forest. The woody debris was then left to dry and later burned before sowing pasture or commencing cultivation (Johnson 1964). However, root systems of the original vegetation remained somewhat intact, allowing species such as *Acacia harpophylla* and *Citrus glauca* (Lindl.) Burkill to resprout, often at densities that compromised pasture establishment. In pre-European times, fire was presumably rare in mature Brigalow forests due to very sparse grass cover (Nix 1994). Following widespread pastoral development, more open Brigalow ecosystems (both mature and regrowth), have become prone to invasion by exotic grass species, particularly buffel grass (*Pennisetum ciliare* (L.) Link). Exotic grass invasion increases fuel loads and promotes more frequent, hotter fires, which kill native woody stems and facilitate further grass invasion (Butler and Fairfax 2003).

Study design and data collection

A 2004 map of the extent of Brigalow regrowth was used to delineate suitable locations for sampling (Butler 2009). A minimum polygon size of 10 ha was applied to allow replicated sampling over a uniform area. In order to efficiently sample regrowth across the bioregion, we chose three blocks (100×150 km; Fig. 1), which covered most of the latitudinal variation and more than half of the longitudinal variation in the bioregion.

To select sampling locations we used the Survey Gap Analysis Tool developed by the New South Wales Department of Environment and Climate Change (NSW NPWS 1998, Ferrier 2002). The tool was run separately for each block in ArcView 3.3 (ESRI 2002) with four bioclimatic inputs: mean annual rainfall, rainfall variability, temperature seasonality, and maximum summer temperature (Houlder et al. 2000). In total, 60 suitable and accessible sites were sampled. An additional 11 sites in mature forests were sampled opportunistically throughout the study region to provide estimates for reference forests.

At each site four, 50-m transects were established no closer than 50 m apart within the selected polygon. In most cases two transects were run north–south and two were run east–west to avoid sampling along natural patterns such as linear gilgais. The width of transects was consistent within sites, but varied between sites depending on the density of stems encountered (the aim was to sample ~400 stems per site). Along each transect, the species and diameter (30 cm aboveground) of each stem was recorded. At 2-m intervals along the transect, canopy, shrub, and ground cover were recorded (point-intercept method) and the height of canopy trees was measured using a laser range finder (Impulse 200; LaserTechnology, Centennial, Colorado, USA). When assessing canopy cover, the tree crown area was taken as the area within the minimum convex polygon around the outer living and dead branches of the tree (following Fensham and Fairfax 2007). Gilgai development was measured in centimeters as the difference between the highest and lowest points along each transect. Two surface soil samples (5–10 cm depth, ~250–400 g each, leaf litter excluded) were collected along each transect, one at 25 m and the other at 50 m.

Soil samples were analyzed to obtain particle-size distributions using a laser diffractometer particle-size analyzer (Mastersizer 2000; Malvern Instruments, Malfern, Worcestershire, UK). The two samples per transect were mixed thoroughly, sieved (2 mm), and pretreated to remove organic matter and salts (following Bowman and Hutka [2002]). They were then dispersed in a solution of 5.5 g/L sodium hexametaphosphate for 24 h. Just prior to measurement, samples were sonicated for one minute at 10-μm tip displacement to break up remaining aggregated particles. Absorption was maintained between 15% and 20% during particle-size measurement. The output for each sample was a continuous particle-size distribution, which was converted to a ratio of clay (particles < 0.002 mm) to sand (0.02–2 mm) as a measure of soil texture.

Where possible, a management history for each site was obtained from the property owner or manager. This was a list of dates of clearing and control events (from initial
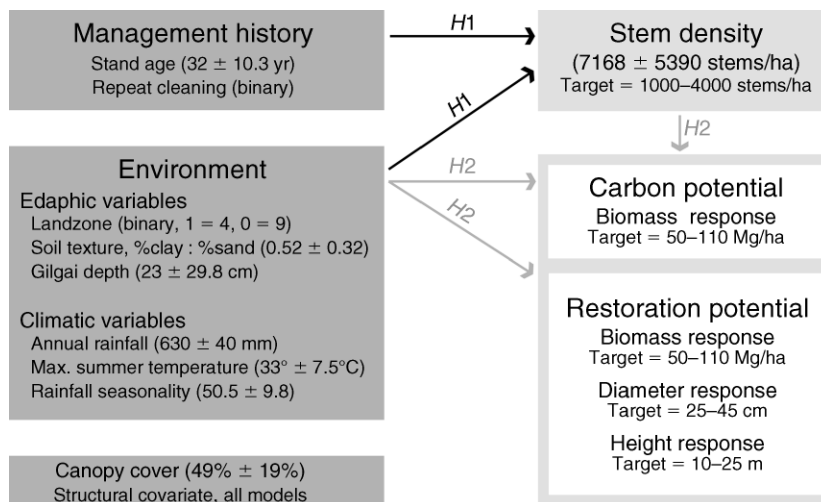
Fig. 2. Conceptual representation of the approach used to address hypotheses 1 (H1) and 2 (H2). Dark gray boxes indicate explanatory variables, and white boxes indicate response variables. Stem density is included in a light gray box because it served as both a response and an explanatory variable in the various models. Values in parentheses are the mean ± SD of each explanatory variable. The target values indicate ranges for each response that have been reported for mature Brigalow ecosystems. For "soil texture" each soil sample was divided into clay, silt, and sand percentages (summing to 100%); the silt component of each sample was ignored, and the clay and sand percentages were expressed as a ratio; the mean ratio of all samples is reported. Hypotheses definitions: H1 indicates management history, in combination with climatic and edaphic factors, has long-term effects on stem density; H2 indicates higher-density stands have lower restoration and carbon sequestration potential, which are also influenced by climatic and edaphic factors.

forest conversion onwards) and corresponding clearing methods. In cases where the current owners could not provide a full management history, historical aerial photography was inspected to determine the initial clearing date and method (e.g., pulling has an obvious photo signature), the number of subsequent control events, and the current age of the regrowth patch. The accuracy of these dates depended on the frequency of aerial photo runs over a particular site, but in general, runs were available for each decade since initial clearing and in many cases it was possible to detect if the clearing was recent (e.g., clearing was in progress or unburned log piles were visible). To our knowledge, none of the sites included in the final data set had been burned since the emergence of the current cohort of suckers. Because detailed management histories were lacking for some sites, all management history data were summarized into two variables—stand age (years since the last control event) and whether the site had been cleared repeatedly (binary). These variables were correlated because sites that had been cleared repeatedly were mostly under 30 years old. To reduce this correlation, sites younger than 12 years were excluded, leaving 50 sites in the final data set.

The "landzone" of each site was obtained from Queensland Government Regional Ecosystem mapping (DERM 2007). Landzones describe the geomorphologic situations that are typical for a particular ecosystem. In our study, Brigalow regrowth was sampled mainly on landzone 4 ("flat to gently undulating Tertiary clay plains") and landzone 9 ("gently undulating landscapes on more or less horizontally bedded fine grained

sedimentary rocks"). Only two sites occurred on other landzones and so we created a binary variable of landzone 4 (1) and "other landzones" (0). This variable can be approximately interpreted as landzone 4 or 9.

Statistical modeling

Four response variables were selected to collectively describe forest structure and aboveground biomass accumulation: (1) density of living woody stems ("stem density"), (2) living aboveground biomass ("biomass"), (3) diameter of the largest living *A. harpophylla* stem ("diameter"), and (4) height of the tallest living *A. harpophylla* stem ("height"). We tested hypothesis 1 (H1) by developing the "stem-density model" in which stem density was modeled as a function of management history and environmental variables. Hypothesis 2 (H2) was tested using the "biomass," "diameter," and "height" models in which these response variables were modeled as a function of stem density and environmental variables (Fig. 2). Two-way interactions between most explanatory variables were considered for inclusion in each model. Due to the correlation between stand age and repeat clearing (the management-history variables) we did not attempt to fit an interaction between these two terms in the stem-density model. Such an interaction would have described patterns in the data that were artifacts of land-management trends over the past 53 years, rather than actual biological trends. Interactions between binary variables were also excluded due to zero inflation. Canopy cover was included as a covariate in all models because we were interested in

potential interactions between it and other variables. Canopy cover was not significantly correlated with any of the environmental variables or repeat clearing, though it was mildly correlated with stem density (Spearman's correlation test, $\rho = 0.40$, $P < 0.001$) and stand age ($\rho = 0.22$, $P = 0.002$). We permitted interactions between these mildly correlated terms.

The biomass response variable included all living and recently dead woody stems ≥ 1 cm in diameter at 30 cm above ground level, with "recently dead" stems defined as those without living leaves, but with bark still attached to small branches. Recently dead stems were included because they retain almost all of their biomass and in the case of *A. harpophylla*, a small percentage of these stems are capable of resprouting from the crown (J. Dwyer, *personal observation*). Published allometric equations are available for the most common species recorded during the survey. For species lacking published allometrics we adopted available equations for species with similar form and wood density (see *Supplement*).

Stem density included all woody stems ≥ 1 cm in diameter at 30 cm above ground level. Multistemmed shrubs were counted as one stem, but for tree species, all stems originating < 30 cm above ground level were counted as separate stems. This was necessary because Brigalow regrowth is characterized by clumps of *A. harpophylla* stems originating near or just below ground level, and it is not possible to determine all members of a clump without excavation.

Survey data were collected at three nested spatial scales: (1) block, (2) site within block, and (3) transect within site within block. The response variables corresponded to the transect scale, but explanatory variables corresponded to either the transect or site scales. We used multilevel models within the hierarchical Bayesian model (HBM) framework to account for the spatial nesting and also to explore the effects of explanatory variables at multiple spatial scales. A multilevel model can be viewed as a set of models, one for each level of grouping, but evaluated simultaneously. Adopting the notation of Gelman and Hill (2007), our transect-level model was

$$y_i \sim \mathcal{N}(\alpha_{j[i]} + \mathbf{X}_i \boldsymbol{\beta},\ \sigma_y^2) \qquad \text{for } i = 1, \ldots, n$$

where $\mathcal{N}$ represents the normal distribution, α_j is the intercept for the jth site, $\mathbf{X}_i$ is a $n \times K$ matrix of transect-scale explanatory variables, $\boldsymbol{\beta}$ is the corresponding K-length vector of transect-level regression coefficients, and σ_y^2 is the within-site variance. Interactions between site- and transect-scale variables were included in the transect-level model because they had unique values for each transect. At the site level, the varying site intercepts (α's) were regressed against the site-scale predictors as follows:

$$\alpha_j \sim \mathcal{N}(\pi_{m[j]} + \mathbf{U}_j \boldsymbol{\gamma},\ \sigma_\alpha^2) \qquad \text{for } j = 1, \ldots, J$$

where π_m is the intercept for the mth block, $\mathbf{U}_j$ is a $L \times J$

matrix of site-scale explanatory variables, $\boldsymbol{\gamma}$ is the corresponding L-length vector of site-scale regression coefficients, and σ_α^2 is the between-site variance. Finally, at the block scale there were no explanatory variables, so the varying block intercepts (π's) were assigned a normal distribution:

$$\pi_m \sim \mathcal{N}(\lambda_\pi, \sigma_\pi^2) \qquad \text{for } m = 1, \ldots, M$$

where λ_π is the overall intercept and σ_π^2 is the between-block variance. Thus, block and site (within block) were treated as random effects and all other variables were treated as fixed effects, reflecting our interest in the "population-wide" effects of the explanatory variables across the Brigalow landscape. The between-block variance was effectively zero in all models after accounting for the age of each stand. Accordingly, all models were reduced to two levels by including the overall intercept in the site-level models as follows:

$$\alpha_j \sim \mathcal{N}(\lambda_\alpha + \mathbf{U}_j \boldsymbol{\gamma}, \sigma_\alpha^2) \qquad \text{for } j = 1, \ldots, J$$

where λ_α is the overall intercept.

Models were fit using WinBUGS 1.4.3 (Lunn et al. 2000) and the R2WinBUGS package (Sturtz et al. 2005) in the R statistical program (R Foundation for Statistical Computing 2009). All four responses required linear transformation due to multiplicative relationships with stand age. Stem density was square-root transformed and all others were log-transformed. Continuous explanatory variables were standardized to provide an indication of relative effect sizes and to speed up convergence of the Gibbs sampler. Overall intercepts and regression coefficients were assigned non-informative normal prior distributions and variance parameters were assigned non-informative uniform prior distributions (Gelman 2006). Multilevel R^2 values were calculated for each level of each model (Gelman and Hill 2007). Refer to Supplement information for further details on model fitting (including annotated WinBUGS code) and simplification procedures.

Probabilistic comparisons were calculated in each HBM between hypothetical 53-year-old stands. For example, in the stem-density model we compared densities after 53 years between hypothetical stands on landzone 9 and landzone 4 (all other variables held at their mean values). To do this we used a missing-data imputation approach and generated a posterior distribution for the difference in predicted values between the two hypothetical sites. The proportion of the resulting posterior distribution that was >0 provided the probability that sites on landzone 9 will have fewer stems than sites on landzone 4 after 53 years.

To further illustrate the relative effect size of certain explanatory variables in the final models, we ran each model on slightly modified data sets. For example, to assess the size of the annual-rainfall effect in the final biomass model, we created two new data sets: one with a high annual-rainfall value assigned to every site and one

with a low value assigned to every site. All other variables were not modified. Predicted values were generated for the two modified data sets and compared using box-and-whisker plots.

Climatic and geomorphologic suitability

With the exception of stand age, the site-scale explanatory variables in the biomass, diameter, and height models were derived from GIS coverages of climate and landzones. By treating stand age as a constant and setting all of the transect-scale variables to their mean values (0), it was therefore possible to extrapolate the models across the entire geographic range of the study area to generate maps of climatic and geomorphologic suitability for biomass, diameter, and height development. Thus, the maps represent relative suitability for development assuming average stem density, canopy cover, gilgai development, and soil texture. All relevant GIS coverages were converted to a common format of 90×90 m grids to correspond approximately with the "site scale" of the survey. The models were spatially extrapolated using the raster calculator in ArcGIS 9.2 (ESRI 2005). Only fixed-effect estimates were used for the extrapolations and map shading was generated using eight quantiles of predicted values for each model.

RESULTS

A number of probability statements are included in the following summaries of each model. These probabilities relate to the specific comparisons shown in the corresponding figures unless otherwise stated. Tables of parameter estimates for the four final models are provided in the Appendix.

Stem-density model

Transect level.—The square root of stem density is defined as

$$\sqrt{\text{stem density}} = \alpha_{j[i]} + \beta_1(\text{canopy cover}_i)$$
$$+ \beta_2(\text{soil texture}_i) + \beta_3(\text{gilgai depth}_i)$$
$$+ \beta_4(\text{canopy cover}_i)(\text{soil texture}_i)$$
$$+ \beta_5(\text{canopy cover}_i)(\text{stand age}_{j[i]})$$
$$+ \beta_6(\text{gilgai depth}_i)(\text{repeat clearing}_{j[i]})$$
$$+ \beta_7(\text{soil texture}_i)(\text{annual rainfall}_{j[i]})$$
$$+ \beta_8(\text{soil texture}_i)(\text{landzone}_{j[i]}) + \varepsilon_i$$

where $\alpha_{j[i]}$ is the intercept for site j that includes transect i, β_{1-8} are the coefficients for the transect-level explanatory variables, and $\varepsilon_i \sim \mathcal{N}(0, \sigma_y^2)$ are the transect-level errors. Variables with the subscript $_{j[i]}$ indicate interactions between site-level and transect-level variables. These interactions are included in the transect-level model because they have unique values for each transect.

Site level.—The definition of the site intercepts is

$$\alpha_j = \lambda_\alpha + \gamma_1(\text{stand age}_j) + \gamma_2(\text{annual rainfall}_j)$$
$$+ \gamma_3(\text{landzone}_j) + \gamma_4(\text{repeat clearing}_j) + \eta_j$$

where the α_j's are the 50 random site intercepts, λ_α is the overall mean (intercept), γ_{1-4} are the coefficients for the site-level explanatory variables, and $\eta_j \sim \mathcal{N}(0, \sigma_\alpha^2)$ are the site-level errors.

Stem density was higher in stands that have been cleared repeatedly (71% probability of higher stem density after 53 years) and on landzone 4 (70% probability after 53 years; Fig. 3a). Predictably, canopy cover interacted with stand age in such a way that older stands with medium to high canopy cover had much lower stem densities than younger stands with comparable canopy cover. Soil texture was present in a number of interactions, but the overall mean effect on stem density was positive (high clay soils were associated with higher densities, not shown), despite having a negative coefficient estimate for the main term. Gilgai (mound and depression) depth also had a positive effect on stem densities, but only in stands that had been cleared repeatedly (95% probability of higher density after 53 years in deeply gilgaied sites; Fig. 3b). The only climatic variable retained in the final stem-density model was annual rainfall, which had a positive overall effect on density (82% probability of higher density after 53 years in high-rainfall sites; Fig. 3c). Annual rainfall interacted with soil texture so that in low-to-medium rainfall regions, sites on clay soils had higher densities than sites on sandy clay soils. In the higher-rainfall regions, the predicted difference in density between clay and sandy clay sites was minor. Multilevel R^2 values for the stem-density model were 0.5 and 0.77 for the site and data levels, respectively.

Biomass model

Transect level.—The definition for the logarithm of biomass is

$$\ln(\text{biomass}_i) = \alpha_{j[i]} + \beta_1(\text{canopy cover}_i)$$
$$+ \beta_2(\text{stem density}_i)$$
$$+ \beta_3(\text{stem density}_i)(\text{rainfall seasonality}_{j[i]})$$
$$+ \beta_4(\text{canopy cover}_i)(\text{stem density}_i)$$
$$+ \beta_5(\text{canopy cover}_i)(\text{max summer temp}_{j[i]})$$
$$+ \beta_6(\text{canopy cover}_i)(\text{annual rainfall}_{j[i]})$$
$$+ \beta_7(\text{stem density}_i)(\text{stand age}_{j[i]}) + \varepsilon_i$$

where all notation is as in the stem-density model.

Site level.—The definition of the site intercepts is

$$\alpha_j = \lambda_\alpha + \gamma_1(\text{stand age}_j) + \gamma_2(\text{rainfall seasonality}_j)$$
$$+ \gamma_3(\text{annual rainfall}_j) + \gamma_4(\text{max summer temp}_j)$$
$$+ \gamma_5(\text{landzone}_j) + \gamma_6(\text{rainfall seasonality})(\text{landzone}_j)$$
$$+ \gamma_7(\text{stand age}_j)(\text{annual rainfall}_j) + \eta_j$$

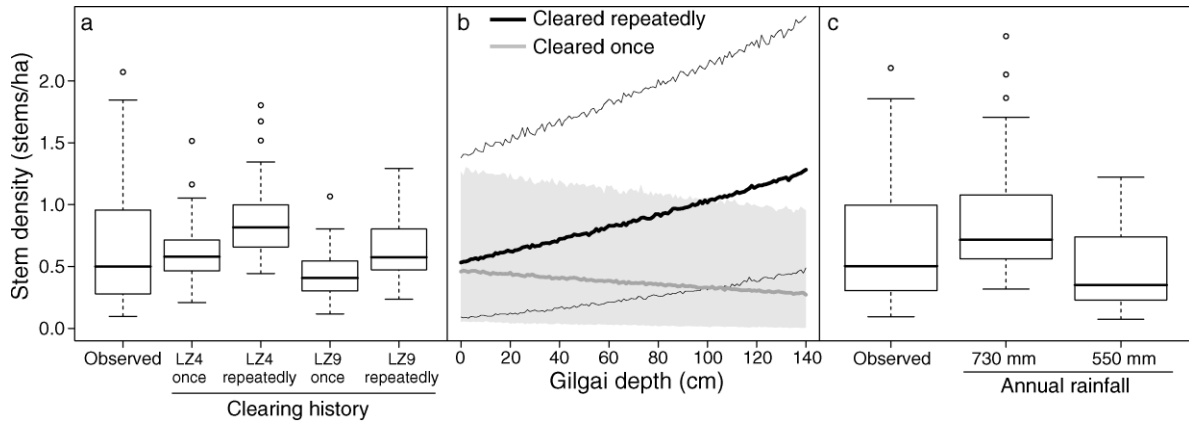where all notation is as in the stem-density model.

FIG. 3. Selected plots from the stem density model: (a) predicted effect sizes for landzone and repeat clearing on stem density; (b) predicted relationship between gilgai (mound and depression) depth and stem density for sites cleared once and sites cleared repeatedly; and (c) predicted effect size for annual rainfall. In panels (a) and (c) thick lines are medians, boxes are interquartile ranges, and whiskers indicate total ranges excluding outliers (circles). In panel (b) the thick lines are predicted (median) relationships and were generated while holding all other variables at their mean values and landzone at 0 (landzone 9). The light-gray envelope and the thin black lines are 95% credible intervals.

Stem density interacted with stand age in such a way that less dense stands had a higher rate of biomass accumulation. A comparison of predicted accumulation for high- and low-density stands revealed an 81% probability of greater biomass in low density stands after 53 years (Fig. 4a). Canopy cover interacted with stem density in a very similar fashion to stand age (Fig. 4b). In fact, canopy cover and stand age exhibited very similar trends with biomass, despite the two terms only being moderately correlated. The interaction between stand age and annual rainfall predicts that lower-rainfall sites have higher biomass initially but the rate of accumulation is considerably higher in high-rainfall sites (85% probability of greater biomass in high-rainfall sites after 53 years, Fig. 4c). Sites on landzone 9 had a 64% probability of higher biomass after 53 years compared to sites on landzone 4, assuming average values for all other variables. Rainfall seasonality and maximum summer temperature had

negative overall effects on biomass accumulation. Multilevel R^2 values for the biomass model were 0.68 and 0.83 for the site and data levels, respectively.

Diameter model

Transect level.—The definition of logarithm of the maximum diameter is

$$\ln(\text{max. diam.}_i) = \alpha_{j[i]} + \beta_1(\text{canopy cover}_i)$$
$$+ \beta_2(\text{stem density}_i) + \beta_3(\text{gilgai depth}_i)$$
$$+ \beta_4(\text{canopy cover}_i)(\text{stem density}_i)$$
$$+ \beta_5(\text{stem density}_i)(\text{stand age}_{j[i]})$$
$$+ \beta_6(\text{canopy cover}_i)(\text{annual rainfall}_{j[i]})$$
$$+ \beta_7(\text{stem density}_i)(\text{annual rainfall}_{j[i]})$$
$$+ \varepsilon_i$$

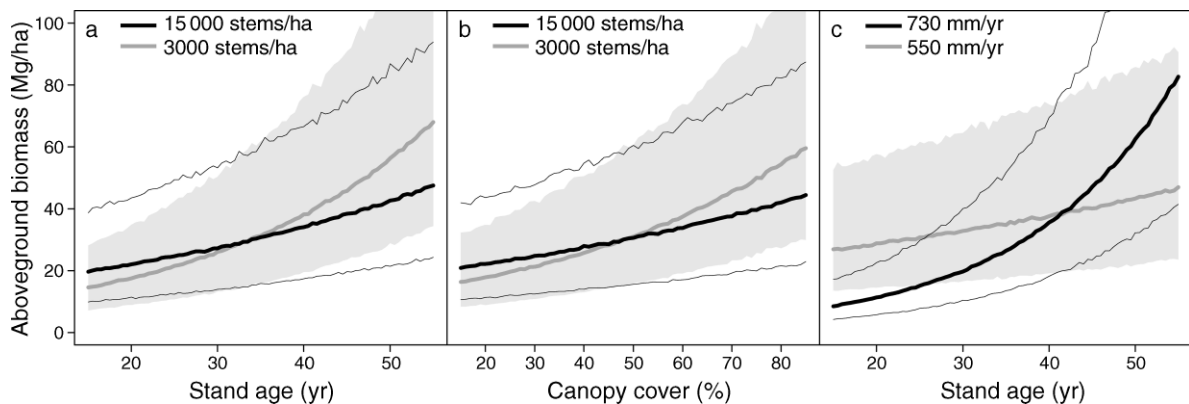where all notation is as in the stem-density model.

FIG. 4. Selected plots from the biomass model. Plots are predicted relationships between living aboveground biomass and (a) stand age for high-density and low-density stands, (b) canopy cover for high-density and low-density stands, and (c) stand age for high- and low-rainfall sites. Line conventions are as in Fig. 3b.
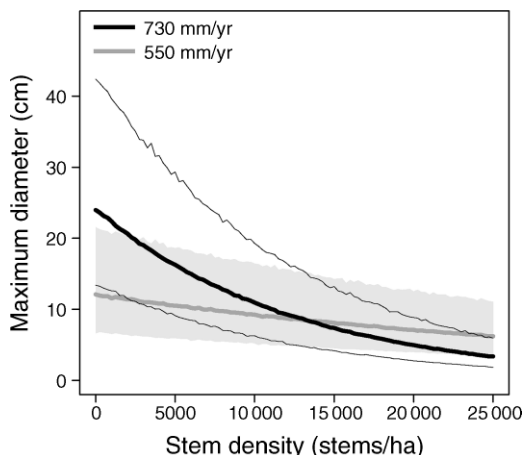
FIG. 5. The predicted relationships between maximum *Acacia harpophylla* stem diameter and stem density for high- and low-rainfall sites. Line conventions are as in Fig. 3b.

Site level.—The definition of the site intercepts is

$$\alpha_j = \lambda_\alpha + \gamma_1(\text{stand age}_j) + \gamma_2(\text{rainfall seasonality}_j) + \gamma_3(\text{annual rainfall}_j) + \eta_j$$

where all notation is as in the stem-density model.

As in the biomass model, stem density interacted with stand age to explain higher diameter growth rates in less dense stands (99.7% probability of larger diameters after 53 years in 3000 stems/ha stands compared to 15 000 stems/ha stands). This reflects the likely importance of neighborhood competition on stem growth. Stem density also interacted with annual rainfall so that sparse stands in higher-rainfall areas had the largest diameters; however, at very high stem densities the effect of rainfall is negligible (Fig. 5). Gilgai depth had a positive effect and rainfall seasonality had a small negative effect. Multilevel R^2 values for the diameter model were 0.52 and 0.8 for the site and data levels, respectively.

Height model

Transect level.—The definition of logarithm of maximum height is

$$\ln(\text{max. height}_i)$$
$$= \alpha_{j[i]} + \beta_1(\text{canopy cover}_i)$$
$$+ \beta_2(\text{stem density}_i) + \beta_3(\text{soil texture}_i)$$
$$+ \beta_4(\text{gilgai depth}_i) + \beta_5(\text{canopy cover}_i)(\text{soil texture}_i)$$
$$+ \beta_6(\text{canopy cover}_i)(\text{gilgai depth}_i)$$
$$+ \beta_7(\text{stem density}_i)(\text{stand age}_{j[i]})$$
$$+ \beta_8(\text{soil texture}_i)(\text{max summer temp}_{j[i]})$$
$$+ \beta_9(\text{soil texture}_i)(\text{annual rainfall}_{j[i]}) + \varepsilon_i$$

where all notation is as in the stem-density model.

Site level.—The definition of the site intercepts is

$$\alpha_j = \lambda_\alpha + \gamma_1(\text{stand age}_j) + \gamma_2(\text{annual rainfall}_j) + \gamma_3(\text{max summer temp}_j) + \eta_j$$

where all notation is as in the stem-density model.

Stand age and stem density had similar effects on maximum stem height as they did on maximum stem diameter (99% probability of taller stems after 53 years in 3000 stems/ha stands compared to 15 000 stems/ha stands). Soil texture interacted with annual rainfall and maximum summer temperature. In warmer, higher-rainfall regions, clay soils support the growth of taller stems; however, in drier, cooler regions, stems are taller on sandy clay soils. Multilevel R^2 values for the height model were 0.53 and 0.83 for the site and data levels, respectively.

Climatic and geomorphologic suitability

Stand age was treated as a constant when extrapolating the models across the study region. The biomass model included an interaction between annual rainfall and stand age (Fig. 6), so it was necessary to set stand age to the upper limit of the data (53 years) to represent the longer term effect of rainfall on biomass accumulation. The diameter and height models did not include interactions with stand age, so the value set for stand age did not affect the relative differences between predicted values.

The maps generated from the site-level models for biomass, diameter, and height were similar in that the areas of highest predicted suitability were in the eastern and central regions (Fig. 7). The regions southwest of Roma and north of Emerald had consistently low suitability for stand development. Landzone was retained only in the biomass model and its effect was most evident in the Tara district. Landzone 4 predominates in this district, contributing to lower predicted suitability compared to surrounding areas of landzone 9 that experience similar climate. Landzone 4 also contributed to lower biomass suitability in the northwest of the study
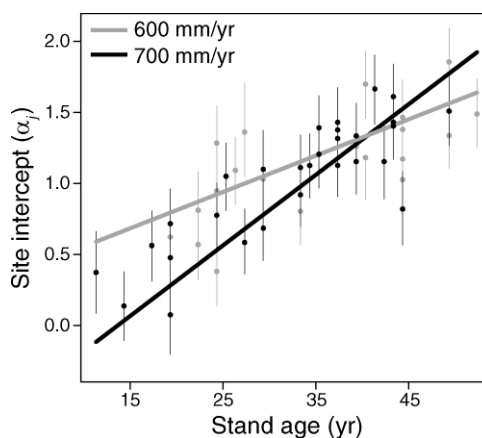

FIG. 6. Plot of site intercepts (α's) vs. stand age from the biomass model. Black and grey points denote sites with above- and below-average annual rainfall, respectively. The lines were fit while holding all other site-level variables at their mean values and landzone at 0 (landzone 9). Bars are 95% credible intervals for each intercept. Note the higher predicted value at age 53 years for the 700 mm/yr line.
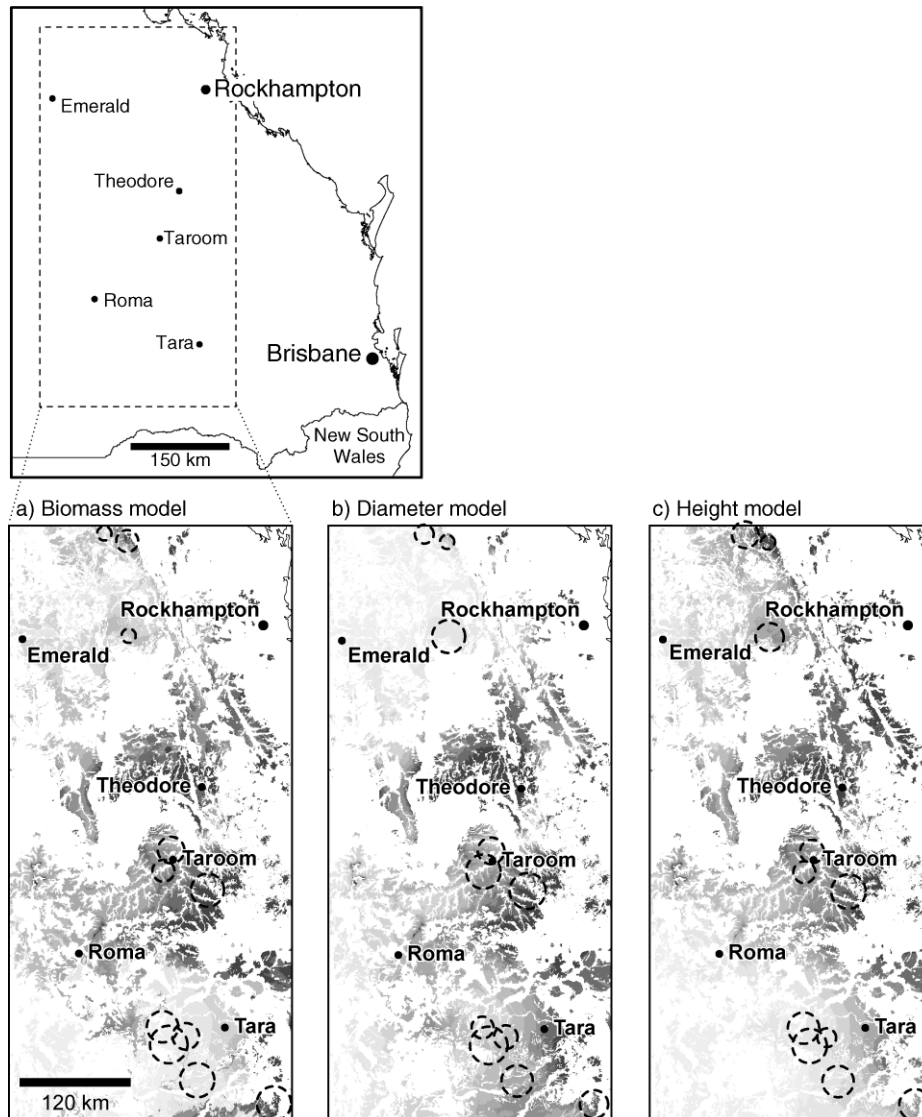
F<small>IG</small>. 7. Maps of relative suitability generated from models for (a) biomass, (b) diameter, and (c) height. Dark areas indicate highest suitability for the development of each structural attribute, and light areas indicate lower suitability. The dashed circles are the locations of 11 mature sites, with circle size proportional to (a) aboveground biomass, (b) maximum *Acacia harpophylla* diameter, and (c) maximum *A. harpophylla* height. Only areas that supported Brigalow ecosystems before European settlement (Accad 2001) were considered; all other areas are shown in white. Shading was generated using eight quantiles of predicted values for each model.

region, where the negative influences of higher seasonality and lower annual rainfall were also evident.

Visual comparisons between the suitability maps and the values recorded for mature reference sites suggest that areas of highest suitability for biomass accumulation and diameter and height development may not always correspond to the areas that have the greatest aboveground biomass, diameters, or heights in mature forests. For example, the surveyed mature forests in the Tara district support considerable amounts of biomass, but the biomass model predicts relatively slow biomass accumulation for the district due to lower annual

rainfall and the negative effect of landzone 4 (Fig. 7a). We identified a strong and significant negative correlation between mature forest aboveground biomass and rainfall seasonality (Spearman's rank correlation test, $\rho = -0.90$, $P = <0.001$). No significant correlations were found between any of the site-level variables and the maximum diameter and maximum height of *A. harpophylla* stems in the 11 mature reference forests.

DISCUSSION

We found strong support for hypotheses 1 and 2, confirming that the rate of progress towards long-term

carbon sequestration and landscape restoration goals is influenced by the agricultural legacy as well as climate, geomorphology, and soil factors.

Brigalow regrowth and the legacy of pastoral development

Suding et al. (2004) incorporated the theory of feedbacks and biotic and abiotic thresholds (Whisenant 1999) with that of alternative stable states (e.g., Gunderson 2000) into a decision framework for restoration projects. Once a restoration goal has been established (step 1), the framework includes the following steps: (2) identify constraints to restoration (both biotic and abiotic) including altered feedbacks, (3) prioritize constraints, (4) address constraints, (5) characterize the changed system and (6) once restoration goals are met, maintain the system. From the results presented here it is possible to identify and prioritize constraints and suggest means to address these constraints for regrowth Brigalow ecosystems.

Considering our restoration goal for Brigalow (*Acacia harpophylla*) regrowth, the constraints to structural restoration appear to be mainly biotic because we focused only on sites that retained some capacity for resprouting. Additional constraints, including abiotic factors, would certainly apply to areas of cultivation or long-term grazing. Notwithstanding, the legacy of initial clearing, burning, sowing of pasture and subsequent regrowth control will result in some abiotic changes in regenerating Brigalow systems. Reductions in nitrogen availability have been recorded in long-developed pasture (Graham et al. 1981), but this is reversible where regrowth persists, due to nitrogen fixation by *A. harpophylla* (Moore et al. 1967) and co-occurring species (e.g., *Casuarina cristata* Miq.). Nutrient cycling and soil hydrology are also altered by pasture establishment (Lawrence et al. 1991, Sangha et al. 2006, Thornton et al. 2007), but as woody species regain dominance these processes are probably reversed to some extent. No significant difference has been detected in soil organic-carbon levels between mature forests and adjacent developed pastures (Harms et al. 2005, Radford et al. 2007).

In terms of biotic constraints, we showed that high stem densities delay structural development and biomass accumulation in the long term, confirming that the apparent conflict between restoration and carbon goals outlined in the *Introduction* (above) does indeed diminish over time. Densities are increased by multiple clearing attempts, particularly on landzone 4, deeply gilgaied (mound-and-depression) soils and high-clay soils. These edaphic effects are consistent with early research into short-term suckering responses following pulling (Johnson 1964), confirming that these factors, in conjunction with management history, have long-term impacts on structural development. Another major biotic constraint is the aforementioned feedback between the widely sown buffel grass and fire. This grass–fire cycle is likely to be particularly problematic in less dense regrowth stands with more open canopies.

Even though our restoration goal focused only on structural development, it is important to consider biotic constraints to community assembly as well. Given the rate and extent of landscape transformation in the Brigalow Belt of northeastern Australia, it is likely that some native species will not be able to disperse to new forest patches. A long-term study by Johnson (1997) found that most plant species were able to recolonize regrowth (albeit at low densities) within 30 years. However that study was undertaken on a property where large areas of mature vegetation were retained for scientific purposes, so the observed recruitment is probably well above average due to small dispersal distances and a large regional species pool.

To prioritize these constraints, the most important is the grass–fire cycle because it has the potential to diminish the resprouting capacity of Brigalow forest species and shift the system, at least temporarily, to a grassland state. Grazing by livestock appears to be the only feasible option to manage grass fuel loads in stands across entire regions. The next most important biotic constraint to structural development is stem density. Restoration thinning can be applied to accelerate stem growth and native plant species recruitment (Dwyer et al. 2010; however, cost-effective methods for implementing this management approach are needed. Assuming that fire can be excluded and stem densities reduced to appropriate levels, it will still be necessary to monitor development to ensure that secondary suckering by *A. harpophylla* (and co-occurring re-sprouting species) is not too prolific and, conversely, to promote suckering or undertake supplementary planting if natural mortality reduces woody stem densities below those of mature reference forests. Once stands have developed structure akin to reference forests, grass fuel loads should have declined to low levels (Scanlan 1991); however, in more open stands, such as those in the northwestern Brigalow Belt, it may be necessary to maintain control of fuel loads indefinitely.

Recommendations to meet carbon and restoration goals

To achieve the carbon goal we recommend selecting younger sites with moderate stem densities in regions with higher rainfall and lower seasonality. Such sites will accumulate biomass relatively quickly and, based on the aboveground biomass estimates for the 11 mature reference sites, they will also accumulate more biomass in the long term. In the event that sites in high-rainfall areas are not available, regions of moderate rainfall and low seasonality should be considered before regions of high seasonality. The rate of biomass accumulation was also greater on fine-grained sediments (landzone 9), but landzone appeared to have little bearing on the amount of biomass that can be accumulated in mature Brigalow forests. Older stands (40–55 years old) with moderate stem densities also have considerable carbon potential

because they have the capacity to substantially increase their aboveground biomass. For example, some of the well-developed older sites in the southeastern portion of the study area had aboveground biomass of ~70 Mg/ha, compared to nearby mature reference sites with 110 Mg/ha. However, current global carbon policy prevents the use of such older sites because the Kyoto Protocol requires that reforestation takes place in areas that were not "forest" in 1990 (refer to discussion in Dwyer et al. [2009]).

To achieve the restoration goal, we recommend selecting older stands with moderate densities because they have biomass, diameter, and height values closer to that of mature ecosystems. Older Brigalow regrowth also supports a greater diversity of woodland-dependent birds (Bowen et al. 2009). Older sites are relatively rare in the bioregion, so it will be necessary to also select younger sites, such as those with the greatest carbon potential, to reinstate some level of habitat connectivity and increase forest area. The suitability maps indicate that the central and eastern regions are more suitable for structural development, but given our restoration goal, it is also necessary to consider regional variation in mature forest structure when considering restoration potential. While the seasonal climate in the northeast is less suitable for structural development, the target biomass and maximum heights for forests in this region are also lower. Climate is less important for restoration because it influences both the rate of development and also the target structure and biomass carrying capacity. Thus in regions of similar climate, stem density will be the major determinant of restoration potential.

Whether it be for carbon or restoration purposes, it is almost inevitable that stand selection will involve choosing among young, high-density stands in some situations. The important variables identified in the stem-density model influence both the initial suckering response and also the subsequent rate of self-thinning. Within regions of similar annual rainfall, sites with limited gilgai development on landzone 9 tend to have fewer stems in the long term. Less clayey soils are also associated with lower densities, but more so in low-rainfall regions. Thus it may be possible to choose between similarly dense stands based on these edaphic factors. When choosing between high-density stands in different climatic regions, the lower rainfall sites might be preferable for restoration projects because self-thinning appears to be faster, presumably due to more frequent and prolonged periods of rainfall deficit. Obviously the context of a site within the broader landscape is also crucial when selecting sites for landscape restoration, but such considerations were beyond the scope of this study.

The regions with greatest carbon potential are among the most heavily cleared (Seabrook et al. 2007, Butler 2009) and in desperate need of landscape-scale restoration. With this simplistic assessment, biomass accumulation and the most urgent conservation objectives would appear to be congruent. However, a more detailed analysis is required to examine emerging land use in an economy where carbon will have a monetary value. This study shows that the rates of biomass accumulation and the potential biomass stored in mature forests are not necessarily aligned across the bioregion. The response of the carbon market to the short-term or long-term imperatives of rates and stocks will be strongly influenced by the rules of carbon trading. On pure economic grounds, factors that will affect the geography of carbon projects will not only include biomass accumulation rates and carrying capacity, but also land values, the price of carbon, secondary income streams, and the net opportunity costs of changing management. In northern areas, Brigalow forests support comparatively less biomass, but tend to be more open, presenting opportunities for a larger income stream from grazing during and after forest development. Grazing may be crucial for managing grass fuel loads to reduce fire risk, but would be precluded in higher biomass forests in southern areas that develop more closed canopies. Conservation planners will need to understand these economic imperatives in order to deflect the carbon market to important areas for the recovery of biodiversity that have apparently low carbon potential.

Limitations

In this study we only explored part of the total carbon budget of Brigalow forests, however aboveground biomass is likely to account for a large portion the total budget. The regrowth stands sampled in this study all had low levels of dead aboveground biomass compared to mature stands because of the practice of burning woody debris following pulling. The pulling and burning method effectively removes the aboveground components of woody plants, but lateral roots remain largely intact and it is likely that regrowth stands have root biomass comparable to mature forests. As previously mentioned, available comparative studies of soil organic carbon have not identified significant differences between mature Brigalow forests and adjacent developed pastures, indicating that soil carbon stocks in regrowth are probably similar to mature forests.

Conclusions

We conclude that site-selection strategies required to achieve both carbon and restoration goals are largely congruent within regions of similar climate. Between regions however, spatial prioritization of restoration and carbon projects may only be aligned where carbon benefits will be high. From a landscape-restoration viewpoint it is crucial that regrowth be restored throughout the bioregion, regardless of the carbon benefits.

LITERATURE CITED

Accad, A. 2001. Remnant vegetation in Queensland: analysis of pre-clearing, remnant 1997–1999 regional ecosystem information. Queensland Herbarium, Toowong, Queensland, Australia.

Aide, T. M., and H. R. Grau. 2004. Ecology: globalization, migration, and Latin American ecosystems. Science 305: 1915–1916.

Augustine, D. J., and L. E. Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conservation Biology 12:995–1004.

Australian Government Department of Climate Change. 2008. Carbon pollution reduction scheme: Australia's low pollution future. White paper, volume 1. ⟨http://www.climatechange.gov.au/publications/cprs/white-paper/cprs-white-paper.aspx⟩

Bekessy, S. A., and B. A. Wintle. 2008. Using carbon investment to grow the biodiversity bank. Conservation Biology 22:510–513.

Bowen, M. E., C. A. McAlpine, A. P. N. House, and G. C. Smith. 2007. Regrowth forests on abandoned agricultural land: a review of their habitat values for recovering forest fauna. Biological Conservation 140:273–296.

Bowen, M. E., C. A. McAlpine, L. M. Seabrook, A. P. N. House, and G. C. Smith. 2009. The age and amount of regrowth forest in fragmented Brigalow landscapes are both important for woodland dependent birds. Biological Conservation 142:3051–3059.

Bowman, G., and J. Hutka. 2002. Particle size analysis. Pages 225–239 in N. McKenzie, K. Coughlan, and H. Cresswell, editors. Soil physical measurement and interpretation for land evaluation. CSIRO Publishing, Collingwood, Victoria, Australia.

Buckley, Y. M., D. T. Briese, and M. Rees. 2003. Demography and management of the invasive plant species Hypericum perforatum. I. Using multilevel mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. Journal of Applied Ecology 40:481–493.

Butler, D. W. 2009. Planning iterative investment for landscape restoration: choice of biodiversity indicator makes a difference. Biological Conservation 142:2202–2216.

Butler, D. W., and R. J. Fairfax. 2003. Buffel grass and fire in a gidgee and Brigalow woodland: a case study from central Queensland. Ecological Management and Restoration 4:120–125.

Castellon, T. D., and K. E. Sieving. 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. Conservation Biology 20:135–145.

Chandler, S. T., Y. M. Buckley, and J. M. Dwyer. 2007. Restoration potential of Brigalow regrowth: insights from a cross-sectional study in southern Queensland. Ecological Management and Restoration 8:218–221.

Cramer, V. A., R. J. Hobbs, and R. J. Standish. 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends in Ecology and Evolution 23:104–112.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

DERM [Department of Environment and Resource Management]. 2007. Copy of the certified regional ecosystem map for the purpose of the Vegetation Management Act of 1999, Version 5.1. Department of Environment and Resource Management, Brisbane, Queensland, Australia.

Dwyer, J. M., R. J. Fensham, and Y. M. Buckley. 2010. Restoration thinning accelerates structural development and carbon sequestration in an endangered Australian ecosystem. Journal of Applied Ecology, 47:681–691.

Dwyer, J. M., R. J. Fensham, D. W. Butler, and Y. M. Buckley. 2009. Carbon for conservation: assessing the potential for win–win investment in an extensive Australian regrowth ecosystem. Agriculture Ecosystems and Environment 134: 1–7.

ESRI [Environmental Science Research institute]. 2002. ArcView 3.3. Environmental Science Research Institute, Redlands, California, USA.

ESRI [Environmental Science Research institute]. 2005. ArcGIS 9.2. Environmental Science Research Institute, Redlands, California, USA.

Feldpausch, T. R., M. A. Rondon, E. C. M. Fernandes, S. J. Riha, and E. Wandelli. 2004. Carbon and nutrient accumulation in secondary forests regenerating on pastures in central Amazonia. Ecological Applications 14(Supplement):S164–S176.

Fensham, R. J., and R. J. Fairfax. 2007. Effect of photoscale, interpreter bias and land type on woody crown-cover estimates from aerial photography. Australian Journal of Botany 55:457–463.

Fensham, R. J., and G. P. Guymer. 2009. Carbon accumulation through ecosystem recovery. Environmental Science and Policy 12:367–372.

Ferrier, S. 2002. Mapping spatial pattern in biodiversity for regional conservation planning: Where to from here? Systematic Biology 51:331–363.

Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models. Bayesian Analysis 1:515–533.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multi-level/hierarchical models. Cambridge University Press, New York, New York, USA.

Graham, T. W. G., A. A. Webb, and S. A. Waring. 1981. Soil nitrogen status and pasture productivity after clearing of Brigalow (Acacia harpophylla). Australian Journal of Experimental Agriculture and Animal Husbandry 21:109–118.

Gunderson, L. H. 2000. Ecological resilience—in theory and application. Annual Review of Ecology and Systematics 31: 425–439.

Harms, B. P., R. C. Dalal, and A. P. Cramp. 2005. Changes in soil carbon and soil nitrogen after tree clearing in the semi-arid rangelands of Queensland. Australian Journal of Botany 53:639–650.

Hobbs, R. J., and J. A. Harris. 2001. Restoration ecology: repairing the earth's ecosystems in the new millennium. Restoration Ecology 9:239–246.

Houlder, D. J., M. F. Hutchinson, H. A. Nix, and J. P. McMahon. 2000. ANUCLIM 5.0. Centre for Resource and Environmental Studies, Australian National University, Canberra, A.C.T., Australia.

Johnson, R. W. 1964. Ecology and control of Brigalow in Queensland. Queensland Department of Primary Industries, Brisbane, Queensland, Australia.

Johnson, R. W. 1997. The impact of clearing Brigalow communities and consequences for conservation. Pages 359–363 in D. Lamb and P. Hale, editors. Conservation outside nature reserves. Centre for Conservation Biology, University of Queensland, Brisbane, Queensland, Australia.

Lawrence, P. A., P. J. Thorburn, and M. Littleboy. 1991. Changes in surface and subsurface hydrology after clearing Brigalow (Acacia harpophylla) forest in a semiarid climate: measurements and modelling. Pages 374–380 in Challenges for sustainable development. Proceedings, International

Hydrology and Water Resources Symposium, Perth, October 1991. National Conference Publication number 91/22. Institution of Engineers, Barton, A.C.T., Australia.

Lugo, A. E., and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. Forest Ecology and Management 190:145–161.

Lunn, D. J., A. Thomas, N. G. Best, and D. J. Spiegelhalter. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325–337.

McMahon, S. M., and J. M. Diez. 2007. Scales of association: hierarchical linear models and the measurement of ecological systems. Ecology Letters 10:437–452.

Moore, A. W., J. S. Russell, and J. E. Coaldrake. 1967. Dry matter and nutrient content of a subtropical semiarid forest of *Acacia harpophylla* F. Muell (Brigalow). Australian Journal of Botany 15:11–24.

Nix, H. A. 1994. The Brigalow. Pages 199–233 *in* S. Dovers, editor. Australian environmental history: essays and cases. Oxford University Press, Melbourne, Victoria, Australia.

NSW NPWS [New South Wales National Parks and Wildlife Service]. 1998. Vertebrate fauna survey: NSW Comprehensive Regional Assessment Project Report. NSW National Parks and Wildlife Service, Sydney New South Wales, Australia.

OECD [Organisation for Economic Co-operation and Development]. 2007. OECD - FAO Agricultural Outlook 2007–2016. OECD Publications, Paris, France.

R Foundation for Statistical Computing. 2009. The R environment for statistical computing and graphics, version 2.9.2. R Foundation for Statistical Computing, Vienna, Austria. ⟨http://www.r-project.org/⟩

Radford, B. J., C. M. Thornton, B. A. Cowie, and M. L. Stephens. 2007. The Brigalow catchment study. III. Productivity changes on Brigalow land cleared for long-term cropping and for grazing. Australian Journal of Soil Research 45:512–523.

Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. Global Biogeochemical Cycles 13:997–1027.

Sangha, K. K., R. K. Jalota, and D. J. Midmore. 2006. Litter production, decomposition and nutrient release in cleared and uncleared pasture systems of central Queensland, Australia. Journal of Tropical Ecology 22:177–189.

Scanlan, J. C. 1991. Woody overstorey and herbaceous understorey biomass in *Acacia harpophylla* (Brigalow) woodlands. Australian Journal of Ecology 16:521–530.

Seabrook, L., C. McAlpine, and R. Fensham. 2007. Spatial and temporal analysis of vegetation change in agricultural landscapes: a case study of two Brigalow (*Acacia harpophylla*) landscapes in Queensland, Australia. Agriculture Ecosystems and Environment 120:211–228.

Silver, W. L., R. Ostertag, and A. E. Lugo. 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restoration Ecology 8:394–407.

Stouffer, P. C., R. O. Bierregaard, C. Strong, and T. E. Lovejoy. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. Conservation Biology 20:1212–1223.

Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: A package for running WinBUGS from R. Journal of Statistical Software 12:1–16.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology and Evolution 19:46–53.

Thornton, C. M., B. A. Cowie, D. M. Freebairn, and C. L. Playford. 2007. The Brigalow catchment study: II. clearing Brigalow (*Acacia harpophylla*) for cropping or pasture increases runoff. Australian Journal of Soil Research 45:496–511.

Whisenant, S. G. 1999. Repairing damaged wildlands. a process-oriented, landscape-scale approach. Cambridge University Press, Cambridge, UK.

APPENDIX

A table summarizing the stem density, biomass, diameter, and height models (*Ecological Archives* A020-068-A1).

SUPPLEMENT

Allometric equations, HBM details, and HBM code (WinBUGS model as called from R) (*Ecological Archives* A020-068-S1).