

Potential aboveground biomass in drought-prone forest used for rangeland pastoralism

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Abstract. The restoration of cleared dry forest represents an important opportunity to sequester atmospheric carbon. In order to account for this potential, the influences of climate, soils, and disturbance need to be deciphered. A data set spanning a region defined the aboveground biomass of mulga (*Acacia aneura*) dry forest and was analyzed in relation to climate and soil variables using a Bayesian model averaging procedure. Mean annual rainfall had an overwhelmingly strong positive effect, with mean maximum temperature (negative) and soil depth (positive) also important. The data were collected after a recent drought, and the amount of recent tree mortality was weakly positively related to a measure of three-year rainfall deficit, and maximum temperature (positive), soil depth (negative), and coarse sand (negative). A grazing index represented by the distance of sites to watering points was not incorporated by the models. Stark management contrasts, including grazing exclosures, can represent a substantial part of the variance in the model predicting biomass, but the impact of management was unpredictable and was insignificant in the regional data set. There was no evidence of density-dependent effects on tree mortality. Climate change scenarios represented by the coincidence of historical extreme rainfall deficit with extreme temperature suggest mortality of 30.1% of aboveground biomass, compared to 21.6% after the recent (2003–2007) drought. Projections for recovery of forest using a mapping base of cleared areas revealed that the greatest opportunities for restoration of aboveground biomass are in the higher-rainfall areas, where biomass accumulation will be greatest and droughts are less intense. These areas are probably the most productive for rangeland pastoralism, and the trade-off between pastoral production and carbon sequestration will be determined by market forces and carbon-trading rules.

Key words: *Acacia aneura*; Australia; biomass; carbon accounting; carbon sequestration; drought; dry forest; grazing; mulga; tree mortality.

INTRODUCTION

Substantial amounts of carbon are lost through the clearing of dry forest and savanna (Klink and Machado 2005), but there are opportunities to recover atmospheric carbon through reforestation in these environments (Fensham and Guymer 2009). Determining the relative role of physical factors (climate and soil) and disturbance on biomass stocks in dry forests and savannas not only informs our understanding of ecosystem function, but also contributes to determining sequestration potential of reforestation. The inherent instability of dry forests, savannas, and grasslands suggests that these ecosystems may be particularly relevant to quantifying global carbon budgets (Asner et al. 2003, Bradley and Fleishman 2008). Experimental studies and simulations have shown that many savannas occur in climate zones capable of supporting forest (Bond et al. 2005).

However, the factors changing grassland to forest are debated and include reduced burning resulting from rangeland pastoralism (Roques et al. 2001, Burrows et al. 2002), relief from browsing (Augustine and McNaughton 2004, Sharam et al. 2006), enhanced atmospheric CO₂ (Wigley et al. 2010), and climatic fluctuations (Fensham et al. 2009, Huang et al. 2010). The latter position is bolstered by numerous recent studies documenting drought-induced tree mortality, possibly exacerbated by global climate change (Allen et al. 2010). There are also important interactive feedbacks, including, for example, increased woody dominance without nutrient supplement by herbivore defecation (van der Waal et al. 2011), and increased tree mortality through density-dependent effects (Dwyer et al. 2010) and insect herbivory (Ganey and Vojta 2011).

A large data set representing tree cover in African savannas revealed that 71% of the variance could be explained by mean annual rainfall, fire return interval, soil attributes, and indices of grazing intensity, in that order of importance (Sankaran et al. 2008). The

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influence of rainfall was particularly important in the semi-arid spectrum (annual rainfall 200–700 mm), and disturbance variables became important where annual rainfall exceeded 700 mm. A similar attempt to describe basal area across a rainfall gradient in northern Australia was less successful, accounting for only 35% of the variance by a model incorporating annual rainfall and clay content (Williams et al. 1996) without integrating land use factors. Only one continental-scale study has incorporated rainfall variability as a determinant of tree stocks (Good and Caylor 2011) despite recognition of its importance (Rodriguez-Iturbe et al. 1999, Fensham et al. 2009).

A recent high-profile report to the government of Australia, reviewing potential responses to mitigating climate change (Garnaut 2008), estimated that the restoration of degraded and marginal grazing lands could offset up to 250 Tg CO₂-e (CO₂ equivalents, the standard unit for carbon accounting, IPCC 2007; Tg represents teragrams), ~40% of Australia's annual emissions, per year for several decades. This report is unclear as to its definition of "restoration," but encompasses forest cover and soil carbon, and identified the Mulga Lands biogeographic region of eastern Australia (Thackway and Cresswell 1995) as a prime candidate for this sequestration opportunity. There is a dominant view among rangeland scientists that woody biomass in the mulga (*Acacia aneura*) dry forest of eastern Australia is largely driven by management, including increases resulting from pastoral grazing via the suppression of fire (Harrington et al. 1984, Pressland 1984, Noble 1997), but also a recognition that sheep grazing can prohibit recruitment of trees (Harrington 1979, Brown 1985). These impacts have been modeled (Howden et al. 2001) and forecast profound changes in carbon stocks, depending on management. With divergent management the models predict outcomes between 2000 kg C/ha for a grazed and annual burnt scenario to 18 000 kg C/ha for an ungrazed and never-burnt scenario over a century time scale, with this contrast representing 0.58 Mg CO₂-e·ha⁻¹·yr⁻¹. A recent study (Witt et al. 2011) estimated that total protection from grazing in the mulga dry forest of eastern Australia would result in increased density of woody trees contributing between 0.74 and 0.83 Mg CO₂-e·ha⁻¹·yr⁻¹, with an additional 0.18 Mg CO₂-e·ha⁻¹·yr⁻¹ from soil carbon.

If disturbance is paramount, then the optimization of carbon stocks will require active management. Eliminating grazing in the Mulga Lands would involve radical land use change, not only because of a well-established commercial grazing industry, but also because the region supports high densities of native macropods. Another potential sink, the restoration of aboveground carbon through the reforestation of cleared lands, may be more practical, and currently has a greater potential to be included in formal trading schemes than manipulating carbon stocks in existing forest (Keenan 2002). The

potential for recovery of mulga dry forests with relatively passive management is possible because mulga trees can persist after clearing, and furthermore, vascular plant diversity is not substantially affected (Fensham et al. 2012). While feasible, the recovery of forest will conflict with the goals of the grazing industry to maximize pasture production, and will require appropriate market incentive.

The current paper analyzes an extensive data set recording the structure and aboveground biomass of mulga vegetation from throughout the Mulga Lands biogeographic region in Queensland. The surveys were conducted after a recent drought (2003–2007), and allow for the assessment of associated tree mortality. The study also incorporates a grazing intensity surrogate, and documents fence-line contrasts comparing divergent management histories that prohibit or favor mulga recruitment and growth. It addresses the following questions: (1) How accurately can the aboveground woody biomass of mature mulga forest be modeled in relation to climate and soil attributes? (2) How does the magnitude of recent drought, soil attributes, and tree density influence dead biomass? And (3) what influence does the range of management activities within the region have on live and dead biomass?

Biomass stocks of forests are incorporated in the Australian Government's National Carbon Accounting System (NCAS) 3PG (physiological principles predicting growth) model (Richards and Brack 2004). This model has been assessed with forest data from *Eucalyptus* forest in the high-rainfall environments of eastern Australia, where it seems to substantially underestimate aboveground biomass (Keith et al. 2010), but its predictions in the more extensive forests in low-rainfall environments has never been evaluated. This study also examines how field estimates of aboveground biomass compare to the national modeled estimates.

This study concludes by employing models to predict biomass across the region and examines the sequestration potential of cleared portions of the mulga forest in the study area. It also forecasts woody biomass losses under future drought events and discusses the role of management for enhancing carbon sequestration.

METHODS

Study area

The Mulga Lands bioregion in Queensland is characterized by mulga (*Acacia aneura*) dry forest occurring in a flat landscape consisting of decomposed Tertiary sandstone and peneplains occasionally outcropped by lateritic surfaces. The climate is semiarid with average annual rainfall ranging from 264 mm in the west to 550 mm in the east, with a slight bias toward the summer months. Overstory canopies in the mature mulga dry forest range from 6 to 12 m in height and have variable densities. *Eucalyptus populnea*, *E. intertexta*, *E. melanophloia*, and the *Eucalyptus* ally *Corymbia* can occur among the mulga, especially in the eastern

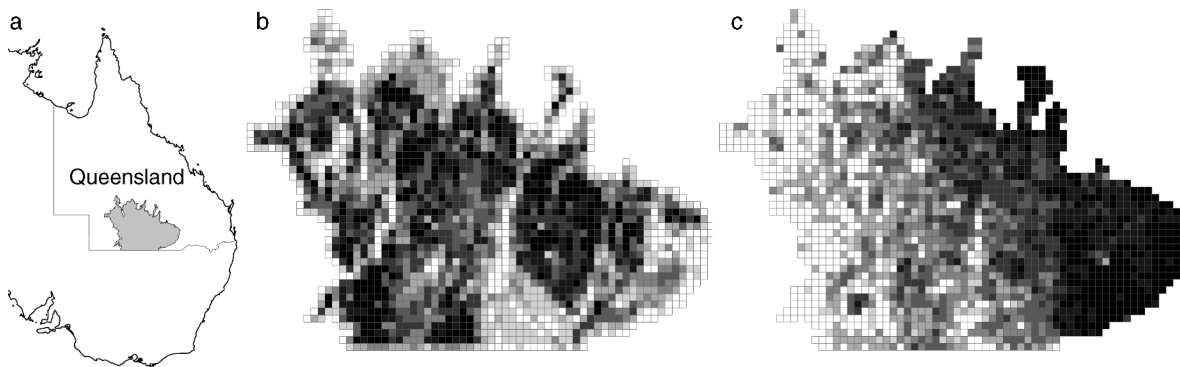


FIG. 1. (a) The Mulga Lands biogeographic region in the Australian state of Queensland. (b) The same region represented by eight equal segments across the range of values for the proportion of mulga dry forest in each 0.1° cell prior to clearing, increasing from white (0%) to black (100%). (c) As for panel (b) but representing the proportion of cleared forest in each 0.1° cell. The data are derived from Regional Ecosystem mapping base (Wilson et al. 2002) with clearing updated to 2006.

part of the region. The soils of the mulga forest have variable texture (sand to light clay), have little profile development, poor structure and are generally acidic with low levels of macronutrients (Dawson and Ahern 1973). The region also includes more fertile and productive landscapes including *Eucalyptus* woodland on alluvium fringing the major streams and gidgee (*Acacia cambagei*) woodland on fertile clay soils that have been extensively cleared (Fensham et al. 2011a).

The region has been subject to extensive rangeland pastoralism, mostly with sheep for wool production, but recent years have seen a transition toward cattle production. Typical stocking densities in the mulga forest range between 0.1 and 0.6 dry sheep equivalents per hectare, but paddocks are often rested during drought. Macropods, particularly the eastern grey kangaroo (*Macropus giganteus*), also occur in densities of about 0.16 dry sheep equivalents per hectare (Pople 2006). During times when herbaceous biomass is diminished, for example during drought, it is common practice to fell mulga trees in order to allow stock to access foliage, a practice known as fodder harvesting (Everist et al. 1958). Historically this practice was conducted with an axe, but is more recently conducted over larger areas with chainsaws and tractors. Furthermore, large areas in the east of the region have been cleared for pasture improvement.

The Mulga Lands biogeographic region in Queensland extends over an area of 18.6 Mha and has been mapped at 1:100 000 scale into Regional Ecosystem mapping units (Wilson et al. 2002). This coverage represents these units prior to mechanical clearing when the Regional Ecosystems containing mulga represented 61% of the region (Fig. 1). A separate mapping base represents cleared (including areas mechanically cleared for fodder harvesting) and uncleared areas (Wilson et al. 2002). These coverages indicate that in 2006, 24% of the mulga-dominated vegetation had been mechanically cleared (Fensham et al. 2011a). Although mulga can be killed by fire (Hodgkinson and Harrington 1985), it is

extremely infrequent in the mulga forest (Hodgkinson et al. 1984), and is only possible after well above average rainfall. Long-term landholders recall fires in the mulga forest of the study area during the 1950s, but much more limited fires during the wet years of the 1970s (J. Mills, *personal communication*).

Field methods

Potential sites were randomly generated within 200 m of road corridors in mulga-dominated Regional Ecosystems classified as remnant. A final set of 182 sites was selected after ensuring there was no evidence of previous mechanical clearing (although 5% of sites had axe-cut stumps from historical fodder harvesting) and contained at least 10 ha of homogenous vegetation cover and pattern.

From each site data were collected in 2008 and 2009 from four, 50 m long plots, spread within the 10 ha and positioned to minimize effects of fence-lines, tracks, and selective tree harvesting. Plot width varied depending on tree density, but was typically 10 m wide; within each plot the diameter at breast height (dbh) was taken for every woody plant with stems ≥ 1 cm dbh originating within the plot. All stems > 30 cm dbh were measured in a 25 m wide plot. For multistemmed plants the surface area of each stem was summed and back-transformed to a single dbh for further analysis. Stems were identified to species and assigned one of four health categories: (1) healthy, (2) barely alive and recently dead with bark hugging trunk, (3) dead with bark present but not hugging trunk, (4) long dead, without persistent bark. A soil sample from 1–5 cm depth to avoid surface organic matter was taken from the beginning and end of each plot, and these eight samples were bulked and then subsampled for each site.

Domestic stock graze both cleared and uncleared areas, and grazing intensity declines with distance to water for both cattle and sheep, although cattle will forage at much greater distances than sheep, which rarely range beyond 3.5 km from watering points

(Fensham and Fairfax 2008). The overwhelmingly dominant native herbivore (eastern grey kangaroo) also has a relatively narrow home range and a high demand for water (Dawson 1995). The minimum distance to a watering point was determined using satellite imagery and provides a surrogate for long-term grazing history given the difficulties associated with obtaining information on stock type and stocking rates over long time periods.

During the course of fieldwork and through inspection of satellite imagery, a site (Quilpie site: 26.355° S, 144.580° E) was selected that represented the sharpest fence-line contrast in tree cover that was unrelated to mechanical clearance. After interviews with the landholder (G. L'Anson, *personal communication*) it was ascertained that the area currently with dense mulga had been grazed exclusively by cattle at moderate stocking rates (0.32 dry sheep per hectare) over the course of a mulga recruitment event during the wet 1970s decade (Fig. 2). In the adjoining open area, sheep grazing with moderate stocking rates (0.25 dry sheep equivalents per ha) was continuous through the 1970s. Unlike cattle, sheep can substantially reduce mulga seedling establishment. The recent drought has resulted in widespread death in the paddock where the mulga is dense.

To quantify the impact of this history, 15 plots were located along 800 m bearing lines, parallel and 50 m either side of the fence-line marking the management contrast at the Quilpie site. Plots were randomly located along the lines, and were 120 m² and 600 m² in the thick mulga and open mulga paddocks, respectively. The identity, size, and health of trees were measured as described.

Data were also collected from three sites (Croxdale, 26.467° S, 146.140° E; Lanherne, 26.739° S, 145.084° E; Wallen, 27.602° S, 145.798° E) with exclosures prohibiting access by sheep for 25–28 years, but allowing access by browsing and grazing by native herbivores. The identity, dbh, and health of woody plants was recorded as described earlier within 2 × 20 m regularly spaced plots within the exclosures ($n = 20$) and also in adjacent areas subject to grazing by domestic stock ($n = 20$) (Fensham et al. 2011b).

Soil analysis

Particle size distributions were determined using laser diffraction (Mastersizer 2000, Malvern Instruments Limited, Malvern, UK). This is a cost-effective and reproducible technique (Arriaga et al. 2006), although it has a tendency to underestimate clay and overestimate silt particles compared with the traditional hydrometer and pipette methods (Pieri et al. 2006, Eshel and Levy 2007). Samples were sieved (2 mm), a portion added to distilled water, then sonicated for 1 min at 10- μ m tip displacement to break up remaining aggregated particles. Absorption was maintained between 15% and 20% during particle size measurement. Outputs represent averages of seven repeat measurements. The output of

continuous particle size distribution was categorized as clay (particles <0.002 mm), silt (0.002–0.02 mm), fine sand (0.02–0.2 mm), and coarse sand (0.2–2 mm), and represented as percentages. Soil pH was determined using a TPS WP-81 pH meter (TPS Pty Limited, Brisbane, Australia) with a 1:5 solution.

Biomass estimation

Allometric equations that predict total aboveground dry mass from tree diameters were sourced from the literature (Appendix A). As some allometric equations estimate biomass from diameters or circumferences at 30 cm aboveground, both the dbh and diameter at 30 cm (D30) were measured for each tree at four sites spread throughout the region ($n = 328$). The relationship between dbh and D30 was explored and found to be linear with 94% of the variance explained. $D30 = dbh \times 1.2125$. All stems were assumed to be circular in cross section.

Spatial climate data

Monthly climate data records were obtained from SILO (*available online*)⁵ (Jeffrey et al. 2001), which is a modeled surface informed by a network of climate stations that has increased in density since reliable records commenced in 1890 (Fig. 2). In addition to survey site locations, SILO data were obtained for every 0.1° used in the analysis and were manipulated to represent standard climate attributes and indices of drought (Table 1).

Soil depth

A two-factor representation of soil depth for all sites was derived from the Regional Ecosystem mapping (Wilson et al. 2002). The regional ecosystems within this mapping base include a land zone category that represents broad geology and soil classes. The mulga regional ecosystems are represented as either Land zone 5 (soils generally >50 cm depth) or Land zone 7 (soils generally <50 cm depth) based on detailed land use studies across the region (Mills 1980a). The two groups will be referred to as deep and shallow soils, respectively.

Modeling design

Separate statistical analyses were undertaken for biomass and recent tree mortality. All environmental explanatory variables corresponded to the site scale, and both biomass and tree mortality were modeled at this scale. We used Bayesian model averaging (BMA) to assess the relative support for a range of ordinary least squares regressions (Raftery et al. 1997) for each response and to estimate averaged coefficients and associated standard errors for subsequent spatial forecasting. BMA circumvents the problems associated with choosing the “best” model by averaging over a

⁵ <http://www.longpaddock.qld.gov.au/silo/>

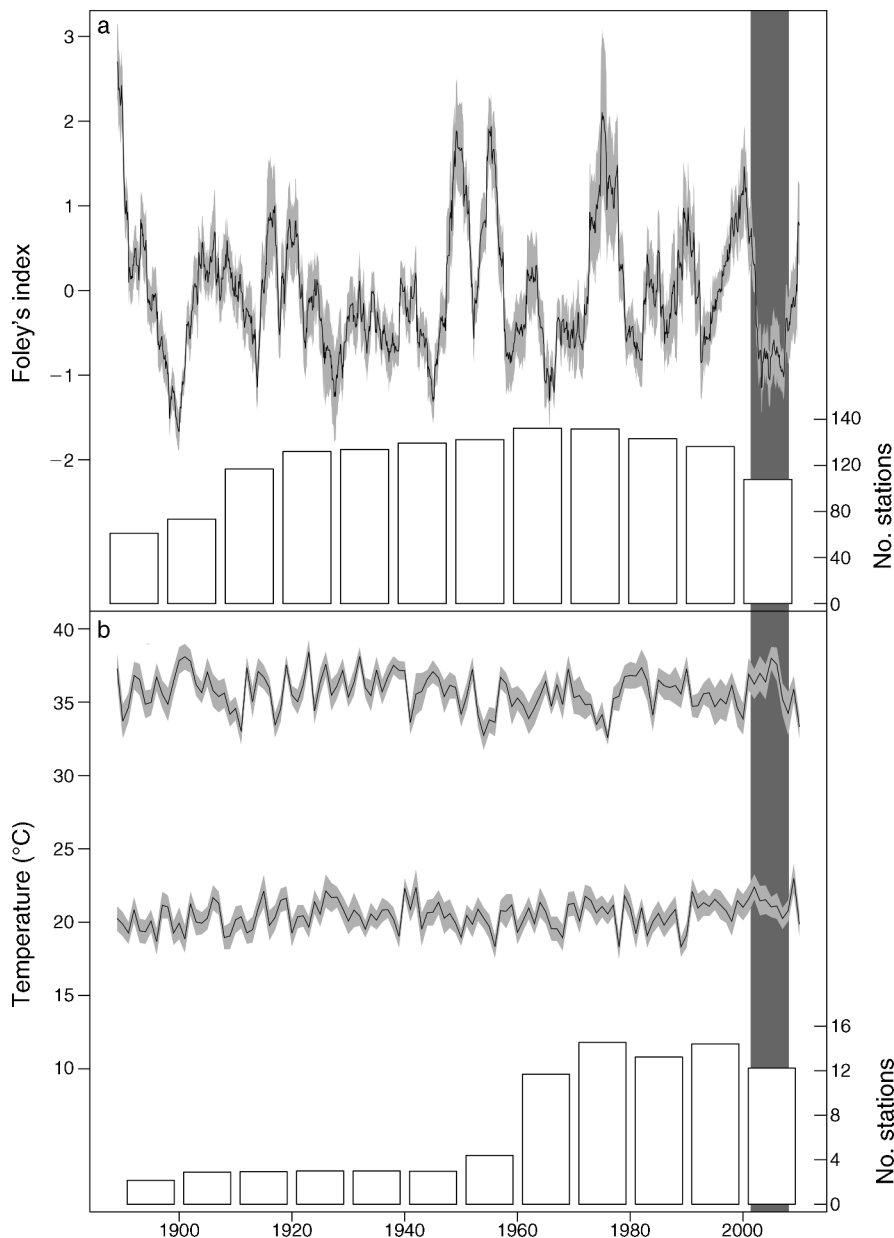


FIG. 2. Climate history for the Mulga Lands biogeographic region averaged from the SILO climate surface (see footnote 5) for every 0.1° cell, including (a) the three-year Foley's index representing relative rainfall over three-year periods, and (b) summer maximum temperature (averaged December–February) (upper line), and winter maximum temperature (averaged June–August) (lower line). The trend lines are buffered by one standard deviation. The dark gray vertical stripe identifies the conditions of the recent drought, 2003–2007. The bars identify the number of climate stations that inform the record within 100 km of the study area.

group of candidate models according to approximate posterior model probability. The R^2 values reported in Tables 2 and 3 are averages weighted by the posterior probability of each model (i.e., each combination of explanatory variables), and are provided to give an indication of the fit of the averaged model. Averaged coefficient values, their corresponding standard errors, and the probability of each coefficient not equaling zero are also reported.

Biomass model

Pre-drought biomass (healthy, barely alive, and recently dead trees) was modeled against annual rainfall, rainfall seasonality, mean maximum temperature, soil depth, surface coarse sand content, surface clay content, and distance to water-point (as an inverse surrogate of grazing intensity). The biomass response was square-root transformed to meet the assumptions of linear modeling. *Eucalyptus* and *Corymbia* form large trees

TABLE 1. Climate variables used in the analysis.

Variable	Derivation
Annual rainfall (mm)	Mean annual rainfall, 1890–2009.
Rainfall seasonality	Coefficient of variation of average monthly values, 1890–2009.
Mean maximum temperature	Average of annual maximum temperatures, 1890–2009 (°C).
Minimum Foley's index	Rainfall for three years preceding a given month less the three-year expected rainfall (equal to three times the mean annual rainfall), divided by mean annual rainfall for 1890–2009. The minimum of all values is selected.
Maximum temperature for Foley's period	Highest mean maximum temperature for three-year periods preceding a given month, 1890–2009.
Minimum Foley's index (recent drought)	Minimum three-year Foley's index, 2003–2008.
Maximum temperature at time of minimum Foley's index (recent drought)	Mean maximum temperature coinciding with the minimum three-year Foley's index, 2003–2008 (°C).

within the mulga forest in some areas. Their contribution to the residual variance of the averaged model was explored graphically.

Tree mortality model

A tree mortality model was developed using the proportion of pre-drought biomass that died following the drought (i.e., barely alive and recently dead biomass/pre-drought biomass) as the response variable. The response required logit transformation to meet assumptions of linear modeling. A small number of sampled proportions were zero or one, which respectively yield $-\infty$ and $+\infty$ on the logit scale. We adopted the approach of Warton and Hui (2011) and substituted zeros with the minimum nonzero proportion (0.005) and ones with 1 – the minimum nonzero proportion (0.995). Using more extreme arbitrary proportions produced outliers on the logit scale that could not be satisfactorily modeled using linear regression. Explanatory variables (Table 1) included minimum Foley's index (recent drought), maximum temperature at time of minimum Foley's index (recent drought), soil depth, distance to water-point (as an inverse surrogate of grazing intensity) and pre-drought tree density. Patchiness in tree mortality may be a function of localized rainfall events; however, available rainfall data is only likely to capture such local-scale rainfall events at or near operational stations. Thus, the reliability of rainfall records probably declines

with distance from nearby climate stations. We were interested to see if the reliability of rainfall records was related to the goodness of fit of the tree mortality model. We first estimated reliability using a density surface informed by the spatial configuration of weather stations, and the amount of information they provided during the recent drought. Specifically, a kernel smoothed intensity function was applied to station locations, with stations weighted by the number of months they were operational between March 2003 and December 2007. This reliability measure was then correlated with the absolute value of the residuals from the averaged tree mortality model.

Comparison of field and NCAS biomass estimates

Modeled aboveground biomass estimates for each site were also extracted from the NCAS (Richards and Brack 2004) for each 0.1° cell containing a site to compare with the field estimates presented here. Within NCAS these estimates are referred to as the maximum aboveground biomass (maxbio), and are the values at which aboveground biomass curves asymptote when modeling natural forest growth.

A meta-analytical approach was used to compare the field estimates with the NCAS maxbio estimates. The relative difference between field and NCAS estimates was expressed as a response ratio, i.e., $\ln(\text{field estimate}/\text{maxbio})$. Positive values of this ratio occur where field

TABLE 2. The Bayesian model averaging results for the biomass response (Mg/ha) based on 26 selected models.

Variable	Posterior probability $\neq 0$	Posterior mean of coefficient	Posterior SD of coefficient
Intercept	1.00	4.880	0.224
Annual rainfall (mm/yr)	1.00	0.026	0.003
Rainfall seasonality	0.346	-2.313	3.612
Mean maximum temperature	0.611	-0.378	0.346
Coarse sand (%)	0.058	-0.001	0.005
Fine sand (%)	0.271	-0.012	0.022
Soil pH	0.103	0.031	0.117
Soil depth (0 = shallow, 1 = deep)	0.607	0.374	0.361
Distance to water (km)	0.087	0.006	0.027

Note: The posterior-weighted average R^2 value of all models was 0.75.

TABLE 3. Bayesian model averaging results for the proportion of tree mortality response (logit transformed) based on 31 selected models.

Variable	Posterior probability $\neq 0$	Posterior mean of coefficient	Posterior SD of coefficient
Intercept	1.00	-0.730	0.190
Minimum Foley's index (recent drought)	0.596	-0.711	0.699
Maximum temperature at time of minimum Foley's index (recent drought)	0.578	0.217	0.220
Coarse sand (proportion)	0.49	-0.017	0.020
Fine sand (proportion)	0.019	0.0002	0.003
Soil pH	0.228	0.102	0.221
Soil depth (0 = shallow, 1 = deep)	1.00	-1.033	0.282
Distance to water (km)	0.098	-0.009	0.032
Tree density (stems/m ²)	0.144	0.631	1.874

Note: The posterior-weighted average R^2 value of all models was 0.21.

estimates are higher than maxbio, and negative values indicate the converse. The associated variances for each response ratio were calculated as follows:

$$\text{Variance of difference} = \text{f.var}_i / (\text{n.tran}_i \times \text{f.bio}_i^2)$$

where f.var is the variance of field biomass estimates from the four plots at site i , n.tran is the number of plots used to calculate f.var _{i} (four in all cases), and f.bio _{i} is the field biomass estimate for site i . Error associated with the maxbio estimates was not available at the time of writing, and was therefore not included in the calculation of the variance of differences. Response ratios were modeled as a function of annual rainfall in a random effects meta-regression. Linear and quadratic terms for annual rainfall were tested.

Spatial predictive modeling

The averaged biomass and tree mortality models were forecasted spatially using a 0.1° grid of climate variables and the land zone category (5 or 7) that was most dominant in each cell as determined from the regional ecosystem mapping. Explanatory variables that were not available for each grid cell (i.e., soil variables, distance to water, tree density) were held at their mean values. This approach was justified a posteriori given the weak support for models with these variables, and because they all had small averaged coefficients (relative to their units) with large standard errors (see *Results*). For predicting restoration potential, the 2006 cleared area of each land zone represented by a Regional Ecosystem mapping unit dominated by mulga was determined within each 0.1° grid cell. Predicted values of biomass and mortality were forecast separately for each land zone and then summed. The assumption underlying these projections that it is possible to recover the biomass of the original forest is generally justified given the potential for mulga regeneration (Fensham et al. 2012) and widespread practice of repeated clearing of woody regrowth.

The magnitude of future droughts under projected climate-change scenarios for the Mulga Lands is highly uncertain (CSIRO 2007), and forecasts for potential tree mortality under severe drought were developed by

incorporating the most severe rainfall deficit (minimum Foley's index) in the climate record (mainly 1902–1904) with the maximum temperature from any three-year period on record (generally 2000–2008).

All statistical analyses were undertaken in the R statistical program (R Development Core Team 2010). The BMA package (Raftery et al. 2010) was used for all Bayesian model averaging and the kernel smoothed intensity function from the Spatstat package (Baddeley and Turner 2005) was used to produce the rainfall station density surface. The random-effects meta-analysis was run using the Metafor package (Viechtbauer 2010).

RESULTS

Climate history

Using the three-year rainfall deficit, the major droughts in order of decreasing severity culminated in 1902, 1946, 1929, 1967, and 2003. Maximum temperature does not show any clear trend, but has relatively high summer values during the period of recent drought.

Biomass model

The coefficients for annual rainfall, maximum temperature, and soil depth all had >0.5 posterior probability of being nonzero (Table 2), with annual rainfall having a posterior probability of 1. Annual rainfall had a strong positive, almost linear relationship with aboveground biomass (Fig. 3), while the relationship of maximum temperature was negative and soil depth positive (Table 2).

The proportion of each site's biomass represented by *Eucalyptus* or *Corymbia* tends to increase toward the high-rainfall end of the gradient, but does not appear to provide substantial explanation for the residual variance in the averaged model (Appendix B).

The sites representing management contrasts suggest a partial explanation for unexplained variance. The biggest disparity is represented by the Quilpie contrast (Fig. 3), spanning 71% of the residual variance on the square-root biomass scale. Long-term grazing protection had lesser and more variable effects (Croxdale,

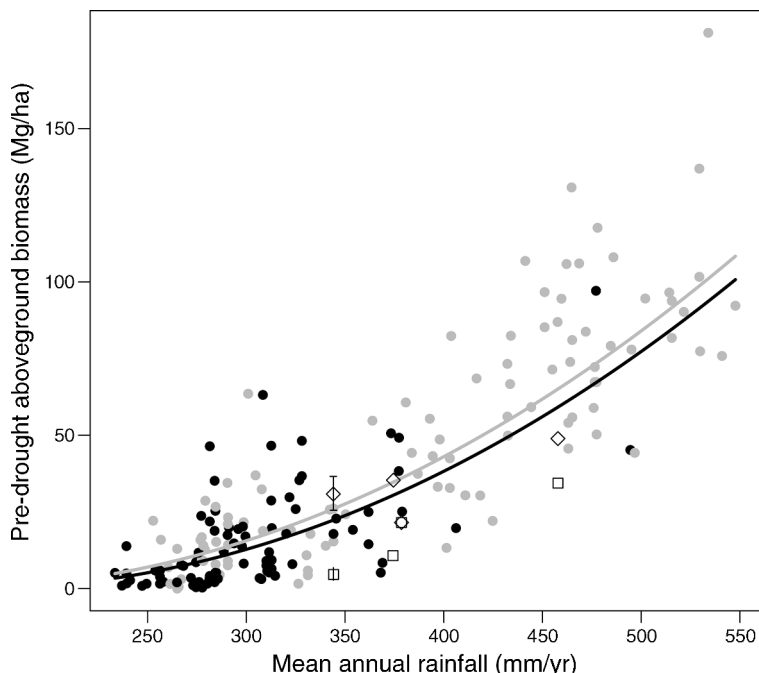


FIG. 3. Pre-drought aboveground biomass in relation to annual rainfall. Data points and trend lines are attributed according to land zone (gray, deep soil; black, shallow soil). All other variables were held at mean values for representation. The management contrasts are paired lightly grazed (diamonds) and heavily grazed (squares) areas in each of four sites (Quilpie, Wallen, Lanherne, and Croxdale). The values for lightly grazed and heavily grazed values at Lanherne are virtually identical. Vertical bars shown for the Quilpie sites indicate \pm SE.

18%; Lanherne, 2%; Wallen, 52% of residual variance). Soil depth was not informative for explaining variability across management contrasts.

Tree mortality model

Tree mortality was extremely patchy through the study area and ranged from 0% to 100% (Fig. 4). Mortality was not biased for any particular stem size in either the mulga or eucalypts (*Eucalyptus*, *Corymbia* combined) (Fig. 4).

The tree mortality model (Table 3) provided an inferior fit compared to the biomass model (Figs. 3 and 5). The coefficients for minimum Foley's index (recent drought), maximum temperature at time of minimum Foley's index (recent drought), and soil depth all had >0.5 probability of being nonzero (Table 3). Mortality was clearly exacerbated on shallow soils relative to deep soils. There was also strong indication that there was more tree mortality with lower coarse sand content.

There was no discernible relationship between the reliability index reflecting the quality of the rainfall record and the absolute residual values from the averaged tree mortality model (Spearman's $\rho = -0.044$; $P = 0.556$). The sites representing management contrasts suggest a partial explanation for unexplained variance because they indicate a consistent trend of greater tree mortality with reprieve from grazing (Fig. 5); however the magnitude of these contrasts varies greatly between sites. The percentages of residual

variance (on the logit scale) spanned by the contrasts were: Lanherne, 8%; Croxdale, 17%; Quilpie, 63%; Wallen, 92% (Fig. 5). Soil depth was not informative for explaining variability across management contrasts.

Comparison of field and NCAS biomass estimates

There was a significant and strong quadratic relationship between the response ratio (relative difference between estimates) and annual rainfall, indicating that field-based estimates are consistently higher than NCAS estimates in higher-rainfall regions, and consistently lower in low-rainfall regions (Fig. 6). Relative differences were greatest in low-rainfall regions, but in these areas the measured values of biomass exhibited a very substantial range (Fig. 6).

Spatial and temporal projections

The biomass of mature mulga forest shows a clear increasing trend from west to east (Fig. 7a), reflecting the strong trend of increasing rainfall but also a preponderance for deeper soils in the east. The restoration potential of mulga forest is highest in the eastern areas because this is where clearing has been concentrated and where the potential for high biomass is greatest (Fig. 7b). Modeled tree mortality after the recent drought (Fig. 7c) is less than projected tree mortality for a projected drought scenario represented by the combination of the most intense historical drought and maximum temperature for Foley's period

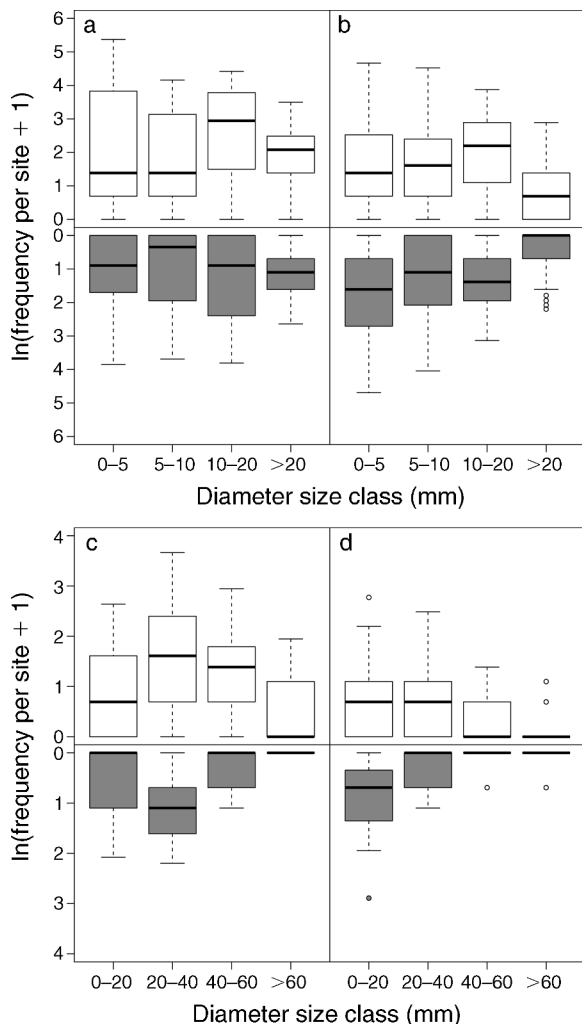


FIG. 4. Box-plots of size classes with live stems above the line (open bars) and dead stems below the line (shaded bars) for mulga in (a) high-rainfall environments (>400 mm annual rainfall) and (b) low-rainfall environments (<400 mm annual rainfall); and for eucalypts (*Eucalyptus*, *Corymbia*) in (c) high-rainfall environments (>400 mm annual rainfall) and (d) low-rainfall environments. Frequencies were log-transformed to enhance visual representation. Boxes represent the 25th and 75th percentile, error bars represent the 10th and 90th percentile, and the median is the horizontal line within a box.

(Fig. 7d). Under the recent drought the mean observed mortality was 21.6%. Fitting our extreme drought scenario to the mortality model suggests that this would increase to 30.1%.

DISCUSSION

The mulga-dominated vegetation in eastern Australia varies from stunted shrubland (canopy cover, $<10\%$; height, <5 m) in the southwest to forest (canopy cover: $>70\%$, height: ~ 12 m) in the northeast (R. Fensham, unpublished data). Aboveground biomass approaches zero in low-rainfall environments (i.e., <250 mm annual

rainfall), but exceeds 100 Mg/ha where rainfall is 550 mm in the northeastern part of the region (Figs. 3 and 7).

Mean annual rainfall is the dominant explanatory variable, with temperature (collinear with rainfall seasonality) and soil depth providing only modest additional explanatory power. Studies from other ecosystems, including *Eucalyptus* forest from eastern Australia (Keith et al. 2010), savanna from northern Australia (Williams et al. 1996), and African savanna (Sankaran et al. 2008) have also found rainfall an important predictor of structural attributes. Variation in statistical procedures makes a quantitative comparison difficult, but rainfall would appear to have a greater control over biomass in the mulga dry forest than the vegetation in other studies.

The role of grazing/browsing on aboveground biomass was evaluated using three methods: (1) with the incorporation of the inverse grazing index of distance to water in the modeling; (2) by locating a site with a stark contrast in woody biomass and identifying the underlying management history; (3) by evaluating difference in biomass across the fences of three long-term grazing exclosures. The grazing surrogate based on the distance-to-water index had limited explanatory power within the biomass model that explained a high degree of variation using climatic and edaphic attributes. This index should represent the range of feasible grazing intensities across the mulga dry forest, because it is represented by 10% of sites beyond the 3.5-km threshold when the dominant herbivores, sheep and grey kangaroos, exhibit substantial declines in density. The sites representing more extreme management contrasts, including the long-term removal of domestic stock, suggest that management may account for some of the unexplained variability in the biomass model. The critical combination of events needed to promote mulga recruitment seems to be grazing relief during the wet periods that are required for mass germination (Harrington 1979), and extending for at least six years (including at least two years with above-average rainfall) when mulga growth can exceed the browsing height of sheep (Brown 1985). An even longer period of grazing relief would be necessary with cattle grazing, because young mulga trees (as opposed to seedlings) are also palatable to cattle, which have a longer browse reach than sheep. Mulga does not seem to have a substantial long-lived seed bank (Wright and Clarke 2009), and the lack of recruitment in some long-term grazing exclosures (Fig. 3) may reflect a lack of coincidence between high rainfall and seed production. Our study did not include contrasts represented by total grazing protection, as the exclusion of macropods is unrealistic and undesirable (cf. Witt et al. 2011). Given the weak effect of distance to water, the patchy response of mulga protected from livestock, and the ubiquity of macropods in the region, the manipulation of aboveground biomass with practical grazing management is

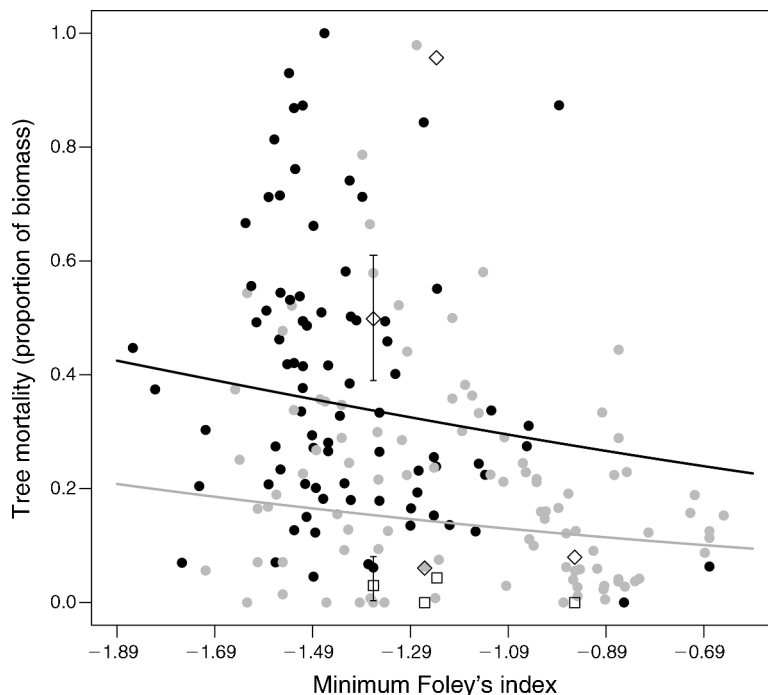


FIG. 5. Tree mortality as a proportion of pre-drought biomass in relation to the minimum Foley's index for the 2003–2008 period. Data points and trend lines are attributed according to soil depth (gray, deep; black, shallow). All other variables were held at mean values for representation. The grazing management contrasts are paired lightly grazed (diamonds) and heavily grazed (squares) areas in each of four sites (from left to right, Quilpie, Lanherne, Wallen, and Croxdale). Vertical bars shown for the Quilpie sites indicate \pm SE.

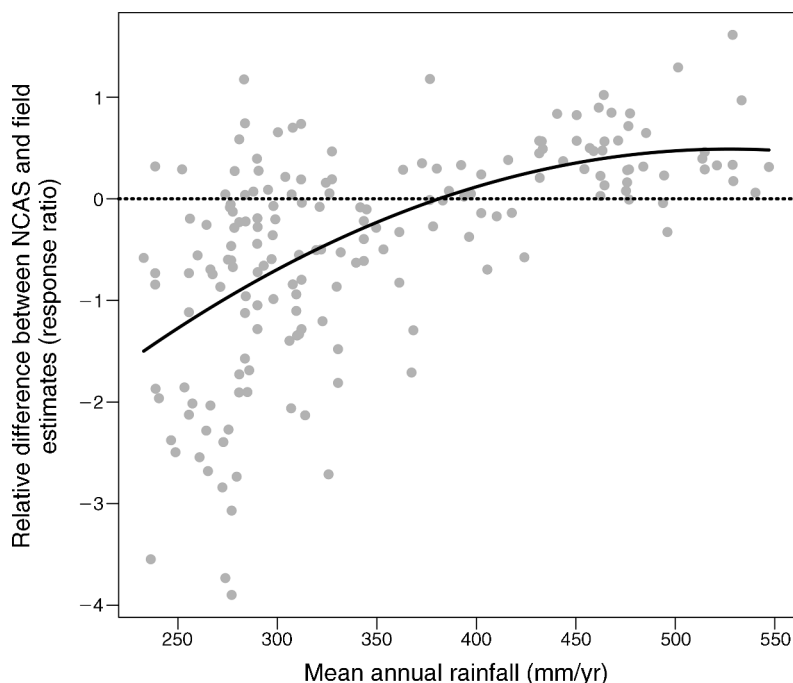


FIG. 6. The relative difference between field and aboveground biomass estimates modeled from the National Carbon Accounting System (NCAS) (response ratios) in relation to annual rainfall. Positive values on the y-axis indicate that field estimates are greater than modeled estimates; negative values indicate the reverse. The curve is the fitted quadratic relationship with annual rainfall from the random-effects meta-regression.

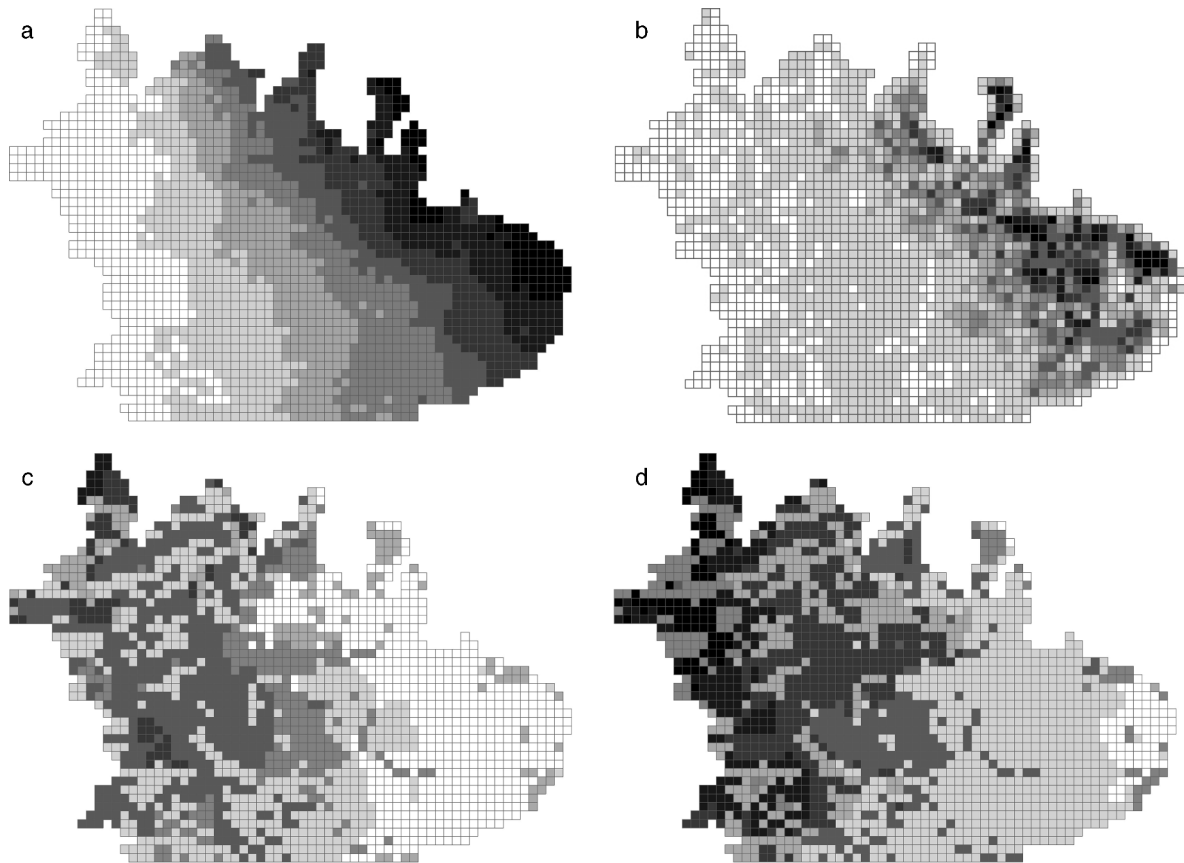


FIG. 7. Modeled projections represented by eight equal segments across the range of values for each 0.1° cell. (a) Mulga forest biomass modeled from climate and the dominant land zone for each cell, assuming that mulga forest occupies the entire area of each cell, range 1.0–122.1 Mg/ha; (b) potential biomass if mulga forest were restored in all areas where it is currently mapped as cleared, range 0–978 162 Mg, with the first segment represented by zero, the second to seventh segment represented by 100 000-Mg increments, and the eighth segment representing >600 000 Mg; (c) modeled proportion of tree mortality in mulga forest after the 2003–2007 drought, range, 0.061–0.531; (d) modeled proportion of future tree mortality in mulga forest based on the coincidence of the minimum recorded three-year Foley's index and maximum recorded temperature for Foley's period, range, 0.113–0.605. Note that forecast projections for tree mortality under recent drought and future severe drought are represented on the same scale, spanning values of 0.061–0.605.

likely to prove unpredictable and have limited overall consequence.

Fire provided an important contribution to continental-scale models describing tree cover in Africa (Sankaran et al. 2005, 2008), and is also heavily implicated as a determinant of structural change based on experimental findings (Sharam et al. 2006, Staver et al. 2009). Boundaries between mulga forest and spinifex (*Triodia* spp. grassland) are thought to be “meta-stable” because of feedbacks that confer fire retardance through fuel suppression within the forest (Bowman et al. 2008, Nano and Clarke 2008). However, spinifex is not common through the Mulga Lands bioregion (Dawson 1974, Mills 1980b) and the low-productivity mulga forest rarely promulgates fire (Hodgkinson et al. 1984). The rarity of fire may contribute to the close relationship between mulga biomass and climatic parameters.

Tree mortality is extremely patchy, and was represented by an average loss of 7.2 Mg/ha live biomass as a result of the 2000s drought. The overall average mortality of 21.6% was slightly less than after another drought event in the 1990s occurring in *Eucalyptus* woodland of north Queensland (Fensham and Holman 1999), and this is substantially less than estimates from droughts in pinon–juniper dry forest in the southwestern United States (Huang et al. 2010). Tree mortality can only be poorly explained by models incorporating rainfall deficit, temperature, soil characteristics, and various measures representing density dependence. The network of 105 rainfall stations through the region partially represents the patchiness of rainfall (Appendix C), but we found no relationship between the information index (based on proximity of sites to rainfall stations) and the tree mortality model residuals.

Tree mortality was ameliorated with increasing concentration of coarse sand. While this finding is not universal (Galiano et al. 2010), there are explanations for this “inverse texture effect” (Noy-Meir 1973) that are consistent with other studies. First, roots penetrate to greater depths on coarse-textured soils (Hacke et al. 2000, Sperry and Hacke 2002) and the importance of this is confirmed in the current study by the influence of soil depth on drought susceptibility represented by the broad mapping data. Second, capillary movement is disrupted in coarse surface soils as drying progresses, with the consequence that deep moisture reserves are diminished less during drought than in fine-textured surface soils (Alizai and Hulbert 1970).

Enhanced drought-induced tree mortality through density-dependence effects has been reported by some North American studies (Savage 1997, Guarín and Taylor 2005), but the most targeted study failed to realize these effects (Ganey and Vojta 2011). There is also limited evidence of density dependence (as represented by tree density) on mortality at the site scale. At two of the management contrast sites (Quilpie and Wallen), stems had accumulated substantially in the lightly grazed relative to the heavily grazed treatment (Fig. 3), and then exhibited substantial tree mortality during drought in 2007 (Fig. 5). Another site (Croxdale) had elevated stem densities in the lightly grazed treatment, but mortality was negligible during the drought. Thus while density-dependent mortality can occur in mulga, it did not emerge as a dominant influence within this regional data set, and is probably less important than in eucalypt woodlands (Fensham et al. 2005, 2009, Dwyer et al. 2010).

Clearly there are factors other than rainfall deficit and density dependence influencing the patchiness of tree mortality. Deep-soil characteristics that are difficult to investigate may play a role (Fensham and Fairfax 2007), and biological interactions (other than competition) are poorly understood in Australia and require further investigation. In North America bark-feeding beetles are implicated (Santos and Whitham 2010), although death can certainly occur due to drought alone (Floyd et al. 2009). There is no published information implicating a biological agent in the drought-induced tree mortality of mulga, but based on anecdotal reports, grasshoppers may be a candidate, having been reported to have stripped trees which, in a drought-stressed condition, are unable to recover (R. Kerr, *personal communication*). Biological interactions with drought-induced stress are difficult to study, requiring attention during the small windows when trees are in the grip of drought.

The field-based measurements of biomass in uncleared mulga forest are probably close to carrying capacity because the sites are uncleared, fire is rare, grazing disturbance has negligible or negative impact on tree stocks, there is no evidence of a sustained increase in tree cover during the course of pastoralism (Witt et al. 2006, Fensham et al. 2011a), and most importantly, measure-

ments were made at the end of a relatively wet second half of the 20th century (Fig. 2) when biomass will be higher than average. The maxbio estimates from the Australian National Accounting System seem to overestimate biomass of mature mulga forest, particularly in the low-rainfall part of the study region. This comparison belies the very substantial range of biomass values in the low-rainfall areas, which for the low-biomass sites may be a legacy of past drought-induced tree mortality. The overestimation of maxbio contrasts with findings from *Eucalyptus* forest in high-rainfall regions of Australia, where maxbio is a substantial underestimate of aboveground biomass (Keith et al. 2010). In the higher-rainfall areas of the mulga dry forest, where there are the greatest opportunities for restoration (Fig. 7), maxbio modestly underestimates field-based measurements.

In most cases mulga survives as young plants after clearing, and pastoralists who want to maintain treeless pasture are forced to continue a cycle of reclearing on a 15-year time frame. Based on our predictions, the restoration of the 27 019 km² of cleared mulga forest in Queensland represents 331 Tg (teragrams) of CO₂-e of aboveground biomass. After adding 20%, a conservative estimate of root biomass (Snowdon et al. 2000), and assuming that restoration occurs over 70 years (Vargas et al. 2008), this would account for 1.04% of the 548 Tg CO₂-e/yr recently reported as Australia's total annual emissions (Department of Climate Change and Energy Efficiency 2010), 2.3% of Garnaut's (2008) estimate for reversing “degradation” in Australian rangelands, and about 44% of the Witt et al. (2011) estimate for changed grazing management in the Mulga Lands of New South Wales and Queensland. The estimated future drought scenarios would diminish stocks in mature mulga forest, although death will be more pronounced in the western areas where soils are shallower in these areas and droughts are more intense. It should be noted, however, that the mortality of live biomass does not necessarily reduce overall aboveground biomass stocks. In the semi-arid environments of the mulga dry forest, decomposition is slow, and because fires are rare, dead wood will persist and accumulate. This represents an unknown additional sink.

The potential for restoring mulga forest for carbon accumulation is revealed by this study. However, the areas in the east of the study area with higher potential biomass stores are also the most productive pastoral lands, and the restoration of derived grassland to forest will adversely impact ecosystem services associated with pasture production (Pressland 1976, Silcock et al. 1985); this trade-off will have to be factored into land management decisions and planning. There may be additional trade-offs for carbon sequestration with clearing vs. restoration of mulga dry forest involving soil carbon (Dalal et al. 2005, Harms et al. 2005) and reduced livestock methane emissions from livestock (Hegarty et al. 2010). The extent to which restoration

of aboveground woody biomass and other sequestration opportunities are embraced will depend on which components of the fluxes are accredited under carbon accounting policies and the price of carbon.

This study identifies an opportunity to sequester carbon through restoration of mulga dry forest that is modest in the grand scheme of global or even Australia's emissions. The role of disturbances in determining aboveground biomass stocks is unpredictable, and we are less confident than Witt et al. (2011) about manipulating substantial increases in aboveground woody stocks through grazing management. This finding appears to be inconsistent with other studies from Africa (Tobler et al. 2003) and the USA (Asner et al. 2003) that have exhibited a prolonged increase in tree cover with pastoralism. The findings suggest that the mulga dry forest is a resilient ecosystem, livestock grazing has a variable but overall small impact on stand biomass, and that only particular and unlikely combinations of management (i.e., wet weather and grazing protection) can generate substantial increases in tree densities, which are then vulnerable to collapse in subsequent droughts. The resilience of the mulga dry forest to human-induced disturbance is consistent with some forests of similar climatic regimes (Tefera et al. 2007), but contrasts sharply with other dry forests where fire is an important disturbance agent (Smit et al. 2010).

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SUPPLEMENTAL MATERIAL

Appendix A

Allometric equations used in the current study for aboveground biomass (*Ecological Archives* A022-049-A1).

Appendix B

The proportion of aboveground biomass at each site contributed by eucalypts (*Eucalyptus/Corymbia*) biomass (*Ecological Archives* A022-049-A2).

Appendix C

An example of the rainfall station density surfaces used to estimate the reliability of rainfall records (*Ecological Archives* A022-049-A3).