



Ecohydrological feedback as a land restoration tool in the semi-arid Brigalow Belt, QLD, Australia

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ABSTRACT

In this study of native plant communities in the Brigalow Belt – a semi-arid bioregion of Queensland and New South Wales, Australia – an ecohydrological model was designed to investigate the complex feedback relationships existing between plant community traits and soil water dynamics among post-disturbance (i.e. mining and agricultural) landscapes. Two distinct locations (having similar composition and climatic environment, yet different soil water dynamics) were selected to compare the interaction and sensitivity of these traits towards water evaporation from soil or from plant transpiration. The model is constrained by soil physical attributes and climate data monitored at the Brigalow Catchment Study, and plant community parameters were derived using Latin hypercube sampling and pattern oriented modelling.

Our findings indicate that, under the given soil–climate constraint, plant communities could only thrive if they were able to avoid prolonged periods of water stress (e.g., by minimising their physiological wilting point). Further, the influence of vegetation dynamics on evaporation from soil was deemed to be critical for the simulated soil water dynamics, whereas plant transpiration affected soil moisture only marginally.

Moreover, both monitoring sites were dominated by the same species but co-dominated by different tree species, suggesting that evaporation from soil was probably influenced by the co-dominant species, whereas transpiration was probably controlled by the dominant species.

For the re-establishment of native plant communities on post-mined landscapes and for agro-forestry and resource management in the Brigalow Belt, this implies that inherent ecosystem processes exist, which control plant community development and, hence, ecohydrological functions such as regulation of evapotranspiration.

Therefore, restoration strategies should carefully reflect on species composition and their ecohydrological functions rather than attempting to re-establish the pre-disturbance ecosystem form and function – which could be less robust and even unsuccessful given post-disturbance conditions and under altered soil conditions of post-mined landscapes or the uncertainty of future climatic environments.

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1. Introduction

The integration of native plant communities for the purpose of restoring degraded landscapes (e.g., post-mined and long established field agricultural sites) is often desirable because of their inherently low maintenance requirements. Also, these native species often have more robust physiological adaptations in relation to environmental stress (Lamb et al., 2005), for instance, in relation to extreme weather events like intense rainfall or prolonged drought periods (Fey et al., 2002; Price et al., 2011; Rodrigues et al., 2011; Simmons et al., 2011). Still, a particular

challenge for any post-disturbance environment is the establishment of suitable conditions for the revegetated native communities to achieve essential levels of functionality and resilience (Suding et al., 2004; Harris et al., 2006). This is especially true for highly disturbed landscapes that are exposed to potentially irreversible modifications to the rehabilitated landforms (e.g., soil texture, topography, ecosystem fragmentation) (Grant, 2006). Hence, the comprehensive assessment of environmental drivers (both biotic and abiotic) within these post-disturbed landscapes should be a key step towards any successful rehabilitation effort (King and Hobbs, 2006; Hobbs, 2007).

In the case of semi-arid areas having rare or highly erratic rainfall, the depiction of hydrological cycles (namely the soil water balance) is regarded as an important broad-scale factor for predicting ecological development. In these water-controlled ecosystems,

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where water is the limiting factor because of its scarcity and/or its erratic and unpredictable occurrence (Rodríguez-Iturbe and Proporato, 2004), soil water content is a fundamental determinant of many ecological processes due to the inherent feedback between vegetation and hydrological processes (Eamus et al., 2006; Newman et al., 2006). Meanwhile, evapotranspiration plays a key role in linking ecosystem and soil water dynamics, particularly during dry periods when water availability is limited (Zhang et al., 2001; Kurc and Small, 2007; Yaseef et al., 2010). Based on these criteria, we consider that such ecohydrological relationships could be used as potential bio-indicators of ecological function and, perhaps, even predictors of rehabilitation success among water-controlled environments through the pairing of plant community traits in relation to various climatic scenarios.

Given the interplay between native plant communities and ecohydrological factors, the Brigalow Belt (Queensland, Australia) offers a unique opportunity to study the function of water-controlled ecosystems in the context of post-industrial and post-agricultural land rehabilitation. The Brigalow Belt (also referred as the Brigalow Tropical Savannah) is a bioregion located between the sub-tropical coastline and the semi-arid interior of Queensland and New South Wales (Appendix A). The bioregion is climatically and edaphically distinct from surrounding areas due to the proliferation of brigalow plant communities (Lloyd, 1984), which typically form open-forests and woodlands dominated by brigalow trees (*Acacia harpophylla*) (Isbell, 1962; Johnson, 1980). This region is characterised by highly erratic rainfall events (in regard to both intensity and seasonality) (Lloyd, 1984) as well as vertosol soils that are rich in clay, have high fertility and good water-holding capacities (Gunn, 1984). Since the 1950s, much of the overall native brigalow woodland had been cleared for agricultural purposes (e.g., cropping and grazing) with little of the pre-disturbance vegetation currently remaining. Likewise, in the Northern Brigalow Belt, significant areas are concurrently affected by coal mine developments. Besides the primary goal of achieving a stable and sustainable ecosystem, part of the discussion for rehabilitating these anthropogenically impacted areas involves the re-establishment of brigalow plant communities in hopes of serving “as biological corridors for the circulation of biodiversity across large-scale agricultural landscapes” (Altieri, 1999). Fortunately, these ecosystems have been the focus of environmental monitoring and active research in the form of a long-term paired catchment study since the 1960s (Brigalow Catchment Study I–III) (Cowie et al., 2007; Radford et al., 2007; Thornton et al., 2007). And so, extensive data have been collected for the parameterisation of ecohydrological processes occurring within the region (including infiltration, evapotranspiration, deep drainage, and runoff formation) which could be used for predicting revegetation development within affected areas.

Building from these findings, the primary objective of this study was to investigate the sensitivity of soil moisture dynamics in relation to plant community traits within the Brigalow region. To achieve this, the partitioning of evapotranspiration into soil evaporation and plant transpiration was targeted for determining vegetation responses to changes in land use and other management decisions, and eventually, the productivity of the ecosystem (Law et al., 2002; Huxman et al., 2005; Booth and Loheide, 2010). A feature of the analysis was the identification of interlacing biotic (plant transpiration) and abiotic processes (soil evaporation) occurring at two sites in a catchment of native brigalow stands. Ultimately, we aimed to build a predictive model of ecosystem function (biomass and soil moisture) which would allow us to depict plant community traits and provide an ecohydrologically based monitoring tool for the purpose of ecological restoration and agro-ecological/forestry management.

2. Material and methods

The study was conducted within the Brigalow Catchment Study (BCS) – an Australian Long Term Ecological Research site – which has been conducting monitoring activities regarding climate, soil properties and soil water dynamics since 1965 (Cowie et al., 2007). Study sites (described below) were selected since they shared the same climatic environment and soil type, but had different soil water dynamics. This investigative strategy assumed that such differences should be governed by plant community traits eventually feeding back within the ecosystem to result in different rates of soil evaporation and plant transpiration. To maintain the model analytically tractable and parsimonious, species interactions were neglected and simplifying assumptions were carried out and stated clearly. Since this study focused on temporal dynamics of ecohydrological interactions, we excluded any spatial components.

2.1. Data sources

The BCS site is located in the northern brigalow bioregion, in central Queensland. The site (24.81°S, 149.80°E) is in the Dawson sub-catchment of the Fitzroy basin (Thornton et al., 2007). The BCS site is a long-term paired catchment study consisting of three catchments chosen as being representative of the broader bioregion based on climate, soil type and native vegetation. The site has a semi-arid subtropical climate, is dominated by uniform, fine-textured, dark cracking clay soils (Black and Grey Vertosols (Isbell, 2002)) and non-cracking clays (Black and Grey Dermosols (Isbell, 2002)), and the dominant overstorey species is brigalow (*A. harpophylla*) (Cowie et al., 2007; Thornton et al., 2007).

The investigative focus of this study was the native vegetation communities that exist within the 16.8 ha ‘virgin’ brigalow scrub catchment and, in particular, those communities existing on clay soils. Permanent monitoring sites were established in the catchment using double stratification based on soil type and landscape position, with two sites occurring on clay soils. While these sites have similar soil type and micro-topography their vegetation is dominated by different native plant communities in terms of species abundance (Johnson, 2004; Cowie et al., 2007). One site is dominated by a brigalow-Dawson gum canopy (*A. harpophylla* and *Eucalyptus cambageana*), hereafter described as BDG site. The other site is dominated by a brigalow-belah canopy (*A. harpophylla* and *Casuarina cristata*), hereafter described as BB site. Understoreys of all major communities are characterised by *Geijera* sp. either exclusively, or in association with *Eremophila* sp. or *Myoporum* sp. (Johnson, 2004). Both vegetation stands have similar age, rooting depth, no access to ground water, and their phenology is governed by water availability. Litter levels (both leaf and wood) range from 1.9 t ha⁻¹ in non-vegetated areas to 29 t ha⁻¹ in ‘tree’ areas (Dowling et al., 1986).

Soil water content at each monitoring site was determined using a combination of gravimetric (0–0.2 m) and neutron scatter techniques (0.2–2.0 m or rock interference). Rainfall data was obtained from a recorder at the head point of the catchment, while pan evaporation was obtained from a Bureau of Meteorology station (No. 035149) located 2 km to the south. Being dominated by a subtropical climate with wet summers and low winter rainfall, most of the annual average rainfall of 720 mm falls between October and March. Moreover, rainfall is highly variable in terms of spatio-temporal occurrence and intensity, ranging from 246 to 1460 mm per year. The annual average potential evaporation is 2133 mm (Cowie et al., 2007; Thornton et al., 2007). Combined soil and climate data were available for three time periods (1983–1985, 1987–1988, 2003–2004), which have been used as model training periods (calibration) and for validation. While the climate data were available at daily time intervals, soil moisture has been

measured only irregularly (Fig. 3c and d) at intervals of 10 cm along a vertical soil profile of 2 m thickness.

2.2. Parameter estimation

The model was parameterised using pattern oriented modelling (Grimm et al., 2005; Lambert and Rochard, 2007; Rangel et al., 2007; Wiegand et al., 2008; Piou et al., 2009; Swanack et al., 2009; Topping et al., 2010; Railsback and Johnson, 2011; Grimm and Railsback, 2012). This strategy acted as a filter to identify whether a given set of parameters was able to reproduce the observed patterns, because they contain information on the internal organisation of a system in an integrated form and are often indicators of essential underlying processes and structures. Latin hypercube sampling was used to identify parameter sets which are able to reproduce three observed patterns, namely the soil water content of the upper and lower soil layer, and the susceptibility¹ to sustain plant communities in the Brigalow Belt. The observed soil water content denotes a quantitative pattern, which was assumed to be accepted when the observed and predicted soil water content (Eq. (1)) did not vary more than $0.1 \text{ m}^3 \text{ m}^{-3}$ and $0.02 \text{ m}^3 \text{ m}^{-3}$ for the upper and the lower soil layer, respectively. The susceptibility to sustain plant communities in the Brigalow Belt for many decades/centuries is a rather 'soft' or qualitative pattern, which was assumed to be accepted if the predicted biomass (Eq. (13)) was calculated greater than 0.1 t ha^{-1} . The sampled parameter sets were checked for plausibility to avoid the identification of unrealistic or physically impossible parameter combinations. For example, (1) if the transpiration rate per unit green biomass converges to zero no biomass growth is possible (Eq. (12)), (2) the soil water potential leading to plant water stress must be larger than the soil water potential at the permanent wilting point, or (3) the total plant community transpiration must not exceed the unsaturated hydraulic conductivity of the soil (Eq. (7)).

The pattern oriented calibration of the model results in a set of possible parameter combinations, which are able to reproduce the observed patterns. Each unique set of these parameter values was used as being representative of a possible native or 'true' plant community of the Brigalow Belt (following Kleidon and Mooney (2000)), assuming that it defines the ecohydrological function of the plant community. In this context, it is possible to use the ensemble of parameter sets to investigate whether parameters which represent response traits (plant functional traits considered in terms of their response to abiotic ecosystem components (Chapin et al., 2000; Lavorel and Garnier, 2002; Gross et al., 2008)) are different between two monitoring sites of native brigalow plant communities. For both monitoring sites three training periods were used (1983–1985, 1987–1988, 2003–2004) to identify the set of parameter combinations, which fulfil the observed patterns (calibrated parameter sets). We validated them by application for time periods not used previously for calibration. Eventually, only those parameter sets were used for further investigations that were able to predict the observed empirical patterns of soil water content and susceptibility to sustain plant communities for all three time periods.

2.3. Model

The focus of this study was to gain principle understanding of the interplay between brigalow plant communities and soil moisture dynamics. Therefore, we followed a 'top-down' approach (Kot, 2001; Zhang et al., 2001) and used a simple aggregated plant community model linked to a storage based soil water model. The

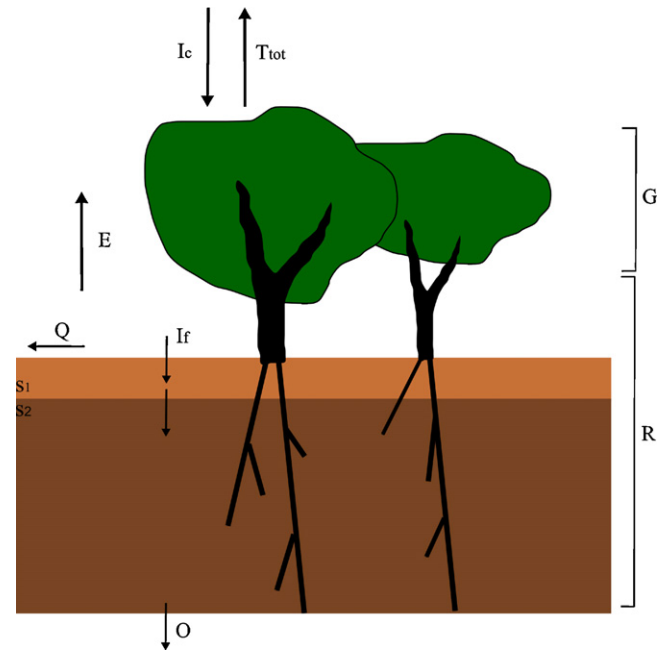


Fig. 1. Model scheme of the applied ecohydrological model. The arrows denote the relevant processes where I_c is the interception, I_f the infiltration, O the overflow into deeper soil layers or ground water, T_{tot} the transpiration from plants, E the evaporation from vegetation covered soil, and Q the runoff. The ecohydrological system is described by four state variables where s_1 and s_2 is the soil moisture content of the two soil layers, respectively, and G and R denote the green and reserve biomass of the ecosystem.

plant community model summarises all relevant effects caused by processes at the individual and population scale (e.g., growth and mortality, response to stress periods) (Frank and Wissel, 2002) without explicitly considering species interactions and spatial components (e.g., recruitment, dispersal). The model is applied on a daily time scale and is illustrated in Fig. 1. Parameter value ranges and units are given in Table 1.

The model calculates the soil water balance at a point expressed as

$$s_i(t) = s_i(t-1) + \left(\frac{(I_{f,i}(s,t) - O_i(s,t) - E_i(s,t) - T_{tot,i}(s,t))}{n_i \cdot Z_{r,i}} \right), \quad (1)$$

where $s_i(t)$ denotes the relative soil moisture content of soil layer i at time step t , $I_{f,i}(t)$ is the infiltration, $O_i(t)$ is the overflow into deeper soil layers, $E_i(t)$ is the evaporation from soil, $T_{tot,i}(t)$ is the total transpiration from the plant community, n_i is the soil porosity, and $Z_{r,i}$ is the depth of 'active' soil (root depth).

It is assumed that infiltration into the upper soil layer is governed by the intensity of rainfall $P_i(t)$ and the saturated hydraulic conductivity of the upper soil layer $K_{s,1}$ (to be calibrated). If the lower soil layer has enough available storage, infiltration into the lower soil layer is assumed to be equal to the overflow from the upper layer (Eq. (5)):

$$I_{f,1}(s,t) = \min[[P_d(t) - I_c(t)], [1 - s_1(t) \cdot n_1 \cdot Z_{r,1}]] \quad \text{for } P_i(t) \leq K_{s,1} \quad (2a)$$

$$I_{f,1}(s,t) = \min \left[\left(\frac{K_{s,1}}{P_i(t)} \right) \cdot P_d(t), (1 - s_1(t) \cdot n_1 \cdot Z_{r,1}) \right] \quad \text{for } P_i(t) > K_{s,1} \quad (2b)$$

$$I_{f,2}(s,t) = \min[O_1(s,t), (1 - s_2(t) \cdot n_2 \cdot Z_{r,2})], \quad (2c)$$

¹ Susceptibility refers to the potential of the soil and climate to sustain the desired plant communities (e.g., brigalow).

Table 1
Symbols used in this study, *i* denotes the reference to a layer.^a

Symbol	Description	Value (unit)	Eqn
<i>a</i>	Shape parameter of g_G-function	{0.01–0.1} (-)	(12)
<i>b</i>	Shape parameter of g_G-function	{–4 to 0} (-)	(12)
<i>c</i>	Shape parameter of Ψ^*-function	{–0.7 to –0.3} (-)	(9)
<i>d</i>	Shape parameter of Ψ^*-function	{9–11} (–ln hPa)	(9)
<i>E_i</i>	Evaporation from vegetation covered soil	Calculated (mm d ^{–1})	(6)
<i>E_{max}</i>	Maximum evaporation from soil	Calculated (mm d ^{–1})	(6a)
<i>G</i>	Green biomass	Calculated (kg m ^{–2})	(10)
<i>g_{Gmax}</i>	Maximum growth rate of green biomass	{0.01–0.1} (d^{–1})	(12)
<i>g_G</i>	Growth rate of green biomass	Calculated (d ^{–1})	(12)
<i>g_R</i>	Growth rate of reserve biomass	{0.01–1} (d^{–1})	(13)
<i>I_c</i>	Canopy interception	Calculated (mm d ^{–1})	(3)
<i>I_f</i>	Infiltration	Calculated (mm d ^{–1})	(2)
<i>K_{s,i}</i>	Saturated hydraulic conductivity	{1–10000} (mm d^{–1}) for <i>i</i> = 1, {1–1000} (mm d^{–1}) for <i>i</i> = 2	(2)
<i>K_{u,i}</i>	Hydraulic conductivity of unsaturated soil	Calculated (mm d ^{–1})	(5)
<i>m_R</i>	Mortality of reserve biomass	{0.01–0.1} (d^{–1})	(13)
<i>n_i</i>	Porosity	Observed data (m ³ m ^{–3})	(2)
<i>O_i</i>	Overflow into deeper soil layers	Calculated (mm d ^{–1})	(5)
<i>P_d</i>	Rainfall depth	Observed data (mm event ^{–1})	(2)
<i>P_t</i>	Rainfall intensity	Observed data (mm d ^{–1})	(2)
<i>PET</i>	Potential evapotranspiration	Observed data (mm d ^{–1})	(6)
<i>Q</i>	Runoff	Calculated (mm d ^{–1})	(4)
<i>R</i>	Reserve biomass	Calculated (kg m ^{–2})	(13)
ρ_i	Evaporative portion of PET	{0.01–0.5} (-) for <i>i</i> = 1, {0.01–0.1} (-) for <i>i</i> = 2	(6a)
<i>s_i</i>	Relative soil moisture content	Calculated (-)	(1)
<i>T_G</i>	Transpiration rate per unit green biomass	Calculated (L kg ^{–1} d ^{–1})	(8)
<i>T_{max}</i>	Maximum transpiration rate per unit green biomass	{0.01–5} (L kg^{–1} d^{–1})	(8)
<i>T_{tot,i}</i>	Total plant community transpiration	Calculated (mm d ^{–1})	(7)
<i>t</i>	Time step	(d)	(1)
<i>Z_{r,i}</i>	Active soil (root) depth	Observed data (mm)	(1)
α	Shape parameter of I_c-function	{0.01–0.04} (-)	(3)
β	Shape parameter of I_c-function	{0.11–0.16} (-)	(3)
λ	Empirical soil parameter	Literature value {15} (-)	(5)
Ψ_{fc}	Soil water potential at field capacity	Calculated (h Pa)	(6)
Ψ_h	Soil water potential at hygroscopic point	Calculated (h Pa)	(6)
Ψ_w	Soil water potential at permanent wilting point	{1–100,000} (h Pa)	(8)
Ψ^*	Soil water potential leading to plant water stress	Calculated (h Pa)	(8)

^a Parameters being calibrated are highlighted bold. The value ranges represent the upper and lower bound of plausible conditions for calibrations.

$P_d(t)$ denotes the rainfall depth, and $I_c(t)$ is the amount of rainfall intercepted by the canopy of the plant community, which is assumed to be governed by rainfall intensity:

$$I_c(t) = \max \left[\min \left(\frac{(P_d(t) - \beta)^2}{(\alpha - \beta)^2}, 1 \right), 0 \right] \cdot P_d(t), \tag{3}$$

where α and β are shape parameters fitted to the observed annually intercepted rainfall amount of 15% in a Brigalow forest (Tunstall and Connor, 1981). Knowing $I_c(t)$ and $I_{f,1}(t)$ the runoff $Q(t)$ is expressed as:

$$Q(t) = P_d(t) - I_c(t) - I_{f,1}(s, t). \tag{4}$$

Overflow losses into deeper soil layers are assumed to be at their maximum when soil is saturated and reduce with time thereafter, following the decrease of unsaturated hydraulic conductivity for each soil layer $K_{u,i}(s(t))$ (Van Genuchten, 1980; Laio et al., 2001b). We assume that the hydraulic conductivity, and hence the overflow for each layer $O_i(s, t)$, decays exponentially from $K_{s,i}$ at $s_i(t) = 1$ to a value of zero at field capacity $s_{fc,i}$:

$$O_i(s, t) = \left(\frac{K_{s,i}}{\exp^{\lambda(1-s_{fc,i})} - 1} \right) \cdot (\exp^{\lambda(s_i(t)-s_{fc,i})} - 1), \tag{5}$$

where λ is an empirical soil parameter and was set to a value of 15 (see Laio et al. (2001b) for more details).

Since the scope of this study is to investigate whether two variables of the soil water balance (Eq. (1)), namely evaporation from soil and plant transpiration, need to be parameterised significantly

different to fit in with observed patterns at two distinct monitoring sites, we considered these variables separately.² Evaporation $E_i(s, t)$ was assumed to be related to the soil moisture state represented by the soil water potential Ψ_i (Fig. 2a), and the atmospheric water demand given by the observed potential evapotranspiration (PET). As long as the soil water potential is above field capacity $\Psi_{fc,i}$ evaporation from soil is assumed to occur at a maximum rate $E_{max,i}$:

$$E_i(\Psi_i, t) = E_{max,i}, \text{ with } E_{max,i} = \rho_i \cdot PET \text{ for } \Psi_i(t) \geq \Psi_{fc,i}, \tag{6a}$$

where ρ_i (to be calibrated) is a plant community parameter which determines what actual portion of the potential evaporation can be evaporated under soil water conditions above field capacity. This parameter describes the ability of a plant community to protect the soil from free evaporation (given by the observed potential evapotranspiration), e.g. through the vegetation canopy or litter cover at the ground. If ρ_i is low, it represents a dense vegetation stand or high soil cover, whereas sparsely covered soils are represented by elevated plant community parameter values. When the soil water potential drops below $\Psi_{fc,i}$, evaporation decreases linearly until the soil pore adhesive forces at a hygroscopic point

² Note: the objective of this study was neither to compare evaporation and transpiration with each other nor to investigate the partitioning of evapotranspiration per se.

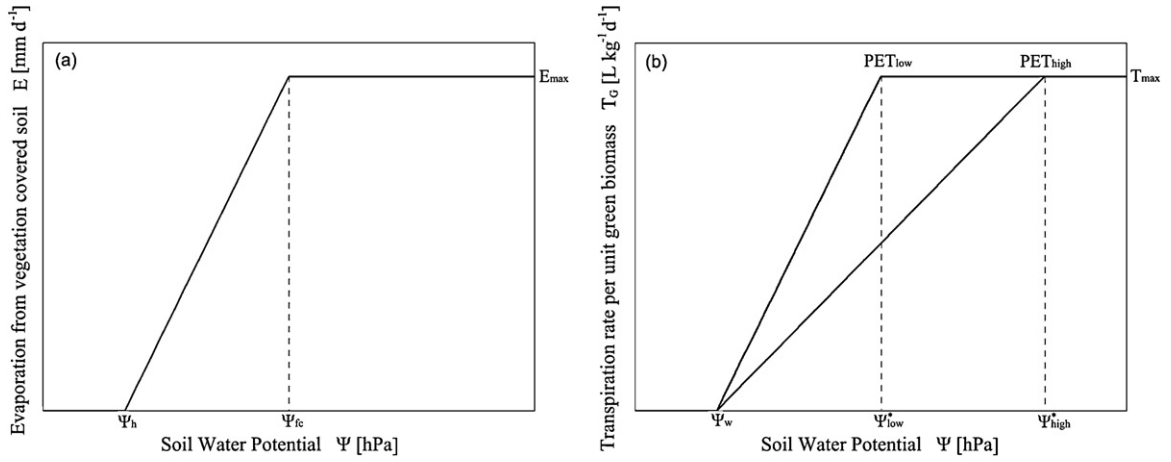


Fig. 2. (a) Evaporation E from vegetation covered soil and (b) transpiration rate per unit green biomass T_G (adopted to water-limited conditions from Feddes et al. (1978, 2004)) as function of the soil water potential Ψ .

$\Psi_{h,i}$ are too strong to further extract water from soil:

$$E_i(\Psi_i, t) = E_{\max,i} \cdot \left(\frac{\Psi_i(t) - \Psi_{h,i}}{\Psi_{fc,i} - \Psi_{h,i}} \right) \quad \text{for } \Psi_i(t) < \Psi_{fc,i}. \quad (6b)$$

The total transpiration of the plant community $T_{\text{tot},i}(t)$ is determined by the transpiration rate $T_{G,i}(\Psi_i, t)$ per unit green biomass $G(t)$ (see Eq. (10)):

$$T_{\text{tot},i}(t) = T_{G,i}(\Psi_i, t) \cdot G(t). \quad (7)$$

Similar to evaporation we assumed that the transpiration rate depends on the soil water potential Ψ_i (Fig. 2b) and the maximum water uptake of a plant community T_{\max} (to be calibrated) is assumed to be a community specific trait, which equals T_{\max} as long as the soil water potential is sufficiently high (Fig. 2b):

$$T_{G,i}(\Psi_i, t) = T_{\max} \quad \text{for } \Psi_i > \Psi^* \quad (8a)$$

when soil water potential falls below the critical value of Ψ^* plants start to reduce transpiration by closing their stomata to prevent internal water losses (Schulze, 1986; Laio et al., 2001b) and the transpiration rate decreases linearly:

$$T_{G,i}(\Psi_i, t) = T_{\max} \cdot \left(\frac{\Psi_i(t) - \Psi_w}{\Psi^* - \Psi_w} \right) \quad \text{for } \Psi_w < \Psi_i \leq \Psi^*. \quad (8b)$$

Eventually, when soil water potential drops below the wilting point Ψ_w (to be calibrated), suction to extract water from soil is so high that it damages the plant tissues (here represented by the transpiring green biomass (Eq. (10))) (Schulze, 1986; Laio et al., 2001b) and the transpiration rate converges to zero:

$$T_{G,i}(\Psi_i, t) = 0 \quad \text{for } \Psi_i < \Psi_w. \quad (8c)$$

Both parameters, Ψ^* and Ψ_w , represent plant community specific traits and regulate, together with T_{\max} , the maximum transpiration rate per unit green biomass and, hence, the total transpiration of the plant community (Fig. 2b). Moreover, the value of Ψ^* depends on the atmospheric water demand and varies with the observed potential evapotranspiration (Feddes et al., 1978; Feddes et al., 2004):

$$\ln \Psi^*(PET, t) = c \cdot PET + d, \quad (9)$$

where c and d are plant community specific parameters (to be calibrated) describing the functional relationship between atmospheric water demand and the response of the community to water limited soil conditions. Under elevated atmospheric water demand

Ψ^* is high, i.e. plants are exposed to water stress even when soil moisture content is high, whereas under low atmospheric water demand Ψ^* is low, i.e. plants are less affected by water stress even under low soil moisture conditions.

The dynamics of the plant community are described by its biomass which is differentiated into transpiring green (G)³ and living active reserve biomass (R) (Noy-Meir, 1982; Muller et al., 2007; Arnold et al., 2009). The green biomass describes all the parts of a plant community, which perform photosynthesis, while the reserve biomass covers all parts that are not photosynthetically active, like woody parts and roots. The dynamic of G depends on short-term water stress and the availability of water:

$$G(t) = (1 - \varepsilon(s, t)) \cdot G(t-1) + g_G(s, t) \cdot R(t-1), \quad (10)$$

where $\varepsilon(s, t)$ is the unitless water stress function, ranging from 0 for no water stress to 1 for maximum tolerable water stress, and $g_G(s, t)$ denotes the growth rate of green biomass:

$$\varepsilon(s, t) = \max \left[\min \left(\frac{(\Psi(t) - \Psi^*(t))^3}{(\Psi_w - \Psi^*(t))^3}, 1 \right), 0 \right], \quad (11)$$

$$g_G(s, t) = \max[\min((a \cdot T_G(t) + b), g_{G\max}), 0]. \quad (12)$$

The plant community specific parameters a and b (to be calibrated) determine how fast green biomass responds to increasing transpiration rates, limited by the maximum growth rate of green biomass $g_{G\max}$ (to be calibrated). Photosynthesis as performed by G results in the production of organic carbon, which maintains both green and reserve biomass. The dynamic of R occurs on a longer timescale and reflects the long-term memory of the ecohydrological system:

$$R(t) = (1 - m_R) \cdot R(t-1) + g_R \cdot G(t), \quad (13)$$

where m_R is the mortality and g_R the growth rate of the reserve biomass (both parameters to be calibrated). The model of biomass dynamics (Eqs. (10) and (13)) enhances the storage effect as described by Chesson (1994) by leading to a markedly increase of R during favourable periods of growth in G , whereas unfavourable periods reduce G fast, but reduce R only slowly.

³ Note: the term "green biomass" only refers to the active transpiring biomass but not to the phenology or the leaf area index of the plant community.

3. Results

The interaction between soil water availability and response of the vegetation (or vice versa) is shown in Fig. 3 by comparing the simulated reserve and green biomass, and soil water content of the upper and lower soil layer for the time period 1983–1985. These time series allow insight into the complex interplay between climate, soil water and vegetation. Deep rainfall events trigger the peaks of soil water content in the thinner upper layer (Fig. 3c). The saturated soil enhanced overflow into deeper soils, as indicated by small peaks of the soil water content in the thicker lower layer (Fig. 3d). During those favourable conditions the green biomass (Fig. 3b) increased resulting in elevated values for transpiration rate (not shown), and reserve biomass (Fig. 3a), eventually leading to rapid depletion of the upper soil layer and slower depletion of the lower layer (e.g., day 150–250, 600–750). In the absence of deep rainfall events the plant community suffers water stress leading to a quick decrease of green and a slower decrease of reserve biomass (e.g., day 400–550).

By applying pattern-oriented modelling we identified several parameter combinations capable of representing the observed patterns of soil moisture in the upper and lower soil layer (Fig. 3). We assumed that these ensembles of parameterisations are possible representations of the natural brigalow plant communities at both monitoring sites. Hence, the distribution of parameters like the permanent wilting point (Ψ_w) provides insight into the ecohydrological functioning of the plant community under the given soil–climate constraints. Fig. 4 illustrates the frequency of all possible values of Ψ_w for both monitoring sites. For both monitoring sites the majority of Ψ_w ranged between -6 and -2 MPa indicating that plant communities must be highly water stress resistant to endure prolonged periods of reduced water availability under the given soil and climate constraints.

To investigate whether each of the soil water balance variables (Eq. (1)) transpiration and evaporation were parameterised significantly different between the monitoring sites, the Wilcoxon rank sum test was applied. The test assesses whether parameters relevant for transpiration and evaporation originate from distributions with equal medians (h_0), against the alternative hypothesis that they do not have equal medians (h_1). The test assumes that the shapes of the distributions are identical, which was tested and confirmed using the Ansari-Bradley test (results not shown). The results (Table 2) had only parameter ρ_2 , which determines the maximum evaporation rate from the lower soil layer (Eq. (6a)), was significantly different among the monitoring sites (at a significance level of 5%). In particular, the maximum evaporation rate was significantly higher at the BB site compared to the BDG site. Fig. 5 illustrates the resulting shapes of the functions of transpiration rate per unit green biomass (Fig. 5a) and soil evaporation (Fig. 5b) for the ensemble average of validated parameter sets for both monitoring sites.

Fig. 6 depicts the functional relationship between the ensemble averages of modelled transpiration rate or evaporation from soil and the observed potential evaporation or the modelled soil moisture content. A strong positive linear correlation could only be identified between potential evaporation and the evaporation from soil (Fig. 6b). Only weak positive linear correlation was revealed for the relationship between soil moisture content and transpiration rate per unit green biomass (Fig. 6c), and no linear correlation was revealed for the relationship between potential evapotranspiration and transpiration rate per unit green biomass (Fig. 6a), and soil moisture content and evaporation from soil (Fig. 6d). Moreover, the figures depict the elevated simulated evaporation at the BB site, reaching values up to 1 mm d^{-1} , compared to the BDG site, where those values ranged only between 0 and 0.5 mm d^{-1} (Fig. 6b and d). On the other hand, the range of simulated transpiration rates

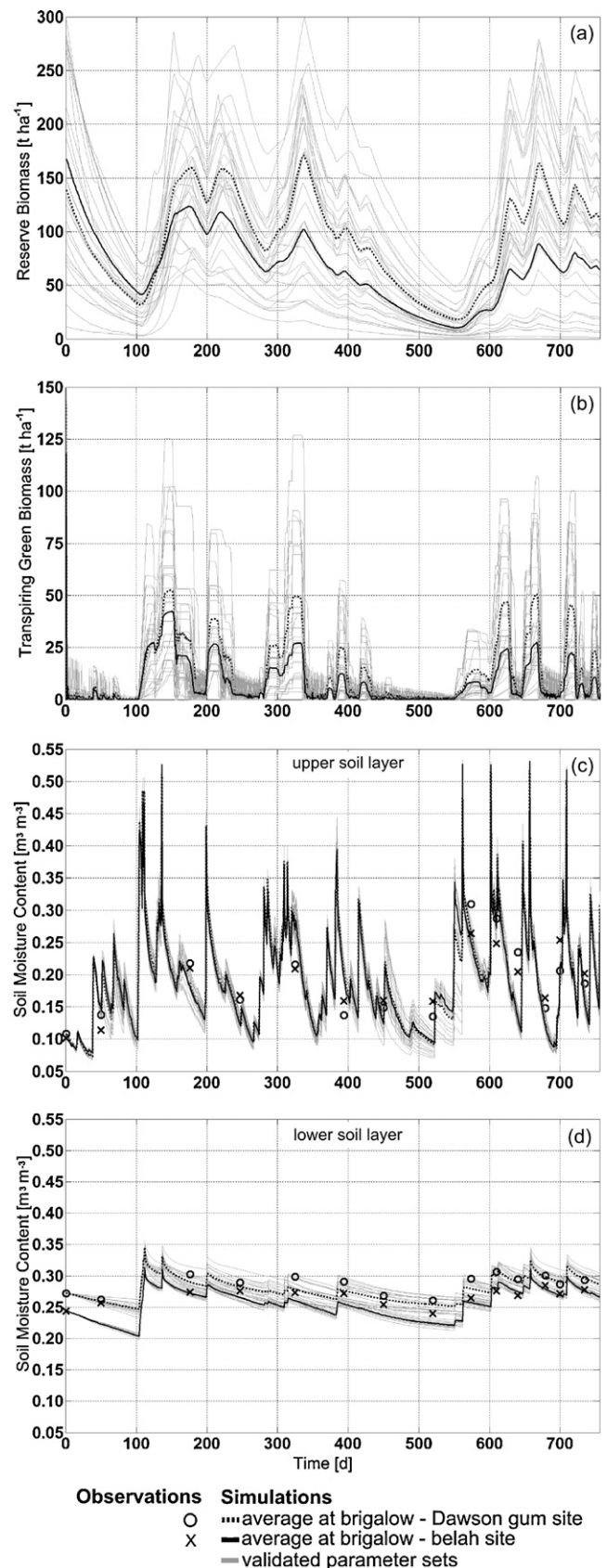


Fig. 3. Simulated biomass (a and b) and observed soil water content (c and d), and observed soil water content (circles and crosses) for time period 1983–1985 at both monitoring sites. Note: simulations depicted in (b) only refer to the photosynthetically active (transpiring) plant community components which, however, not necessarily correlates with observed or simulated leaf area index (LAI).

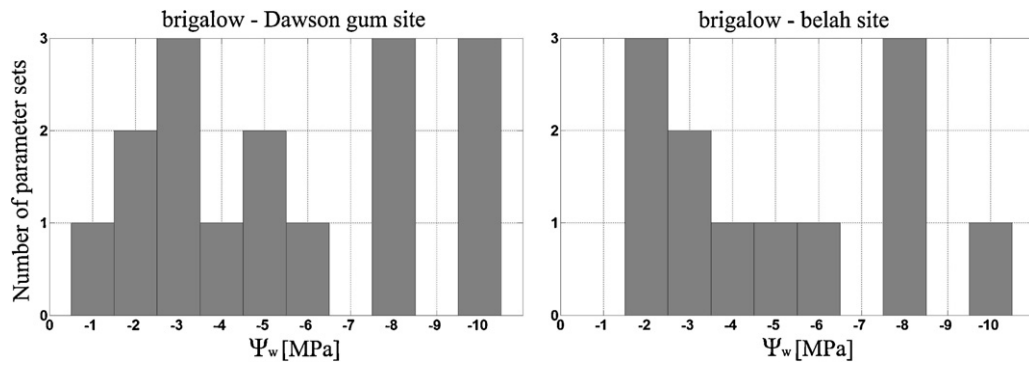


Fig. 4. Histograms of Ψ_w of all validated parameter sets for both monitoring sites.

per unit green biomass was the same among both sites (Fig. 6a and c).

4. Discussion

4.1. Water potential

The wilting point (Ψ_w) of the plant species (among other factors) within the community structure in a semi-arid environment is considered a critical determinant of revegetation success within the Brigalow Belt ecosystem (Connor et al., 1971; Van den Driessche et al., 1971; Tunstall and Connor, 1975, 1981). In water-controlled ecosystems (such as this) which can endure prolonged drought periods, the soil water potential can be an accurate descriptor of extrinsic drought stress whereas the wilting point represents the level of intrinsic stress tolerance of plants. In our model, this relationship is described by a wilting point parameter below which plants would succumb to permanent physiological damage and leaf transpiration rate would converge to zero (Eqs. (8a)–(8c)) (Schulze, 1986; Laio et al., 2001b). In this regard, plants that are better adapted to water-limited conditions (i.e. xerophytes) tend to have lower wilting points than the less water stress resistant mesophyte species which suffer severe water stress already at soil water potentials below -1.5 MPa (Hsiao, 1973). Previous studies have indicated that the wilting point of brigalow (*A. harpophylla*) is very low and ranges between -7.2 and -1.5 MPa (Connor et al., 1971; Van den Driessche et al., 1971; Tunstall and Connor, 1981). Interestingly, this characteristic is supported in the simulation results of our study which reveals that, under the given soil attributes and climate conditions, plant communities can only thrive if they are inherently resistant against periods of exceptionally low soil water potentials, as represented by the range of low values for Ψ_w for both sites under consideration (Fig. 4). This implies that

the understanding of linkages among plant physiological characteristics (here, the aggregated wilting point of the given plant community) and plant water availability are critical for the establishment and management of agro-forestry; particularly for the rehabilitation of post-mining landscapes under the soil–climate constraints of the Brigalow Belt. As such, our simulation outcomes suggest that the successful restoration and conservation of brigalow landscapes seems solely feasible by re-establishing drought tolerant native plant communities. For ecosystem restoration on highly disturbed and degraded post-mining landscapes, there is a unique opportunity to actively and directly manage and (or) modify both these determinants of plant water availability (e.g., soil type and its attributes) and plant community traits (e.g., drought tolerance), as opposed to more passive strategies which may result in either less resilient soil conditions or even a possible shift in ecosystem function given the climate regime (Palmer et al., 1997; Hobbs, 2007). Building on this premise, it would be favourable in future to investigate the sensitivity of native brigalow communities to a variety of different soil types (e.g., considering different water retention characteristics) and landscape attributes (e.g., active soil thickness), or even different weather regime (e.g., rainfall depth and intensity) to verify the susceptibility of the plant community to a broader range of ecological determinants. The merit of such an approach lies in the possibility to integrate the uncertainty arising from unpredictable future rainfall regimes, while the conceptual design of the model presented in this study would provide the basis to work on those challenges (Table 3).

4.2. Evapotranspiration

Besides abiotic factors such as climate and soil, the plants' functional characteristics should also have an important impact on the soil water balance (Chapin et al., 2000; Lavorel and Garnier, 2002;

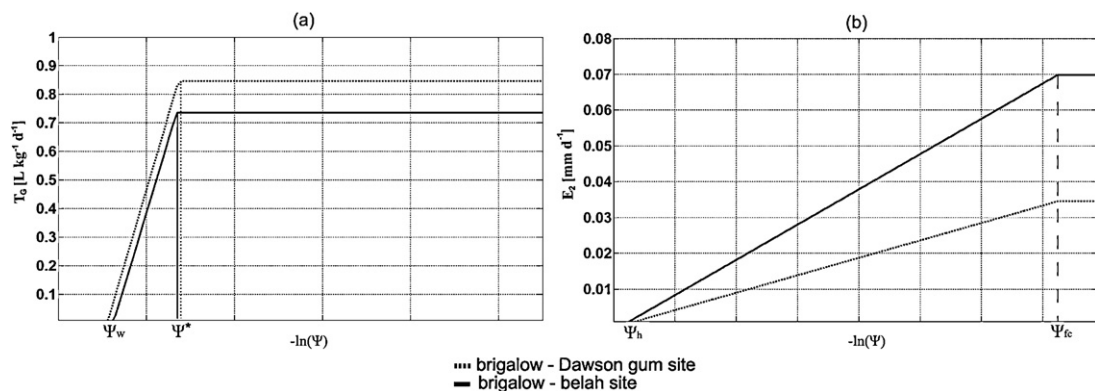


Fig. 5. Average shape of (a) the function of transpiration rate and (b) the function of evaporation from the lower soil layer for both monitoring sites with $PET = 1 \text{ mm d}^{-1}$.

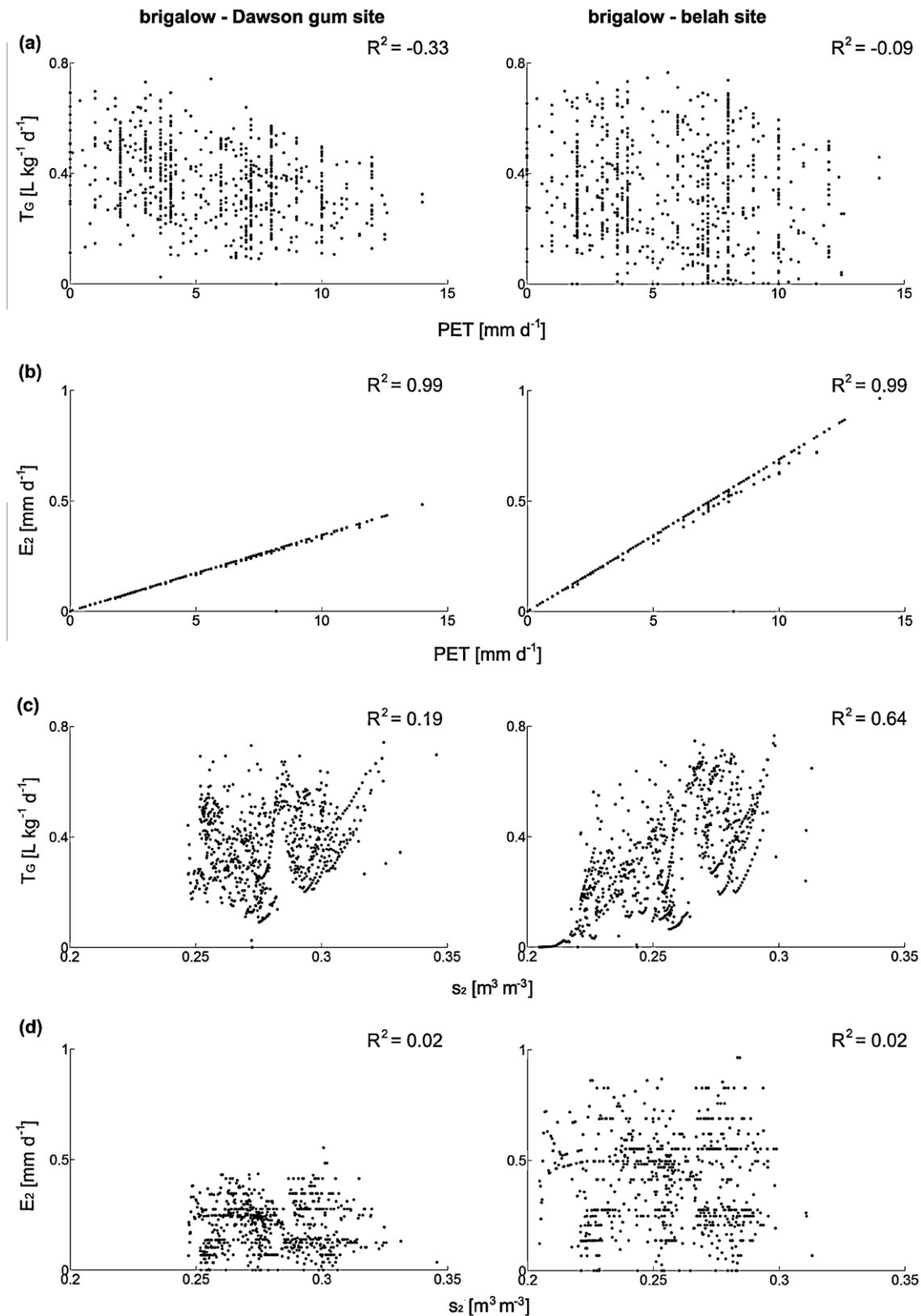


Fig. 6. Scatter plots of the ensemble average of the modelled transpiration rate (a and c) and evaporation (b and d) for both monitoring sites as function of the measured potential evaporation (a and b) and the modelled soil moisture content (c and d).

Gross et al., 2008). Plant evapotranspiration is known to govern soil moisture dynamics of water-controlled ecosystems in combination with the atmospheric water demand, the soil water state and plant community traits (Rodríguez-Iturbe and Proporato, 2004; Eamus et al., 2006; Newman et al., 2006). In agro-forestry, plant available water is a major limitation to forest productivity and losses to

soil evaporation are a significant component in ecosystem hydrology (Raz-Yaseef et al., 2010). For these reasons, our investigation focused on determining the sensitivity of soil moisture dynamics in relation to (a) plant community transpiration and (b) evaporation from soil, each compared among two distinct sites. Comparing the simulated transpiration rates among both monitoring sites has

Table 2
Results of the Wilcoxon rank sum test.

Parameter	P-value	Hypothesis	Modelled process
ρ_1	0.55	h_0	Evaporation
ρ_2	9×10^{-6}	h_1	
α	0.73	h_0	Interception
β	0.61	h_0	
c	0.69	h_0	Transpiration
d	0.31	h_0	
T_{\max}	0.52	h_0	
ψ_w	0.69	h_0	

The Wilcoxon rank sum test performs a test of the null hypothesis h_0 that the parameter vectors for the BDG site and BB site are independent samples from identical continuous distributions with equal medians, against the alternative hypothesis h_1 that they do not have equal medians. The significance level was 5%. The Ansari-Bradley test was used to test if the distributions are identical.

revealed similar value ranges for the ensemble average of all plant communities (Fig. 6a and c), whereas values of simulated evaporation from soil were found to be significantly different. At the BB site (low observed soil moisture) for any value of observed potential evapotranspiration (Fig. 6b), the simulated evaporation was up to two-fold greater than at the BDG site (elevated observed soil moisture) (Fig. 6d). This is a consequence of the functions calibration for transpiration rate per unit green biomass (Fig. 2a) and evaporation (Fig. 2b) for both monitoring sites; which is significantly different for evaporation but not for the transpiration rate per unit green biomass (Table 2). Plant communities affect evaporation from soil through various processes. For instance, the canopy structure influences the microclimate of a stand by modifying radiation, albedo, and the vegetation boundary-layer thickness (Fliervoet and Werger, 1984; Luo and Dong, 2002) and, hence, the water fluxes between soil and atmosphere. In addition, the plant litter can create a barrier to water vapour diffusion (Facelli and Pickett, 1991). Eventually, both canopy structure and plant litter influence the intercepted water amount (Dowling et al., 1986; Raz-Yaseef et al., 2010; Yaseef et al., 2010). However, this effect should only play a negligible role within our model since the parameters for interception (Eq. (3)) were not significantly different (Table 2) between both monitoring sites.

According to our model concept, evapotranspiration was determined by the atmospheric water demand (represented by observed potential evapotranspiration) and simulated soil moisture state (Eqs. (6)–(9), Fig. 2). In this context, it is noteworthy that a strong linear relationship only existed between the observed potential evapotranspiration and simulated evaporation (Fig. 6b). This, however, is a conditioning of the model concept which implies that the transpiration rate per unit green biomass can be regulated actively by plant physiological traits represented by the parameter Ψ^* (Fig. 2b). Whereas, evaporation can only be influenced indirectly through the plant community parameter ρ_i (Fig. 2a), which represents canopy or litter coverage and thereby determines the maximum evaporation from soil (Eq. (6a)). Nevertheless, this conditioning had been chosen thoroughly according to literature (Feddes et al., 1978; Schulze, 1986; Ridolfi et al., 2000; Laio et al., 2001a; Laio et al., 2001b; Porporato et al., 2001; Feddes et al., 2004). For the management of agro-forestry, this would imply that various plant communities can exist under the same soil–climate constraint with distinct magnitudes of ecohydrological functions, as shown here through the regulation of evaporation from soil. Moreover, the differences in simulated evaporation among the monitoring sites indicate that, indeed, different plant communities dominate these distinct sites. This perspective is supported by previous vegetation surveys at the Brigalow Research Station (Johnson, 2004; Cowie et al., 2007). The BDG site, where soil moisture was elevated and simulated evaporation were found to

be lower, the brigalow community was co-dominated by Dawson Gum (*E. cambageana*) – a broad-leaved tree species with similar leaf area index as brigalow. However, the BB site, where soil moisture is lower and simulated evaporation is higher, the plant community is found to be co-dominated by belah (*C. cristata*) – a tree species with long and narrow leaves. Notably, both monitoring sites have no access to ground water, similar soil type, micro-topography, understorey species and canopy cover, stand age, rooting depth, phenology, and are dominated by brigalow species, but co-dominated by either Dawson gum (BDG site) or belah (BB site). This indicates that it was the co-dominant species, which governed ecohydrological function in these semi-arid landscapes.

4.3. Implications for agro-forestry management

The value of using an ecohydrological modelling strategy for depicting agro-forestry management (such as native brigalow species) in an arid landscape lies in the fact that the model is fundamentally derived from and constrained by long-term monitored soil and climate data. Hence, the model provides a minimalist representation of ecological linkages and feedback relationships existing between plant communities, their inherent adaptive physiological traits, and soil water dynamics. In ecohydrological modelling, however, the model structure may have profound effects on model performance and robustness (Arnold et al., 2009). And so, alternative model structures can be critical to determine which physical and biological processes should be considered for inclusion, how equations describing those processes should be implemented, and how the ecohydrological linkages should be invoked (Choler et al., 2011). The fact that different plant communities can exist on two sites constrained by the same soil attributes and climate emphasises that inherent ecosystem processes may exist, which drive vegetation dynamics and eventually lead to different plant communities. This underpins the role of plant community traits in regulating water fluxes in water-controlled ecosystems (McLaren et al., 2004; Gross et al., 2008) and has important implications for water conservation and the management of restoration sites (Fu et al., 2009). Notably, it is desirable to restore degraded landscapes in semi-arid areas with plant communities that prevent the soil from high evaporation rates while being intrinsically tolerant of prolonged periods of water stress. This attention to plant water stress resistance would then result in higher soil moisture which could generate more adequate or buffered conditions for recruitment of seedlings and eventually enhance autogenic recovery (King and Hobbs, 2006), i.e. self-sustaining feedback loops that lead to continued improvements in ecosystem attributes (Whisenant et al., 1995). Moreover, the functional traits of the plant communities themselves can also be associated with the feedback relationships due to the interactions existing between species (i.e. interspecific complementarity) rather than simply the abundance or distribution of species within plant communities (i.e. interspecific competition) (Chapin et al., 2000). Hence, species interrelationships play a critical role in determining ecosystem characteristics and may affect water-controlled ecosystem processes either directly by modifying resource availability (De Ruiter et al., 1995; Arnold et al., 2009) or indirectly by modifying the abundance of species with strong effects on ecosystem functions (Lavorel and Garnier, 2002). Both can dominate the fundamental relationship between biotic and abiotic ecosystem components in the Brigalow Bioregion. The community level functional traits can also change due to the replacement of species with different trait values (Fu et al., 2009) and at species or individual scale organisms can be plastic, i.e. they can alter their development, physiology and life history depending on abiotic conditions (Sultan, 2000). All these aspects may govern the feedbacks among ecosystem and soil hydrology. Therefore, testing the mutual

Table 3
Restoration challenges and strategic management contribution in the context of post-mining ecosystem restoration and potential outcomes of the model framework presented in this study.

Restoration challenges	Strategic management contribution	Potential outcomes
(1) Severely disturbed soils resulting in tenuous landscapes	Testing sensitivity of possible native ecosystems to: a. Soil attributes (e.g. water retention characteristics, soil thickness) and	(1) Provide a deeper understanding of abiotic and biotic factors governing highly disturbed and (or) ongoing rehabilitation agro-ecosystems
(2) Unpredictable and (or) highly variable rainfall patterns	b. Rainfall patterns (e.g. occurrence of rainfall depths and intensities, frequency of prolonged (un)favourable periods)	(2) Provide a minimalist framework for predicting and then monitoring ecosystem function based on mechanistic components
(3) Identification of ecohydrological patterns	Depiction of water dynamics within water-limited ecosystems	(3) Provide a deeper understanding of ecohydrological functions within water-limited ecosystems and potential for efficient water resource use
(4) Difficulty in effectively describing reference points for restored ecosystem function	Depiction of native plant communities in relation to inherent physiological characteristics and observed environmental parameters	(4) Taking into consideration (1)–(3), assess the potential conditions and environmental relationships conducive for restoring and integrating native plant communities within environmental restoration

influence of plant community composition, including competition for the resource water, and soil moisture dynamics in semi-arid restoration areas denotes an important future research task, which requires further model development towards the integration of species interactions and aspects of phenotypic plasticity.

Despite the minimalist description of the native water-controlled ecosystem of the Brigalow Belt, we emphasise the role this model framework be applied towards restoration planning (Table 3). Ecosystem restoration of arid post-mining landscapes requires comprehensive understanding of ecohydrological dynamics before it was modified or degraded to reassemble and reinstate essential processes (Hobbs, 2007). This is often obtained by determining a reference ecosystem (SERI, 2004), which is undisturbed and similar to the original state of the area to be restored (Hobbs, 2007). However, in terms of continuing anthropogenic landscape management and the uncertainty in future weather regimes it might be more reasonable to restore the underlying ecohydrological functions rather than pre-human structures (King and Hobbs, 2006; Hobbs, 2007). The present model framework supports those challenges by providing a variety of unique parameter sets representing native brigalow plant communities and their ecohydrological functions. Moreover, it denotes a starting point of an ecohydrologically based monitoring tool for restoration ecology of post-mined landscapes in the Brigalow Belt (Savenije, 2009; Arnold et al., 2012).

5. Conclusions

This study has introduced a model framework that facilitates the investigation of mutual effects of plant community traits and soil moisture dynamics by ecohydrological attributes that influence plant community transpiration and evaporation from soil. It gives insight into the ecohydrological function of native brigalow plant communities and therefore important implications for post-mining land rehabilitation, and agro-forestry and resource management. Potentially, it can be used to investigate the sensitivity of brigalow communities to attributes of soil (e.g., water retention, thickness) and climate (e.g., frequency of rainfall depth and intensity) and, therefore, predict the suitability of a plant community for establishment on post-mined landscapes under severely disturbed soils and the uncertainty of future rainfall patterns. Moreover, the model parameterisation is an important step towards designation and description of reference ecosystems of the Brigalow Belt, which is critical in restoration planning.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2012.05.020>.

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