Review of soil water models with respect to savanna hydrology

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1 Introduction

Effective management leading towards sustainable rangeland production in arid and semi-arid regions will stem from effective soil water management (Snyman, 1998) and comprehension of the hydrological properties of the soil in relation to pastoralism (Sharma, 1998). However, in such areas, there is great complexity of interaction between the soil, climate and vegetation. Highly variable climates can give rise to extended dry periods in which the majority of rain that does fall is lost to surface evaporation (*e.g.*, Opperman *et al.*, 1977 cited in Bate *et al.*, 1982; Walker & Langridge, 1996).

Soil water dynamics are a function of soil physical processes and the competition between plant species and individuals for soil water and space (*e.g.*, Knoop & Walker, 1985). Spatial distribution of canopy and rooting patterns dictate the outcome of this competition, and the subsequent stability of the vegetation structure (Skarpe, 1992), although soil nutrients may be more important in determining vegetation composition (Cole, 1982). However, rainfall infiltration and the spatial redistribution of runoff water are the predominant factors determining patterns in semi-arid vegetation (Friedel, 1990; Maestre *et al.*, 2003), with grazing impacts and fire also contributing to the generation and maintenance of spatial heterogeneity (*e.g.*, Higgins *et al.*, 2000; Adler *et al.* 2001; but also see *Savanna ecohydrology*, below).

Despite soil water content being the net result of climatic input, soil surface and subterranean characteristics, the extraction of water by plants and it's return to the atmosphere, the integrated approach needed to comprehend the complete cycle is rarely adopted. Systems models assist us in identifying the gaps in our knowledge by integrating mathematical representations of processes operating at local scales in order to simulate larger scale natural phenomena. However, because of the differences between scientific disciplines, and the bias on investigation that different interests support, true fusion of knowledge is hard to achieve. Hydrologists and ecologists are historically ingrained in their view of soil water dynamics.

It is difficult to make comparisons between the approaches taken by hydrologists and ecologists, as they are so dissimilar, despite their mutual aim to predict the water content of the soil profile. Whilst hydrologists consider the physical laws that determine water flow between locations in the soil body, ecologists are more concerned with the volume of water available for plant use during transpiration. Hydrologists imagine a net throughput that ends with accumulation in an acquifer, the rate of which is dictated by soil morphology. Ecologists include plants that intercept percolating water and return it to the atmosphere. Hence, plants are considered to bridge the water-potential gradient between soil and air (Larcher, 1995), with resistance to this movement of water present in the soil body, throughout the plant structure (roots, shoots and leaves), and in the atmosphere. Consequently, some models describe the same processes, but in very different ways, with emphasis being placed on the subject of interest. Perhaps the best approach towards reviewing this literature is to highlight the hydrological content of these models that has some bearing on the relevant ecological processes.

This review reports on the current state of knowledge regarding the modelling of water in soil profiles. Our intention is to present an accessible document that will be useful to ecologists, ecological modellers and other specialists not necessarily familiar with the field of physical hydrology. This introductory section continues with an investigation of the role of soil water in savanna dynamics, to highlight the components of the savanna system that will dictate most(?) the balance of soil water content. This should also provide hydrologists with a concise account of the relevant issues that link their subject with the botanical elements of the environmental sciences (*i.e.*, soil water content), and their treatment within the modelling efforts detailed in the following sections. The report concludes with an appraisal of a recent call to limit reductionism in ecohydrological modelling. Appendix 1 contains a list of the models and their principal source literature referred to by their acronyms in the following text.

Re: appendix list. I have left the full titles and refs in for now.

2 Savanna ecohydrology

Tropical savanna is bounded by the equatorial rainforests and the deserts and semi-deserts of Africa, Australia and South America (Huntley & Walker, 1982). The various climates of these continents exhibit seasonal rainfall falling in summer with a dry winter season. The range of rainfall is between approximately 250 mm and 1300 mm per annum with moist savanna receiving in excess of 650 mm per annum.

These rainfall regimes give rise to a patchy vegetation mosaic exhibiting high spatial heterogeneity. In fact, evidence suggests that a positive feedback between plant density and rainfall infiltration, plus the spatial redistribution of runoff water are sufficient to explain vegetation patterns in savanna, whereas herbivory, slope, plant dispersal, drought tolerance and underlying vegetation heterogeneity (composition/diversity?) are all secondary determinants (HilleRisLambers *et al.*, 2001).

Thus, plant available soil moisture (PAM) is one of the four principal determinants of savanna structure (Frost *et al.*, 1986). The others are plant available soil nutrients (PAN), herbivory and fire. In particular, PAM and PAN are considered to be the most important influences on plant growth in African savanna systems (Rutherford, 1980; Walker *et al.*, 1981; Dye & Spear, 1982; Walker & Noy-Meir, 1982; Sarmiento *et al.*, 1985; Scholes, 1990a and 1993). To some extent, PAM and PAN act synergistically to determine plant primary production, forage quality and vegetation composition. Under conditions of low rainfall, PAM limits production (O'Connor & Bredenkamp, 1997). However, the relative importance of each varies according to site with the effect that rainfall may more ameliorate PAN than control photosynthetic rate (Scholes & Walker, 1993).

The controlling influence of rainfall extends via the interaction of standing biomass, its nutritional content, the resultant pattern of herbivore impacts, and the frequency and intensity of fire, to govern savanna dynamics (*e.g.*, Skarpe, 1992). In turn, there is a feedback of these processes on the levels of PAM (*e.g.*, extraction of moisture by grasses from topsoil, Walker *et al.*, 1981) and PAN (*e.g.*, redistribution of nutrients via dung, Thrash & Derry, 1999). The availability of soil water will dictate whether plants are able to strike the balance required in their water economy underpinning their survival and development (Kelly & Walker, 1976).

2.1 Osmoregulation

The protoplasm of a plant cell is buffered from fluctuating environmental conditions by its large central vacuole. The forfeit is the loss of the cell's ability to tolerate dehydration. Hence, vascular plants only became able to control their water balance upon evolution of a protective cuticle to retard evaporative loss, and of stomata to regulate transpirative loss (Larcher, 1995).

The relative rates of transpiration and carbon dioxide uptake depend on stomatal conductance, which is determined by anatomical, physiological and environmental factors. Carbon assimilation is further modified by tissue respiration, which varies with plant biomass, growth rate and temperature, to leave net photosynthesis. This relationship between net carbon assimilation and transpiration is interchangeably termed 'rain use efficiency' and 'water use efficiency'.

Soil water uptake (see *Uptake*, below) counterbalances the water lost as a symptom of gas exchange via open stomata, a component of transpiration. Water stress causes a decrease in osmotic potential necessitating an osmotic adjustment. Osmoregulation seeks to replace this lost water in order to maintain cell turgor, a requisite for growth (Zimmerman, 1978). Cell membrane permeability is mediated by hydrostatic pressure sensors, membrane pore proteins sensitive to changes in internal pressure (Derry, 1989). Changes in cell turgor that may arise from stresses such as cytorrhysis during drought deform the cell membrane, causing a modification in the stereochemistry of the pore protein, the determinant of its water transport function. If there remains a deficit in PAM, growth is not sustained, cells turgor is lost, cellular osmotic capacity may be permanently lost and the soil is said to have reached wilting point.

2.2 Uptake

Macropore water is held in fissures in the soil structure caused by cracking, root extension and invertebrate activity. Micropores are the result of coarsely textured material and are most numerous in soils containing high concentrations of organic matter.

Soil structure is not static and may undergo substantial reorganization through pores collapsing and new ones being formed. There are no distinct forms of water, and change in soil water content is gradual. PAM is essentially a practical concept defined according to soil water potential (SWP) and is used to describe soil water that may be extracted by plants from micropores. This is the water available at SWPs between -1.5 and –0.01 MPa ($1\ \text{MPa} \equiv 10\ \text{bar}^{-1}$). Following a significant rainfall event, saturated (gravitational) flow (where $\text{SWP} \rightarrow 0\ \text{MPa}$) removes macropore water, reducing SWP to field capacity (approximately –0.01 MPa). When the macropores are emptied, unsaturated (capillary) flow occurs down gradients of matric potential (the soil's ability to absorb or release water). The fine roots of plants absorb water thereby reducing local SWP. In response water moves towards the roots, however, as root-soil contacts may amount to only a fraction of total soil surface area (*e.g.*, < 1%, even though the root area index (RAI: m^2 root area per m^2 of ground) can be as much as 2 to 4 for semi-arid shrubland, Larcher, 1995), water uptake is compensated for by root extension. Therefore, water is sucked towards roots and roots grow in order to forage for water (Ludwig *et al.*, 2004). A plant's maximum productivity typically occurs as SWP nears field capacity, thus conditions for optimal growth do not extend over the complete range of water availability.

Water vapour accounts for only a trivial proportion (~0.003%, REF) of water within the upper 15 cm of the profile under optimal conditions for plant growth. Nonetheless, during extended droughts, vapour movement delivers the most important source of water (REF). A probable mechanism is by daytime transport to surface horizons followed by condensation during the cooler nights (Jackson *et al.*, 1973).

Having trouble retracing these sources for vapour and water holding capacity. Any ideas?

In the absence of soil water recharge from infiltration or hydraulic lift (see *Vegetation Composition*, below), the soil water deficit (the water required to reinstate field capacity) will increase until the remaining hygroscopic water cannot be extracted by the suction pressures exerted by roots (Hewlett, 1982). If this stress is not relaxed the soil will reach wilting point (-1.5 MPa). While clay soils can hold water in excess of 50% of their weight (REF), up to a half of this water is unavailable for extraction by plants (REF) as clay contains fewer pores because of the smaller particle size than those found in, for example, sandy loams. Therefore, clay soils contain more water at a given matric potential, but this does not translate into PAM.

Salt concentrations result in wilting points occurring at lower soil water content. Osmotic potential retains water in the soil at wilting point and has a significant effect in arid and semi-arid soils of high salt content (Brady, 1990).

2.3 Primary Production

The relationship between climate and primary productivity in precipitation-driven systems is well established (*e.g.*, Kelly & Walker, 1976), along with the system level amelioration of water uptake by soil texture (Dye & Spear, 1982). Large mammalian herbivores depend on forage biomass, and therefore on rainfall amounts (*e.g.*, Coe *et al.*, 1976; Fritz & Duncan, 1994) and forage quality which is related to soil fertility (Breman

& de Wit, 1983; Scholes, 1993). Grass yields on fertile soils are larger for high rainfall years than on nutrient-poor soils (Dye & Spear, 1982), and woody vegetation has been shown to grow faster on fertile soils (Prins & van der Jeugd, 1992).

Several researchers have found a linear relationship between rainfall and aboveground production of the herbaceous layer in semi-arid savanna (*e.g.*, Walter, 1971; Lauenroth, 1979; Rutherford, 1980; Dye & Spear, 1982; Sala *et al.*, 1988; Dunham, 1990; Milchunas & Lauenroth, 1993). The relationship can be seen for open savanna receiving $\leq 900\ \mathrm{mm\ yr^{-1}}$ of rainfall. Across sites of differing annual rainfall (*e.g.*, Fig. 1), the gradient is a function of PAM and PAN (McCown & Williams, 1990) and implicates soil texture as a cofactor (Frost *et al.*, 1986; Scholes & Walker, 1993).

`Insert Fig. 1`

Herbaceous canopy height and cover is mediated by herbivory. Extreme defoliation has a greater impact on perennial grasses than annual grasses and the resulting decrease in basal cover (increase in bare soil) can promote the patchiness of the grass layer, reducing litter and increasing runoff (Kelly & Walker, 1976).

While intensive herbivory causes depletion of root-based carbohydrate stores (Kelly & Walker, 1976) there are examples of positive relationships between grazing intensity and aboveground net primary production. In water stressed individuals of a dwarf shrub (Spiny Indigo, *Indigofera spinosa*), defoliation (clipping) increased the photosynthetic rate per unit leaf mass by reduction of total leaf mass, and therefore increased the relative abundance of available water for each unit of residual leaf (Coughenour *et al.*, 1990). Increasing water uptake attempts to maintain aboveground biomass, and, within limits, this response gives the same amount of total aboveground biomass production independent of defoliation intensity. Milchunas & Lauenroth (1993) found no trend in impact on root phytomass and the effects of herbivory (positive and negative) on aboveground net primary production observed across a broad range of studies. Some studies have suggested that other woody vegetation employ defensive survival strategies, reducing growing tips and increasing spinescence in response to utilization pressure (*e.g.*, Umbrella Thorn, *Acacia tortilis*, Dangerfield et *al*., 1996 and Gowda, 1997).

2.4 Vegetation Composition

Differences between the root morphology of savanna vegetation types lend themselves well to interpretations of resource partitioning. Rooting depth thus becomes an adaptive strategy to avoid competition for soil water (Walter, 1971). Within this two-layer exclusion model, dense but short grass roots outcompete the deeper-reaching, extensive root systems of woody vegetation for newly fallen precipitation high in the zone of aeration. Following water extraction by the herbaceous layer, woody biomass is maintained by water drained to greater depths. Survival largely relies on superior rain use efficiency (Scholes & Walker, 1993), although some favorable processes do occur to the woody species' advantage, such as canopy interception and trunk funneling of rainfall. The two-layer model explains vegetation population dynamics by variable rooting patterns. However, other phenomena do effect the tree-grass balance.

Rapid evaporation from topsoil after small rainfall events is a potential threat for the survival of developing plants. To account for this, grass seedling mortality is limited after insubstantial rainfall by no germination occurring for < 12 mm rainfall, and a delay in germination until 3-10 days after a 30 mm rainfall event (which will wet the soil to a depth of about 30 cm). Upon germination, large numbers of seedlings (*e.g.*, 3000 m^{-2} for *Tragus berteronianus*) emerge from within 1 cm of topsoil and litter deposited on the soil surface (Veenendaal *et al.*, 1996) giving rise to the characteristic pulse of herbaceous growth.

Establishment of new woody biomass is limited by the competition for water and light and therefore relies on patchiness in the herbaceous layer along with rapid development of sufficient root phytomass in upper soil layers to compete with the grass. Differential growth rates between woody species originate from some species' differing proficiencies for nitrogen fixation and water conservation (Prins & van der Jeugd, 1992). This can give rise to successional colonizations underneath the canopy of other trees (Scholes & Walker, 1993) or within favorable gaps in the grass canopy, such as the upslope perimeters of vegetation patches (Montaña *et al.*, 1995). Patchiness may be extended by intensive utilization (*e.g.*, Adler *et al.*, 2001, but also see *Primary Production*).

Even since the relatively recent proposal of the two-layer exclusion model for tree-grass balance there has been acceptance that vegetation interaction involves more factors than solely PAM (*see* Scholes & Archer, 1997, for a recent review). Additionally, the two-layer model assumes contrasting root distributions for each vegetation type, along with grass roots being effectively absent from the lower level. Recent studies have shown these root proportions not to differ as dramatically as previously expected.

Mordelet *et al*. (1997) attributed climate as the major determinant of the vertical distribution of root phytomass. They contrasted maximal root densities found for the upper 20 cm of a humid savanna (1200 mm yr^{-1} rainfall) with rooting patterns reported for more arid savannas where only 55% of roots were found in the upper 50 cm of the soil profile. In areas where water is comparatively abundant, soil nutrient status is proposed to be the basis for competitive dynamics. Limited water availability in semi-arid savanna induces rooting patterns that seek to partition this soil resource. In an extensive analysis, Schenk & Jackson (2002) found herbaceous rooting depths related to mean annual rainfalls below 1000 mm yr^{-1}, with shallower and wider root systems in dry and hot climates, and deeper and narrower root systems in cold and wet climates. They found deeper woody vegetation root systems not to be related to mean annual rainfall, reflecting the herbaceous layer's ability to respond quickly to rainfall infiltration into topsoil. Additionally, Ludwig *et al.* (2003) found that grasses benefit from overnight redistribution of moisture by hydraulic lift to topsoil by deeper tree roots (also see

Larcher, 1995), as well as having the capacity to extend their roots deeper to avoid competition with trees for topsoil water (Ludwig *et al.*, 2004).

Thus, overlap in vertical root distribution leads to competition throughout the soil profile and while this occurs predominantly in the upper layers of deep soils, in shallow soils, roots may be forced to overlap completely as in 1 m deep soils at Nelsvley, South Africa (Knoop & Walker, 1985. Fig. 2), concentrating the majority of root mass into the upper 40 cm of soil (Huntley & Morris, 1982). 75% of root biomass occurs within the upper 40 cm of another restrictive rooting zone where the soil profile is only 70 cm deep in its entirety in the southern Chihuahuan Desert, Mexico (Montaña *et al.*, 1995). The rainfall levels in these locations, 630 mm yr^{-1} and 264 mm yr^{-1}, respectively, would imply a more extended root system if not physically constrained.

`Insert Fig. 2`

Water in the upper layers is considered available to all vegetation types (Knoop & Walker, 1985; Montaña *et al.*, 1995; Seghieri, 1995; Mordelet *et al.*, 1997). It follows that plants sharing this rooting domain will be potential competitors. This still allows for some plants avoiding this competition by seeking water from deeper sources, (*e.g.*, Mesquite, *Prosopis glandulosa*). Given the fitness of the herbaceous layer for opportunism, this suggests that the success of shallow rooting shrubs and trees will be dependent on factors other than direct competition for PAM, and these will include soil fertility and texture (Scholes & Walker, 1993). Infiltration is reduced in clay rich soils leading to waterlogged soils in humid areas, and dry soils in low rainfall areas (Frost *et al.*, 1986). Whilst tree:grass ratios have been calculated for a wide range of Australian savannas using the total amount of soil water and the ratio of subsoil to topsoil water, along with total amount of evapotranspiration and the ratio of subsoil to topsoil evapotranspiration, improved estimates are possible by including PAN (Walker & Langridge, 1997).

3 Conflicts in savanna soil water modelling

It has been suggested that integration of simulated hydrological processes and simulated ecological processes is untenable as “Hydrology and ecology have in common an almost complete lack of common fundamental theory to those fields.” (Hatton *et al.*, 1997). It should be noted that probably only classical hydrological concepts were considered for this assessment. At the same time it was suggested, in quite damning terms, that integration of ecohydrological system components, obtained by reducing a complex system to fundamental processes, is also invalid. In preference it was suggested that an abstraction of these processes to an appropriate scale in an attempt to negate the fundamental differences existing between the two sciences, is a more rational exercise.

The conflict arises from the difference in scale that our knowledge operates at within the disciplines (also see *Scale and spatial variability in systems models*, below). The physical laws that govern hydrological processes are adequately understood to allow mechanistic simulation of soil water flow. Whilst transport of water within plant tissues is equally well understood, there is little information on water uptake by roots, rooting patterns and physical interaction of roots with the soil body. Thus, when considering water extraction by plants, abstraction is needed, away from microscopic scales to a more practical volume of soil.

4 Savanna soil water model theory

Soil water models exist as separate hydrological models or otherwise as sub-models of vegetation growth and ecological systems models. Classical approaches have tended to use physical laws to predict unsaturated water flow through hypothetical soil pore networks. Historically, such networks are based on homogeneous porous media. Contemporary forms employ methods that incorporate more realistic variation in pore size. In doing so, the tendency has been a move away from deterministic models to those incorporating stochastic elements to account for uncertainties about soil structure.

4.1 Classical hydrological concepts

Micropore volume is assumed to be a continuous function in space. A series of differential and partial differential equations[1] based on mass, momentum and energy conservation, are used to describe water flow. A widely used formulation is Richards' equation (Richards, 1931), as follows,

$$\frac{\partial \theta(\psi)}{\partial t} = \nabla \cdot \left(K(\psi)\nabla(\psi + z)\right) \qquad 1$$

where, θ is the volumetric water content, ψ is the pressure head (a product of capiliarity), z the elevation head, $\theta(\psi)$ the water retention characteristic, and $K(\psi)$, the conductivity characteristic. This form is one-dimensional, assuming horizontal uniformity and predominantly vertical water flow through soil columns. That is, change in soil water content is a function of conductivity and pressure at a given depth in the soil profile. Extensions of the Richards' equation are most often concerned with providing methods to find optimal solutions for $\theta(\psi)$ and $K(\psi)$. Conductivities are higher in sandy soils as channels in fine clays clog up with particles and cracks swell shut.

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[1] Partial differentials can be of scalar (*gradient*, ∇) or vector (*divergence*, $\nabla\cdot$) quantities. The partial differential of a one-dimensional vector gives a scalar result.

Clemente *et al.* (1994) compared three unsaturated soil water flow models (*Soil Water and Actual Transpiration Rate, Extended* (*SWATRE*), Belmans *et al.*, (1993); *Leaching Estimation and Chemistry Model* (*LEACHM*), Hutson & Wagenet (1992) and *Soil Water Simulation* (*SWASIM*), Hayhoe & de Jong (1982)), each using a form of Richards' equation. Differences between model predictions were found to arise from differing approaches to modelling soil evaporation and plant transpiration

4.2 Contemporary hydrological concepts

Total flow rate, related to a pore network's hydraulic conductivity, is proportional to the combined pore radius raised to the fourth power. This means that 10,000 pores with 0.1 mm radius would contribute a flow rate equivalent to that of a single pore of 1.0 mm, implying that the primary route of water flow is via macropores, pores in excess of 0.06 mm diameter (Brady, 1990).

Classical approaches fail to adequately describe infiltration via macropores (Feyen *et al*., 1998). Microscopic heterogeneity in soil structure concerns the inclusion of a macropore network, contrasted with exclusively a micropore network. Macroscopic heterogeneity refers to the effect of differential soil structure on flow throughout the soil body. Macropore flow can account for three-fold increases in water content, as measured by time-domain reflectometry (TDR) probes, spaced a few centimeters apart, but at an equal depth. Various techniques have been introduced to model water flow through heterogeneous porous media. Dual-porosity models apply the classical approach to a second macropore network. Micropore and macropore networks are considered continuous, and solutions are found that best describe flow within and between these two regions. Typically, bimodal functions are employed to describe differential water retention characteristics and hydraulic conductivities of pore networks (*e.g.*, Zhang & van Genuchten, 1994). Expedited water flow via macropores leads to deeper infiltration and a different spatial redistribution of water than found in macropore-deficient soil. Other microscopic heterogeneous approaches include explicit description of channelling and gravitational flow through macropores.

Modelling of macroscopic heterogeneity has been tackled in two ways, deterministically and stochastically. Deterministic models may use an exact representation of an observed heterogeneity at a given study site. Alternatively, a homogeneous model is parameterized using the scaled-up averages of local site data. Stochastic forms introduce elasticity into soil properties to generate the levels of variability expected for local heterogeneity in a porous medium (*i.e.*, the variance in pore size). For example, stream tube models (*e.g.*, Mallants *et al*., 1996), typically use a probability density function to determine the variance and covariance of the model parameters for the pore series that constitute flow tubes at a given location, but ignore spatial heterogeneity between locations by ignoring flow between tubes. Random space functions extend stochastic forms to account for spatial heterogeneity between locations by generating a covariance between the hydraulic properties of soil at different locations. The remaining 'Stochastic continuum' models are largely distinct by the mathematical techniques used to provide input values and to analyze their output. These techniques include bootstrapping (resampling) of soil properties within a Monte-Carlo framework, and Perturbation-Spectrum Analysis. The latter uses a random space form of Richards' equation to apply stochastic water flow, such as,

$$\frac{\partial \theta(x,\psi)}{\partial t} = \nabla \cdot \left(K\left(x,\psi(x)\right)\nabla\left(\psi(x)+z\right)\right) \qquad 2$$

where, x is the spatial coordinate and $K\left(x,\psi(x)\right)$ and $\psi(x)$ are random space functions.

The main effect of 'channelling flow' is to accelerate infiltration, redistributing water to lower in the soil profile. There is no automatic increase in gravitational through-flow unless the macropore structure is specified to extend uninterrupted to the zone of saturation (groundwater). At the working scale of population (*i.e.*, not individual) plant models, microscopic heterogeneity has no bearing on the calculation of evapotranspiration. Macroscopic heterogeneity will influence estimates of evaporation and transpiration by models that treat the soil profile in terms of layers, and allocate roots to these soil layers (typical of the many ecological models discussed below). The consequence for plant growth models that do not use layers or rooting depth, therefore, is negligible.

4.3 Ecological concepts

Hatton *et al*., (1997) proposed use of Eagleson's statistical-dynamic model of equilibrium water balance. This analytical formulation assumes equilibrial dynamics between the hydrological and biological components of an ecosystem. Vegetation growth is modelled in terms of water alone. The equilibrium state would not be possible without the dampening influence of steady-state water flow on the effects of a stochastic climate. Thus unsaturated flow, which includes [upward] capiliarity, suppresses variability in rainfall. Water flow is modeled by an adaptation of Richards' equation (Eq.1) and uptake is an externally defined proportion of the bare-soil potential evaporation rate.

The optimal solution for the model is assumed to equate to the maximal value for soil water balance, under a stochastic climate. Optimality in this relationship will eventuate via short-term shifts in vegetation composition to maximize transpiration efficiency, and therefore net soil water. These compositional changes seek to equilibrate canopy density with climate and soil. Over a longer time scale, the vegetation will generate changes in soil hydrological properties connected with saturated flow, to maximize biomass growth, whilst maintaining the equilibrium. Essentially, macropores become populated and divided by root systems, giving an increase in micropore density. Growth is assumed proportional to canopy density and canopy rain use efficiency.

Eagleson's statistical-dynamic model provides an estimate of soil water without the use of ecologically relevant parameters such as, soil depth, field capacity and rooting pattern, which are difficult to quantify. Therefore, the model requires only a minimal set of field parameters, which is an advantage, but at the cost of an estimate for evapotranspiration. A complementary algorithm needed to compute the species- and climate-dependent evapotranspiration rate, particularly in the case of patchy savanna, probably would be complex.

Hence, few ecological models are such extensions of the Richards' equation (Eq.1), by simple addition of a vegetation component. A rare example is *Soil Water Infiltration & Movement* (*SWIM*, Ross, 1990) which exhibits reasonable performance (Singleton *et al.*, 1998), but only after parameterization with generally unavailable specialized hydrological data (Walker & Langridge, 1996). Most ecological models restate soil water flow in terms of the entire flow path between soil and leaf. Evaporative losses from leaf surfaces provide a measure of photosynthetic activity and, if rain use efficiency is known, then also of carbon assimilation. A common goal of these ecological models therefore is to estimate evapotranspiration for conversion into growth. The infiltration of rainfall and the availability of soil water for transpiration is an important factor determining savanna dynamics, and the shared requirement for soil water by diverse types of savanna vegetation implies a competition for this resource as supported by evidence of overlap in rooting patterns (see *Vegetation Composition*). Stratifying the soil into layers has provided a computational framework with which to implement Walter's (1971) two-layer exclusion model, but is a perpendicular viewpoint to that of the hydrologist's soil columns.

5 Simulation of processes

So far we have considered cell-, plant- and population-based water relations, and, separately, the theory of water movement in soils and the classical models (and their modern adaptations) that have attempted to represent soil hydrology. In ecological models, the aim is to harmonize differences in scale to enable integration of soil and plant properties towards representation of the system. The attitude that plants are an interface between soil and the atmosphere leads to a more process-oriented interpretation in place of the general analytical forms like the Richard's equation. Processes combine to define components of the system; delivery of water (precipitation) to the soil surface, redistribution according to topography (runoff), loss to evaporation, infiltration through the soil profile, uptake and transport, photosynthesis and transpiration, growth and assimilation.

5.1 Infiltration

Savanna can comprises a sparse canopy, with large areas of bare ground possible between the canopies of individual plants. Low basal and litter cover reduces infiltration and increases runoff. *Productivity, Erosion and Runoff Functions to Evaluate Conservation Techniques* (*PERFECT*, Littleboy *et al.*, 1992, 1993; Littleboy, 1995) explicitly models runoff using a second order function to relate runoff to a retention parameter, an index of soil water content, in a similar way to Dye (1983) who assumed a second order relationship between infiltration and daily rainfall above 12 mm. Comparing the two, independent estimation methods for infiltration across a range of daily rainfall between 0 and 100 mm (Fig. 3), there is greatest similarity for soil water content equal to 69.5 mm in *PERFECT* ($t_{0.5[100]}=4.19$, $p<0.01$). Where the methods differ is in their estimation of infiltration for small rainfall events. Dye (1983) compensated for the local minima occurring for second order curves towards the origin, by imposing a 1:1 linear relationship for infiltration and rainfall below 12 mm. There seems to be no adjustment in *PERFECT*, however, this may be ameliorated in part by capping of the retention parameter for low standing crop cover according to a soil condition curve number which accounts for antecedent moisture conditions. The error in predicting runoff by the unmodified second order function will be largest for dry soils with maximum cover.

`Insert Fig. 3`

Soil sorptivity (mm/min^2) is a measure of infiltration potential, a function of hydraulic conductivity, soil water potential and soil water content (Philip, 1957; cited in Stroosnijder, 1996). In a grazing model applied to the Sahel, sorptivity was related to canopy cover, soil surface crust and rainfall event frequency (Stroosnijder, 1996). Canopy cover also provided a macroporosity factor that increased infiltration. The model was not concerned with soil deeper than topsoil, as rainfall is light and frequent during the growing season. Runoff was assumed to be the difference between precipitation and the sum of infiltration and change in topsoil storage capacity. The model predicted that under grazing, runoff may be increased considerably, *e.g.*, 28% of rainfall for no herbivory to 47% for 2000 kg ha^{-1} removal.

PERFECT contains a set of rules defining the conditions for infiltration via cracks These are; rainfall must be greater than 10 mm, infiltration via cracks is limited to 10 mm of rainfall, the upper profile must be at less than 50% of field capacity, cracks can extend throughout regions which are at less than 50% of field capacity, cracks are filled from the bottom up, and any crack flow can only introduce water up to 50% of field capacity. *Simulation of Daily Water Dynamics* (*WATDYN*, Walker & Langridge, 1996) adoptes the same crack flow routine.

5.2 Evapotranspiration

Evaporation in *PERFECT* is a two stage process. Immediate evaporation of infiltration is followed by long-term evaporation at a rate proportional to the square root of time, constrained by soil water deficit in the topsoil. Transpiration is the minimum of potential extraction rate and potential transpiration rate, which is derived from Leaf Area Index (LAI, a measure of cover expressed as m^2 total leaf area per m^2 of ground). LAI has been widely adopted as a measure of the mean attenuation of incident solar radiation by interception by leaf surfaces. This depends largely on structural aspects of the canopy such as the density of foliage and, the arrangement and inclination of the leaves (Larcher, 1995).

In the modelling of LAI, leaf area is often assumed directly related to green leaf biomass (*e.g.*, *WATDYN* and *Savanna - Landscape and Regional Ecosystem Model* (*SAVANNA*, Coughenour, 1993), or is a user-measured input (*e.g.*, *PERFECT* and *Soil Water, Energy and Transpiration* (*SWEAT*), Daamen & Simmonds, (1994)). LAI measurements vary according to the choice of criteria used in estimation. Assuming LAI to be maximal when *further increases in LAI have an insignificant effect on evapotranspiration* (REF) is notionally distinct from LAI is maximal when *evaporation is nullified as a contributor to evapotranspiration* (REF). Other treatments of LAI relate fluctuation in leaf area to ambient temperature and light interception (*e.g.*, Acock *et al*., 1979 cited in Johnson & Thornley, 1983). However, as Johnson & Thornley (1983) state, such dependencies of LAI on environmental conditions and biomass are limited because two canopies concurrent in their LAIs do not necessarily have identical structures. Additionally, environmental variation often exceeds that observed in associated vegetation growth. Johnson and Thornley's (1983) solution was to treat LAI as an independent state variable in their model. Vegetation structure was generated independent of biomass by allocation of predicted daily growth to a carbon storage pool, and fluxes from there to other compartments representing differential turnover of leaf, sheath and stem material. The result was an independent estimate for LAI buffered from environmental variation, and provision of a mechanism that may be extended by inclusion of known species phenology and plant part allometry (Illius *et al*., 1996).

"LAI is maximal when" in italics? i.e., from quote?

The patchy mosaic of savanna vegetation gives rise to LAIs below those that may be observed for commercial crops (maximally ~10) (REF). Savanna values range between 0 (bare ground) and 5 (closed canopy) (REF).

REFS? Johnson and Thornley (1983)

An important consideration for a patchy matrix is the reduction in transpiration for high evaporation rates; semi-arid regions often have low vegetation cover leading to greater losses by evaporation than transpiration. This can be modelled simply by allocating a fraction of total potential evapotranspiration, with the remainder being used for evaporation (*e.g.*, *SWIM*). However, this method assumes no interaction between evaporation and transpiration, and therefore lacks the capacity for unrelated dynamics from each evaporative source. Alternatively, models that allow interaction between evaporation and transpiration for a single plant species are called 'two source' models as they independently derive more than one estimate for evaporation. Add another plant species to a two source model and you have a 'three source' model, and so on. A representation of water flow from soil to leaf that allows such interaction is with a network of resistances which mediate water flow between the soil, vegetation, and atmosphere, analogous to an electrical circuit (Fig. 4). To draw parallels between such ecological models and the hydrological approaches detailed above, it may be useful to note that hydraulic conductance (g) is related to hydraulic resistance (r) by $g = r^{-1}$.

"Unrelated"? This needs explaining

The Penman-Monteith equation (Monteith, 1965) is a modified expression for soil surface evaporation that assumed the soil and canopy to be a single damp surface separated from a reference height by aerodynamic resistances. Inclusion of the canopy and boundary layer conductances allowed transpiration to be determined as a function of solar radiation (net reflection), vapour pressure and several temperature-dependent physical quantities (Thornley & Johnson, 1990). Models such as *WATDYN* use the Penman-Monteith equation to their advantage in separately estimating transpiration and evaporation.

SWEAT is a two source, crop-based model specializing in the calculation of transpiration for sparse canopies furnishing low aerial cover, a condition associated with droughts in particular. LAI is used to estimate canopy condition, and thus canopy photosynthetic activity. Flux of water and heat are evaluated for soil surface, leaf surface, in air canopy and air at a reference height, each a node within the network of resistances. Penman-Monteith potential evaporation from the soil surface was calculated assuming bare soil conditions. Actual evaporation was obtained using a matrix method to solve a system of linear equations (Gaussian Elimination). An algebraic manipulation of the Penman-Monteith equation involving the ratio between potential and actual evaporation was then used to calculate the hydraulic resistance in the soil (r_{soil}), estimates of which were found to be improved by using soil temperature and layering within the topsoil, rather than an integral volume of water near the soil surface. A linear scale for r_{soil}, from 0 sm^{-1} following rain to 2000 sm^{-1} after about 4 days (based on a sparse stand of millet in Niger) was shown less accurate than using this maximum value throughout, implying complexity in the soil surface flux. Transpiration is limited by leaf water potential (Ψ_L) and the stomatal resistance (r_s). Root water uptake is a function of Ψ_L, optimized in the model to balance root uptake with transpiration. Root density with depth is a required input, along with vegetation height, LAI, and other species parameters.

`Insert Fig. 4`

Inclusion of the aerodynamic resistance in a sparse canopy is important for increased evaporation following large rainfall events as high humidity reduces potential transpiration. Thus a principal component of such models is their representation of r_s. In *SWEAT*, r_s is proportional to the ratio between Ψ_L and a critical value for Ψ_L at which r_s "increases quickly" (~-1.6 MPa), and the energy available at the leaf surface with respect to LAI. This gives a range of r_s between 128 and 167 sm^{-1} for LAI's from 0.5 (sparse canopy) to 2.0 (full canopy), leading to the greatest relative change in transpiration for LAI ≤ 0.5, and maximum absolute change between LAI = 1.0 and LAI = 1.5. This effect is due to soil heat (convection and reflected) being absorbed and dissipated by the canopy. Transpiration is most sensitive to r_s at very low LAI. For models that do not include r_s to regulate transpiration rate, transpiration may be first corrected for humidity (Dye, 1983). In contrast, *WATDYN* uses an adjustment term to increase r_s in response to increasing water deficit, evaluated with respect to soil texture.

5.3 Growth

Transpiration is often converted into plant growth by use of a coefficient of efficiency, (*e.g.*, Dye, 1983; *PERFECT*; Stroosnijder, 1996). *PERFECT* constrains crop growth for saturated soils, by scaling plant biomass down by a wetness factor. *WATDYN* adds the proviso that soil water should exceed 15% of field capacity before growth can commence at 10 kg ha^{-1} per mm of transpiration. *WATDYN* additionally modifies growth with respect to soil fertility, temperature, vapour pressure deficit, and fire history. Hobbs *et al.*, (1994) constructed an analytical model that predicts growth directly from a negative exponential function of PAM expressed in terms of soil water storage capacity (field capacity minus wilting point). This simple approach proved effective, predicting a near constant rate of growth per unit of PAM, 0.33 g mm^{-1} m^{-2}, throughout the growth season, but was validated across a limited range of sites in central Australia.

5.4 Rooting depth

Where a resistance network is used, it does not preclude the use of differential equations to represent water flow through the soil profile. Plainly, delivery of rain water to depths in the soil profile is a precursory stage to flow from soil to leaf. However, understandings about rooting depth, including water competition, suggest apportionment of root phytomass across a stratified soil profile. Calculation of instantaneous mass flow throughout the profile has been substituted by summation of soil water volume within soil layers, thereby facilitating representation of soil water content across the range of rooting depths. A simple mechanism by which rainfall may percolate to increasing soil depths uses the ‘tipping bucket model’ (REF, Manabe?). Working from the topsoil down, each layer is filled to field capacity before excess water is allowed to pass into the next layer. Water flowing from the lowest layer is assumed lost to deep drainage. This is a popular representation employed in models of soil water flow as well as those specializing in soil nitrogen dynamics (*e.g.*, *Water Balance Model* (*WATBAL*), Berghuijs van Dijk, 1990, *Soil Nitrogen Model* (*SOILN*), Eckersten *et al.*, 1996 and *SWATRE*, reviewed in Wu & McGechan, 1998).

Dye (1983) used three soil levels to model grass growth in a semi-arid savanna in south-western Zimbabwe. Infiltration of daily rainfall, after runoff and evaporation from the soil surface, is sequentially allocated to each soil level in order of increasing depth. *PERFECT* allows division of the soil profile into ten layers of variable thickness, each layer characterized by wilting point, soil water content at wilting point, field capacity, total porosity, infiltration and drainage characteristics, evaporation and drainage, and PAM to rooting depth. Daily evaluation of total soil water content is equal to the current soil water content plus daily rainfall, net evapotranspiration, runoff and drainage. Potential extraction is a function of soil water status, root depth, and root density. *WATDYN* is based on the work of Dye (1983) and needs only layer depth, field capacity and wilting point for input. The model uses layer depth to convert between volumetric units and millimeters. Each layer can be split into further sub-layers also used in the volumetric translation. Furthermore, the sub-layering can be used to determine the compensatory rate for water extraction from adjacent sub-layers based on transpiration demands in excess of the local sub-layer's water content.

In addition to the tipping bucket-type flow, macropore flow is another option in *WATDYN* (*c.f.* dual-porosity models, see *Contemporary Approaches*). Macropore flow is assumed to commence at a relative rate (the default is 50% of flow from above) when soil water content surpasses a threshold value (80% of field capacity).

Although not reported as a modelled feature in *WATDYN*, stratified layers may increase the water holding capacity of the upper part of the soil by acting as moisture barriers until a relatively high moisture level develops for infiltration into the stratified layer. The result, a build up of water content in excess of that that would otherwise exist for freely draining soils. For clay above sand, downward movement of water is halted at the layer boundary as the macropores of the sand provide less attraction for water than the fine textured clay above, so the water progresses laterally.

6 Scale and spatial variability in systems models

Although ecological space has been a concern in ecology for some time (*e.g.*, Gause, 1934 cited in Tilman & Kareiva, 1997), it is only the recent advances in computing that have allowed simulations of integrated [heterogeneously] spatial systems. this has led to findings of complex dynamics that emerge through spatial interactions (*e.g.*, ecosystem function, Pacala & Deutschman, 1996; and ecosystem resilience, van de Koppel & Rietkerk, 2004), which would otherwise not be apparent from unidimensional (temporal) simulation (Steinberg & Kareiva, 1997). These spatial studies have elicited pattern formation at individual plant (*e.g.*, Bian *et al.*, 2002), vegetation patch (*e.g.*, Roxburgh *et al.*, 2004), plant population (*e.g.*, Wu & Levin, 1994) and landscape levels (*e.g.*, Wiegand *et al.*, 2000). This organization of structure and function into a spatially ordered hierarchy of scale has necessitated revision of established concepts and primarily led to our current comprehension of ecological systems (Schneider, 1998). Recently, contemporary dicta based on the scale hierarchy even advocate holistic analysis in the place of reductionism (Li, 2000), even though ecological holism (Odum, 1953), and the hierarchical approach are less recent introductions to ecology (in abstraction, *e.g.*, Scholes, 1990b, and simulation, *e.g.*, Auger, 1990). The new understanding has brought with it conflicts when combining observational scales (Atkinson & Tate, 2000), conflicts of scale between observations and models (Bierkens *et al.*, 2000) and conflicts when combining modelled scales (Peterson & Parker, 1998), although geostatistics (*e.g.*, Riply, 1981; Cressie, 1993) and the modern synthesis are also uncovering means for using scale relationships to integrate across those scale hierarchies (Wiegand *et al.*, 1999; Pascual *et al.*, 2002).

7.1 Hydrological Systems Models

Soil–Vegetation–Atmosphere Transfer (SVAT) models are conceptually-based constructs of typically large scale (> 50 km) interactions between the atmosphere and the terrestrial biosphere (Menenti *et al.*, 2004). The broad aim of the SVAT schemes is to estimate the exchange of water, energy and carbon between vegetation and atmosphere over multiple seasonal cycles and diverse climates (Moehrlen, 1999) by the coupling of land surface models (LSM) to large-scale general circulation (climate) models (GCM). SVAT schemes range from single tipping bucket models (to represent the soil-plant-atmosphere interface) to those that incorporate multiple layers for vegetation, soil, and snow (Warrach *et al.*, 2002). They can assume that the biome (the spatial distribution of plant species) is either static or dynamic (Menenti *et al.*, 2004), where most current SVAT schemes and hydrological models do not parameterize vegetation as a dynamic component (Arora, 2002), although a recent approach has included variable root density related to predictions of vegetation biomass (Arora & Boer, 2003). Equilibrial water balance is assumed for most SVAT models (Braud *et al.*, 2005) such that transpiration is assumed to be equal to root water uptake (see *Ecological concepts*, above). Whilst microscopic soil structure (macropores) and vegetation canopy space (aerial cover) are represented, there is often a conflict between the successful integration of processes operating at these small scales with the larger scale processes at the landscape level and those resulting from atmospheric conditions (*e.g.*, air temperature and humidity that are assumed to only vary by height, Menenti *et al.*, 2004).

Extensions to SVAT schemes that introduce spatial variability for runoff and infiltration, to account for spatial heterogeneity in soil moisture, perform best when compared with homogeneous alternatives (Warrach *et al.*, 2002). Also, the accuracy of heat fluxes predictions by a SVAT scheme have been shown to be improved (Yang & Friedl, 2003) by introducing more temporal (diurnal variation) and spatial (3D plant architecture) detail into the atmosphere-canopy interactions (a 'canopy interception reservoir' (Koster & Suarez, 1994), comparable to the hydraulic conductance approaches for modelling transpiration, see *Evapotranspiration*, above). Further improvements have been possible by using LAI to estimate spatially heterogeneous transpiration and rainfall interception by the canopy (*e.g.*, Mo *et al.*, 2004; Wattenbach *et al.*, 2005). Alternatively, the terrestrial biosphere is not explicit in the model, but instead root water uptake is represented by a term for potential [evapo]transpiration (Braud *et al.*, 2005), often within the expression for soil water transfer (*e.g.*, Richard's equation), but transpiration can be underestimated when calculated from potential evapotranspiration in this way (Braud *et al.*, 2005). Improved accuracy of SVAT models can result from more spatial detail, but this carries the cost of needing a large number of spatial parameters (Pachepsky *et al.*, 2004).

A SVAT model applied to savanna has shown that detailing soil surface conductance was more significant than improvements to radiation balance and aerodynamic conductance terms for predicted evapotranspiration (Domingo *et al.*, 1999), highlighting the importance of evaporative losses for dry, low-cover areas. The extent of bare ground in these systems can cause problems for single source SVAT models unless modifications are introduced to allow for low canopy cover (*e.g.*, two source model). The problem then is that single source SVAT models perform better than two source SVAT models for high cover (Boulet *et al.*, 1998) thereby imposing a limit on vegetation parameters. Another sensitive parameter was found to be [hydraulically active] soil depth, which determines the time taken for the soil column to dry out after saturation (32 days when the latent heat flux for semi-arid land was set at 100 W/m^2, Boulet *et al.*, 2000).

7.2 Ecological Systems Models

A total system grazing model tends to involve integration of separate climate, soil, plant and animal mechanistic modules that attempt to synthesize ecological theory and empirical evidence, to give a compound estimate of the system's dynamics. Total system models that exist for semi-arid savanna are few, and those that do exist tend to adopt elements of the ecological modelling approaches already described as their soil water balance module. Vegetation dynamics (competition for soil resources, transpiration and primary production) tend to be expressed in terms of plant functional groups, although varieties (species) may often be parameterized. Here we will focus on the water balance modules of the three most comprehensive, spatially-explicit (in these cases by using grids of cells), process-oriented (mechanistic) systems models currently applicable to semi-arid savanna, *SAVANNA* (Fig. 5a) and *Simulation Model for Australian Savannas* (*SAVANNA.AU*, Liedloff *et al.*, 2004, Fig. 5b), a version extensively modified for Australia, and *Simulation of Semi-arid Grazing Systems* (*SimSAGS*, Illius *et al.*, 1998; Illius & Gordon, 1999; Illius *et al.*, 2000; Derry, 2004, Fig. 5c). Figure 5 includes additional detail about each approach.

`Insert Fig. 5`

Big "if" about this (set of) figure(s)
Picture paints a 1000 words and all that but is it worth it? Quality of figures needs improving if we go with them.

In *SAVANNA* soil profiles are divided into three layers, with grass roots reaching into the second layer and shrub and tree roots exclusively occupying the third layer. The middle layer is shared. Layer thickness, field capacity, wilting point and an index of porosity are used to calculate soil water holding capacities and maximum PAM for each layer. Runoff is calculated by a similar method to that used in *PERFECT* and *Simulation of Production and Utilization of Rangelands* (*SPUR*, Wight & Skiles, 1987), such that runoff depends on daily rainfall, the quantity and distribution of water in the soil relative to water holding capacity, and the condition curve number for the soil according to vegetation cover (*i.e.*, the USDA curve number method, United States Soil Conservation Service, 1964). The range of LAI allowed is between 0 and 4. Grid cells are also partitioned laterally into subareas which captures within cell heterogeneity of topography and soils. Total runoff can therefore be distributed among all runon subareas according to the proportion of the landscape that they occupy.

Bare soil evaporation is simulated using the same method as *PERFECT* and *SPUR*. Precipitation from mean weekly rain days plus additional runon is allowed to infiltrate into the top layer after runoff has been extracted and is redistributed with a tipping bucket model. Evaporation is from the top layer and occurs for the mean number of days between rain events. Surface litter is accounted for in calculation of infiltration and potential evapotranspiration. A water table depth for each soil type may be specified, and this increases soil water in the unsaturated portion of that layer. Layers below that remain saturated. A system of resistances moves water from soil to leaf. r_s is mediated in response to water stress by the ratio of PAM to potential evapotranspiration, a technique also found in *Grassland and Agroecosystem Dynamics Model* (*CENTURY*, Parton *et al*., 1993). Potential evapotranpiration is augmented by root phytomass growth via increased uptake (Coughenour, 1991).

Plant functional groups in SAVANNA are, 'sun-adapted herbs', 'shade-tolerant herbs', 'shrubs', 'deciduous trees' and 'evergreen trees'. Actual transpiration rate for each group is calculated from r_s, the vapour pressure deficit, daylength and green leaf mass. Water demands for transpiration are levied across soil layers to match PAM and do not consider rooting pattern at this stage. Competition for water between vegetation species is modelled by assuming that each plant's competitive ability for water is proportional to it's potential rate of water use (strength for water uptake). If total plant water demands in a layer exceed available water then available water is partitioned among competitors in proportion to their demands. Water use efficiency is allowed to decrease with increasing plant size due to greater maintenance respiration costs, therefore, tree relative growth rates decline with increasing size, accessed with respect to leaf area, maximal relative growth rate and maximal root biomass per plant.

SAVANNA.AU rainfall may be intercepted by canopies and evaporated back to the atmosphere or flows down plant stem to the soil. Water uptake is transpired back to the atmosphere, or falls through to reach the landscape surface, where, for saturated soil, it either ponds on flat areas and evaporates, or runs off if the landscape is sloping. *SAVANNA.AU* treats runoff in a similar way to *SAVANNA* except that runon is partitioned according to elevation differences between neighbouring source and destination cells. Runoff may be impeded by, *e.g.*, vegetation patches, which leads to increased infiltration beneath the patch, or runs off the grid cell as runout. Water may also be lost from the system as deep drainage.

Soil texture defines the sand silt and clay content of the soil, and *SAVANNA.AU* uses this to estimate the potential for water infiltration and conduction. Texture is specified along with depth, bulk density, porosity, and specific water holding capacities, depending on availability of the data, for a variable (user-defined) number of soil layers. Macropore flow is implemented as a multiplier for infiltration and hydraulic conductivity based on predicted root biomass and a parameter for invertebrate activity. This is deemed important because the approach behind *SAVANNA.AU* emphasizes macroporosity of soil layers and soil surface condition in determining infiltration rates into layers and conduction rates between layers. Soil surfaces are impacted through disturbance, for example, from cattle grazing (trampling effects) and fire, so that as soil surface condition deteriorates (*e.g.*, becomes compacted, more bare, *etc*.), infiltration rates decline. Better soil surface condition is awarded for a high cover of perennials and deep litter, which result in higher infiltration rates. Soil surface condition is integrated into the model as a score devised for Landscape Function Analysis (LFA, Tongway & Hindley, 1995, 2004), that assimilates measures of cover for cryptogamic crusts, litter, forbs, and annual and perennial grasses, as well as surface roughness, slope and animal days (exposure to herbivore impacts).

Plant functional groups in *SAVANNA.AU* are, 'resprouting woodies', 'non-sprouting woodies', 'palatable perennial grasses', 'unpalatable perennial grasses', 'ephemeral grasses' and 'forbs'. Competition between groups for PAM (and PAN) is regulated as it is in *SAVANNA* such that, if the water demand exceeds availability, plants are allocated resources based on their proportional demands, Following this estimation of actual transpiration, evaporation and deep drainage are calculated to maintain each soil layer within its field capacity.

[FROM ADAM] *SAVANNA.AU* is a grid-based, spatially explicit, process orientated model, developed from the Savanna model. Savanna was originally devised to study 10,000km2 nomadic pastoral ecosystems in arid east Africa (Coughenour, 1992; 1993) and has been used in the savannas of north Australia (Liedloff et al 1999, Ludwig et al 1999). While *SAVANNA.AU* shares much of the plant production and general model concepts with the Savanna model, it has been completely re-developed to answer a range of management questions relevant to northern Australia.

Accurate modelling of soil water is considered critical for simulating plant production as available plant water directly relates to pant growth. While *SAVANNA.AU* aims to capture the soil water processes involved, it does so using a tipping bucket soil water model which is intended to be easily parameterised using available field data. As this model has a management focus, the landscape hydrology processes used are not as detailed as for other models such as PERFECT (Littleboy et al., 1992), WEPP (Laflen et al., 1991), GUEST (Misra and Rose, 1996) or CENTURY (xxx), from which Savanna devised its soil water and nutrient components. In terms of simulating hydrological processes, *SAVANNA.AU* runs on a daily time step using daily rainfall records. It is recognised that rainfall intensity and duration are critical to understanding infiltration and modelling soil water. For this reason, the daily rainfall is divided into two rainfall events. The first event is of one hour duration accounting for a proportion of the daily rainfall. The second event uses the remaining daily rainfall for a duration determined from a daily rainfall total to duration equation provided for the site. Rainfall may also be intercepted by trees before reaching the soil surface.

Given rainfall of known intensity, the model uses soil properties to determine infiltration rates and move water into the soil rather than calculate runoff from a range of landscape parameters (is slope, litter etc) and assume the remaining water infiltrates. Many of the soil properties used in the model can be obtained from soil maps which provide the depth of various layers and the soil texture of these layers (sand, silt and clay percentages) from which a range of soil characteristics such as saturated capacity, wilting point and base infiltration rate can be estimated (Bristow et al 1997). Alternatively, soil water properties can be determined from bulk density and porosity data. Infiltration and percolation into the various layers is further enhanced or reduced by eco-hydrological processes such as macroinvertebrate activity developing macropores (Dawes), the soil surface condition

(Tongway) and the feedback to factors such as plant biomass, litter production and cover. This is deemed important because the approach behind *SAVANNA.AU* emphasizes macroporosity of soil layers and soil surface condition in determining infiltration rates into layers and conduction rates between layers. Soil surfaces are impacted through disturbance, for example, from cattle grazing (trampling effects) and fire, so that as soil surface condition deteriorates (e.g., becomes compacted, more bare, etc.), infiltration rates decline. Better soil surface condition is awarded for a high cover of perennials and deep litter, which result in higher infiltration rates. Soil surface condition is integrated into the model as a score devised for Landscape Function Analysis (LFA, Tongway & Hindley, 1995, 2004), that assimilates measures of cover for cryptogamic crusts, litter, forbs, and annual and perennial grasses, as well as surface roughness, slope and animal days (exposure to herbivore impacts).

Water that cannot infiltrate into the soil layers in the given time, or is surplus to soil water holding capacity is routed between cells as sheetflow. A digital elevation map provides the height differences between adjacent cells which are used to determine which cells receive runon, and what proportion is sent to each cell as runoff using the basic approach used in the model T-HYDRO (Ostendorf and Reynolds, 1993). An additional creek map can be used to specify when a proportion of sheetflow is channelled into creek flow and lost from the system. Runoff may is captured by moving through cells with high cover and increased macroporosity, resulting in increased infiltration. Water may also be lost from the system as base soil evaporation, plant transpiration and deep drainage to dynamically determine the amount of soil water in the soil.

Any number of plant functional groups or individual species can be used in *SAVANNA.AU* such as, 'resprouting woodies', 'non-sprouting woodies', 'palatable perennial grasses', 'unpalatable perennial grasses', 'ephemeral grasses' and 'forbs'. Competition between groups for PAM (and PAN) is regulated as it is in SAVANNA such that, if the water demand exceeds availability, plants are allocated resources based on their proportional demands, Following this estimation of actual transpiration, evaporation and deep drainage are calculated to maintain each soil layer within its field capacity.

The components modelling the soil moisture balance in *SimSAGS* are based the non-spatial *WATDYN*. To introduce spatial interactions into the processes that determine soil water dynamics, landscape topography is used to move surface water around the landscape from high to low regions in a similar manner to the other two ecosystem models, except that runoff is not partitioned between runon subareas nor neighboring cells, but is delivered entirely to the next highest cell in the sequence of decreasing altitude. Rainwater and runoff that does not soak into the soil or is not evaporated from the soil surface effectively runs across the surface as rivers and streams (Fig. 6). This hydrology is modelled and is important in determining higher soil moisture and the increased plant growth in runon areas that gives rise to the characteristic heterogeneity of savanna vegetation, however the adoption of Dye's (1983) simple relationship for infiltration (see *Infiltration*, above) limits *WATDYN*'s ability to accurately predict runoff for a large range of soil type, slope and soil surface conditions (Walker & Langridge, 1996), which is more possible using the family of curves in the USDA curve number method.

Insert Fig. 6

This figure is probably excessive and a better illustration of WATDYN / SimSAGS output (if beneficial?) is possible, *e.g.*, soil moisture content (even within layers), etc.?

After runoff, changes in soil moisture are predicted as a function of losses to deep drainage, evaporation and transpiration, using a modified version of *WATDYN* for each grid cell in a variable number of layers, and sub-layers therein. Layers allow for accurate estimation of soil water and vegetation species dynamics from the ratios of PAM between layers (see *Vegetation Composition*, above). Sub-layers enable more accurate processing of small changes in local soil moisture. The minimal data set for *WATDYN* requires daily rainfall, wind speed, atmospheric pressure, radiation, temperature and relative humidity plus soil/plant properties including soil depth, proportional root distribution per layer and an index of soil fertility. Soil nutrient budgets are not explicitly modelled, however accurate estimates of soil moisture are possible using this fertility index which encapsulates soil capacity for primary production as a function of the concentration of cations and phosphate (Walker & Langridge, 1997). Additionally soil type (texture) is used to specify clay and sand content.

Evaporation from the soil surface is modelled as a Penman-Monteith function of surface cover (alive and dead biomass), temperature and humidity, and the resistance to further vapour loss as the soil dries out. Calculation of infiltration and subsequent through-flow uses a bucket model. Through-flow is calculated when the water content of each progressive soil layer (after adding rainfall minus runoff and that entering via cracks) is above the user-defined amount (70% of the storage capacity for a medium textured soil). At this point 50% of the incoming water becomes through-flow and infiltrates the next soil layer down the profile. Macropore flow may be invoked in *WATDYN* but is generally advised against because of the difficulties in obtaining parameters for the process. The default settings assume macropore flow to commence at 80% of the soil water storage capacity, and flow at 50% of the rate of the incoming water above this threshold.

Plant functional groups in *SimSAGS* are, ‘annual grasses’, ‘perennial grasses’, ‘forbs’, ‘shrubs’ and ‘trees’. Species within these groups can be distinguished through parameterization. Daily potential transpiration for each species is based on daylight intensity, LAI, light interception, humidity, temperature, the aerodynamic resistance (equivalent to r_a) and the canopy resistance (equivalent to r_s), using a modified Penman-Monteith equation. During the calculation of water uptake for transpiration, an adjustment is made to r_s in response to a vapour pressure deficit (dependent on atmospheric pressure and humidity) and the combined water deficit within the soil layers (also dependent on the soil texture). r_s is also adjusted according to variation of temperature. Actual transpiration is calculated according to the proportions of root biomass within each soil layer. This is capped to the wilting point of the soil, however, an optional function scales water uptake via a Michaelis-Menten function to a maximum (default=150%), to account for compensatory extraction when the relative moisture content of the local soil layer is insufficient to meet demands for transpiration as it approaches wilting point, and the soil moisture in other [deeper] layers is not limiting. Transpiration efficiency, to convert from transpiration into growth, is calculated according to soil fertility, minimum temperature and the vapour pressure deficit. Plant phenology and the allocation of photosynthates to modelled plant parts is handled separately in the *SimSAGS* plant module. Thus, within each cell of *SimSAGS*, daily growth is predicted for each herbaceous and woody species on a per unit area basis before being partitioned across the species present according to their contribution to total photosynthetic biomass.

There is concern about the volume of input data required to parameterize mechanistic models (*e.g.*, Pachepsky et al., 2004). The simulation of an extensive list of soil water balance processes across stratified soil profiles invariably calls for an extensive list of input parameters (*e.g.*, ~50 in *WATDYN* / *SimSAGS*, ~60 in *PERFECT*, ~60 in *SWEAT*, ~90 in *SAVANNA*, and ~145 in *SAVANNA.AU*), which are often difficult to supply or assumptive in their quantification. For soil water models, there is (arguably) a trade off between minimizing a parameter set and maximizing the sophistication and accuracy of the simulated processes.

Other comparisons?

8 Conclusion

The aim of this exercise was to identify the main components of soil water models, compare differences in approaches to their modelling, and assess which approaches were best suited for the modelling of soil water dynamics in semi-arid savanna. To this end, the sections above have identified infiltration, runoff, evaporation and extraction of the water demanded for transpiration.

A major argument echoed by Hatton *et al*. (1997) opposes mechanistic models as they are considered to form too complex a system for interpretation of simulation predictions. Sensitivities in model output require comprehension by comparison with variation in model parameterization, and in the subsequent responses of their sub-models. In spite of this, various mechanistic models have been validated in their simulation of savanna vegetation growth based on soil water dynamics. Furthermore, this was achieved in part by the coupling of mechanistic soil hydrology sub-models with mechanistic vegetation growth sub-models.

Physical hydrology has produced sophisticated models of water flow through variable soil structures providing accurate methods of simulating infiltration and redistribution. There is a claim that these approaches do not lend themselves to ecological modelling as processes work at different scales, necessitating considerable abstraction before contrarieties may be nullified. Even if this claim could not be supported, our knowledge about rooting patterns is insufficient to resolve water uptake with delivery at the scale hydrological models operate, even though one example has been found that attempts this marriage (*SWIM*). Ecologists have responded to this clash by reevaluation of soil physical properties in ecological terms. Previous notions of resource partitioning have been modified so that competition for soil water is thought to occur between differing savanna vegetation by overlap of rooting zones at some point in the soil profile. The association between competition and rooting depth has effected a stratification of the soil profiles into layers that are equivalent to rooting zones. The need to estimate rates of transpiration have necessitated estimation of water loss to processes other than percolation, such as runoff, soil surface evaporation, crack flow and deep drainage.

Much effort has been invested in the construction of ecological models, which, on the whole, differ marginally within this category of models. Generally, runoff is related to vegetation cover and topsoil water potential. A tipping bucket model is typically used to redistribute infiltrating rain. Transpiration is assumed proportional to biomass or LAI, (which is often derived directly from estimates of green leaf biomass). Alternatively, soil surface evaporation is a function of time since the previous rainfall event and may be dependent on canopy sparsity. Most models are single source models, therefore, whichever quantity is not calculated, is effectively the balance between the original rainfall value and the calculated value. However, low canopy cover in semi-arid savanna can lead to unrelated dynamics for transpiration and evaporation, and this is better dealt with in two source models which separately calculate transpiration and evaporation. Growth is often calculated directly from transpiration by conversion with a coefficient of assimilation efficiency that provides a mechanism to differentiate between plant species.

There is some cross over in the hydraulic conductance approaches shared by SVAT schemes and process-oriented ecological models, but they are posed with the same conflicts of spatial resolution when trying to integrate with hydrological models.

Omissions from current modelling efforts

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Appendix 1 - list of models referred to in the text, listed alphabetically by acronym.

Acronym	Name	Principal literature
CENTURY	*Grassland and Agroecosystem Dynamics Model*	Parton et al., 1993
LEACHM	*Leaching Estimation and Chemistry Model*	Hutson & Wagenet, 1992
PERFECT	*Productivity, Erosion and Runoff Functions to Evaluate Conservation Techniques*	Littleboy et al., 1992, 1993; Littleboy, 1995
SAVANNA	*Savanna - Landscape and Regional Ecosystem Model*	Coughenour, 1993
SAVANNA.AU	*Simulation Model for Australian Savannas*	Liedloff *et al.*, 2004
SimSAGS	*Simulation of Semi-arid Grazing Systems*	Illius *et al.*, 1998; Illius & Gordon, 1999; Illius *et al.*, 2000; Derry, 2004
SOILN	*Soil Nitrogen Model*	Eckersten et al., 1996
SPUR	*Simulation of production and utilization of rangelands*	Wight & Skiles, 1987
SWASIM	*Soil Water Simulation*	Hayhoe & de Jong, 1982
SWATRE	*Soil Water and Actual Transpiration Rate, Extended*	Belmans *et al.*, 1993
SWEAT	*Soil Water, Energy and Transpiration*	Daamen & Simmonds, 1994
SWIM	*Soil Water Infiltration & Movement*	Ross, 1990
WATBAL	*Water Balance Model*	Berghuijs van Dijk, 1990
WATDYN	*Simulation of Daily Water Dynamics*	Walker & Langridge, 1996

Figures

Fig. 1

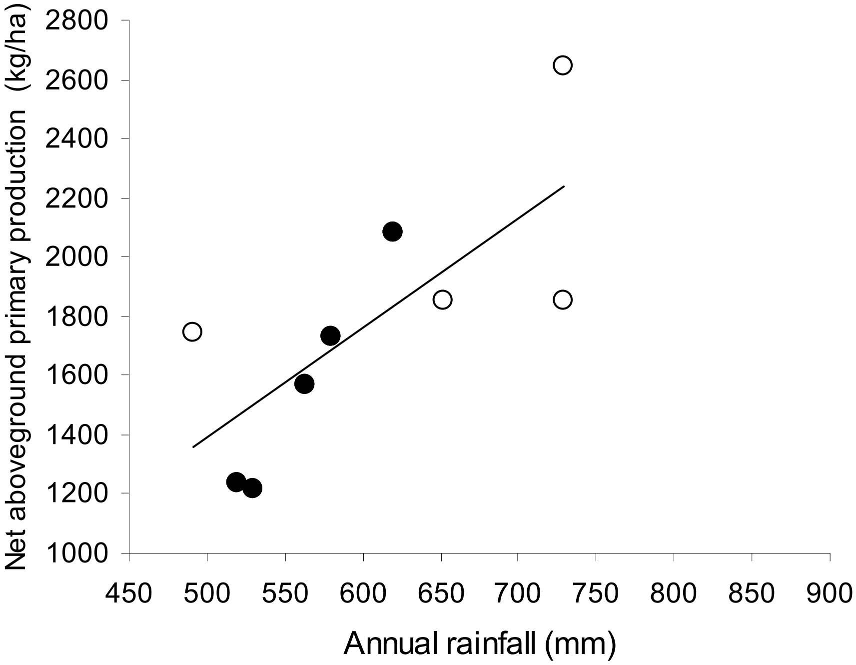


Fig. 2

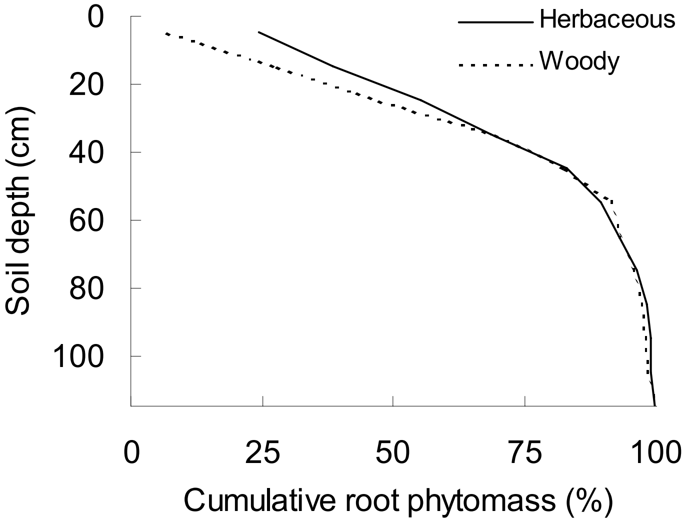
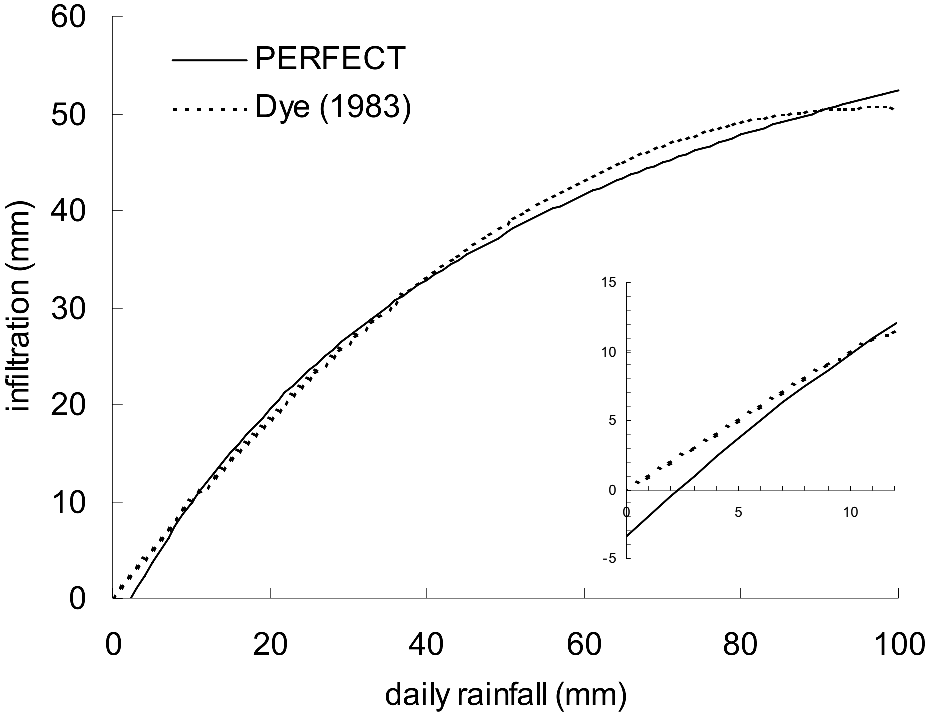
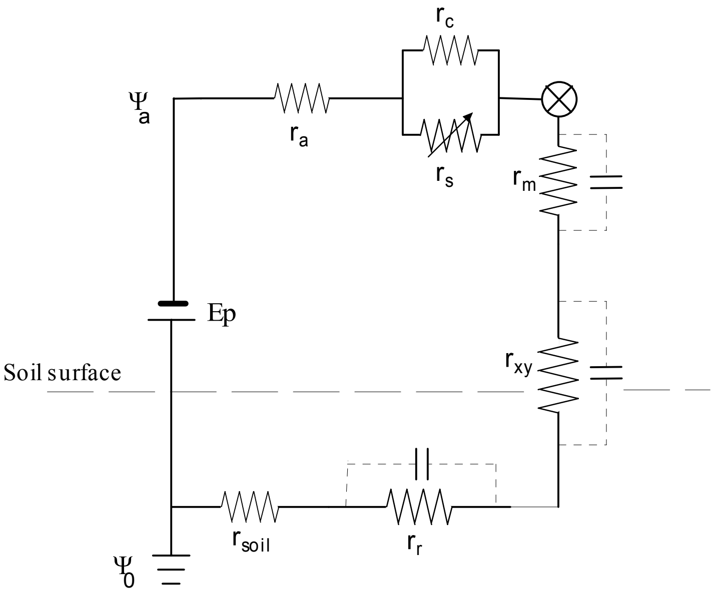


Fig. 3



PERFECT
Dye (1983)
infiltration (mm)
daily rainfall (mm)
0
10
20
30
40
50
60
0
20
40
60
80
100
15
10
5
0
-5
0
5
10

Fig. 4



Ψ_a
r_a
r_c
r_s
r_m
Ep
Soil surface
r_{xy}
r_{soil}
r_r
Ψ_0

Fig. 5a

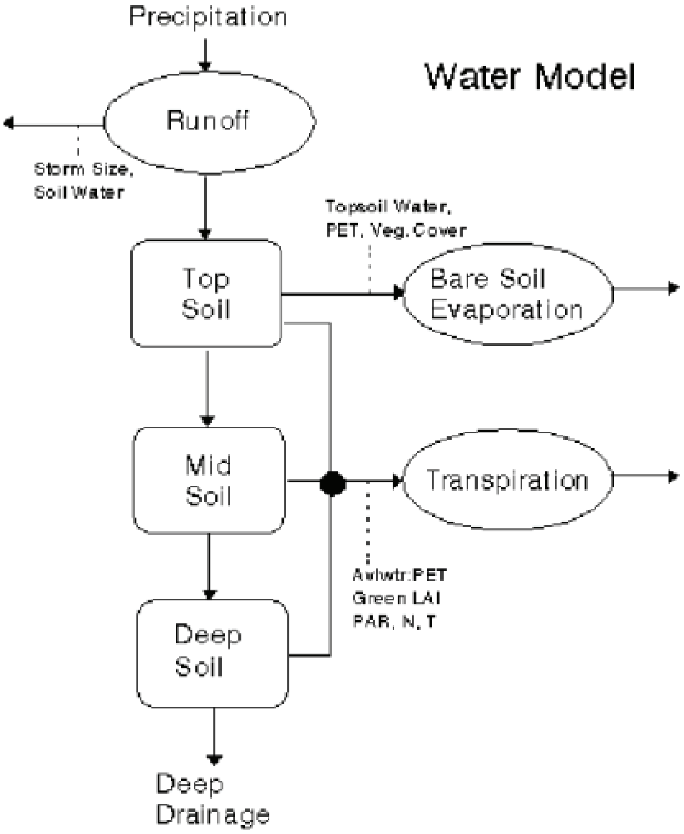

Precipitation
Water Model
Runoff
Storm Size,
Soil Water
Topsoil Water,
PET, Veg. Cover
Top
Soil
Bare Soil
Evaporation
Mid
Soil
Transpiration
Avlwtr:PET
Green LAI
PAR, N, T
Deep
Soil
Deep
Drainage

Fig. 5b

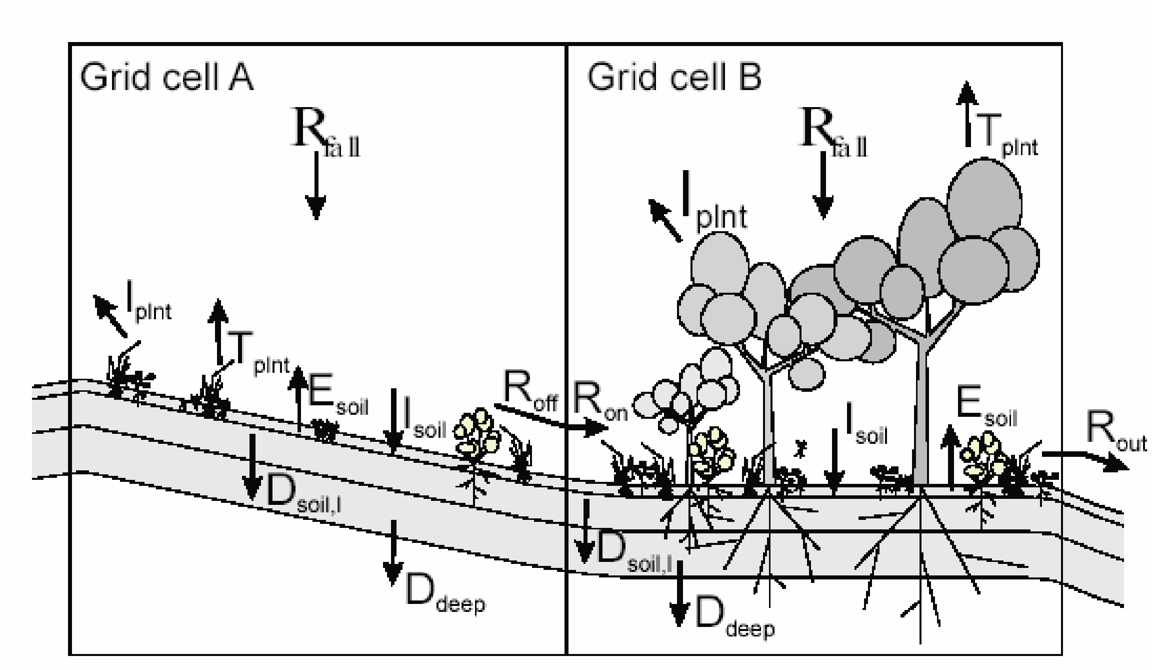

Grid cell A
R_{fall}
I_{plnt}
T_{plnt}
E_{soil}
I_{soil}
R_{off}
$D_{soil,l}$
D_{deep}
Grid cell B
R_{fall}
T_{plnt}
I_{plnt}
R_{on}
I_{soil}
E_{soil}
R_{out}
$D_{soil,l}$
D_{deep}

Fig. 5c

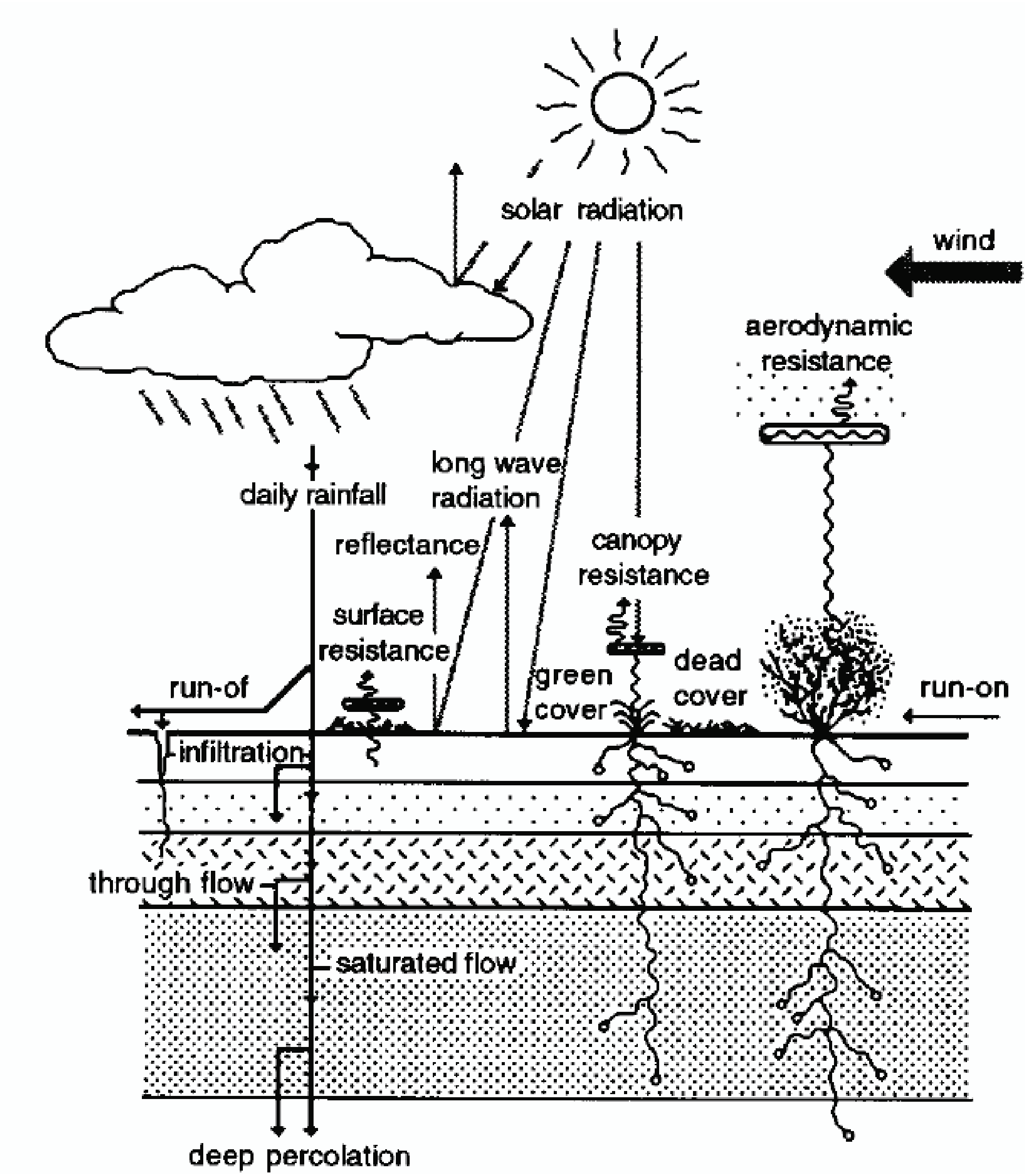

solar radiation
wind
aerodynamic resistance
long wave radiation
daily rainfall
reflectance
canopy resistance
surface resistance
dead cover
green cover
run-of
run-on
infiltration
through flow
saturated flow
deep percolation

Fig. 6

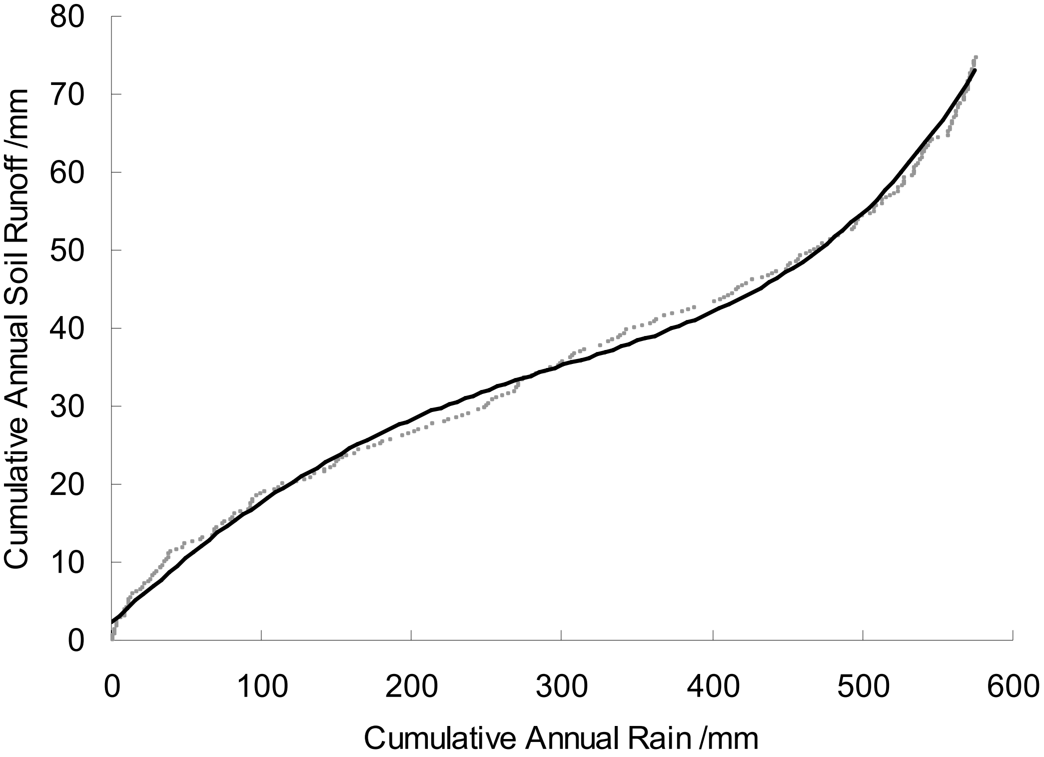

80
70
60
50
40
30
20
10
0
Cumulative Annual Soil Runoff /mm
0
100
200
300
400
500
600
Cumulative Annual Rain /mm

Figure legends

Fig. 1

There is a linear relationship between net aboveground primary production (NAPP) and annual rainfall (R), NAPP = 3.69 R - 452.42 (R^2=0.75, F=8.72, p=0.02). Data from [●] Kelly & Walker (1976) and [○] Dye & Spear (1982).

Fig. 2

Cumulative root proportions in a Burkea community on shallow Nelsvley soils. Under such spatial conditions, root distribution may be similar within each vegetation type. Data from Knoop & Walker (1985).

Fig. 3

Relationship between infiltration (I), daily rainfall (R) and soil water content (W = 69.5 mm) in the PERFECT model, $I = (R - 0.2W)^2 / (R + 0.8W)$ and the model of Dye, $I = -0.4 + 1.05R - 0.0054R^2$ for R > 12 mm. PERFECT predicts runoff using a second order curve with a local minimum at low rainfall values. The insert shows how estimates of infiltration have the potential to go negative for small rainfall events unless the relationship is modified as in Dye's treatment.

Fig. 4

Electrical circuit representation of water flow from soil to point of transpiration. Ep is potential evaporation; Ψ_0 water potential of the liquid phase; Ψ_a water potential of the atmosphere; r_{soil} hydraulic resistance in the soil; r_r transport resistance in the secondary roots and root cortex; r_{xy} conduction resistance in the xylem of roots, shoots, leaf petioles and veins; r_m transport resistance in the mesophyll; r_c cuticular resistance; r_s stomatal resistance (variable); r_a boundary layer resistance at the surface of the shoot; *capacitor symbol* storage capacity in the apoplast and symplast of the root, in the wood and cortex and in the leaves; $\otimes$ transistion from liquid to vapour phase. Adapted from Larcher (1995, Fig. 4.10).

Fig. 5

Comparative approaches to modelling savanna ecohydrology in three ecosystems models: a) *SAVANNA* water model uses three soil layers, where evaporative losses occur from the top soil according to potential evapotranspiration (PET) and vegetation (veg.) cover, and transpiration is calculated from all layers according to plant available water (Avlwtr), PET, leaf area index (LAI), plant available radiation (PAR), nitrogen (N) and temperature (T). After Coughenour (1993). b) *SAVANNA.AU* has variable soil layers which receive water from rainfall (R_{fall}), which may be intercepted by canopies (I_{plnt}), and evaporated back to the atmosphere or flows down stems to the base of the plant. Water uptake is transpired back to the atmosphere (T_{plnt}), or falls through to reach the landscape surface where, for saturated soil, it either ponds on flat areas and evaporates (E_{soil}), or runs off if the landscape is sloping (R_{off}) or, infiltrates into the soil (I_{soil}), adding to water in soil layers ($D_{soil,j}$). Runoff may impeded by, *e.g.*, vegetation patches, as runon (R_{on}), and infiltrates beneath the patch (I_{soil}), or runs off the grid cell as runout (R_{out}). Water may also be lost from the system as deep drainage (D_{deep}). After Liedloff *et al.* (2004). c) *SimSAGS* has variable layers and sub-layers and does not explicitly model canopy interception of rainfall as it is considered to be offset against the reduction in soil surface evaporation and the reduced transpiration from wet plant surfaces. Soil water can move via saturated flow, macropore (through-flow) channels if site-specific parameters are available, and infiltration via cracks. Evaporation and transpiration are calculated separately from modified Penman-Monteith formulae to account for evaporative losses for savanna with typically low vegetation cover. After Walker & Langridge (1996).

Fig. 6
In the SimSAGS ecosystem model, rainfall is lost to neighbouring cells as run-off. Here, model output shows **WHAT? WHY THIS RESPONSE?**