

Published in Aus J Botany (2005) 53, 1-19.

Ecosystem services: an ecophysiological examination

Derek Eamus¹, Catriona M.O. Macinnis-Ng, Grant C. Hose, Melanie J.B. Zeppel, Daniel T. Taylor and Brad R. Murray

Institute for Water and Environmental Resource Management
Department of Environmental Sciences
University of Technology Sydney
PO Box 123
Broadway
NSW 2007
Australia

¹ Corresponding author: Derek.Eamus@uts.edu.au

Key words: Ecosystem services; carbon accounting; biodiversity, NPP, wetlands

1.0 Summary

This review aims to discuss ecosystem services, provide case studies at catchment and local scales and provide ideas for future research. Thus this review discusses the following:

1. Ecosystem services (ES) are those goods and services that are provided by or are attributes of ecosystems that benefit humans. Examples of ES include the timber derived from a forest, the prevention of soil and coastal erosion by vegetation and the amelioration of dryland salinity through prevention of rises in the water table by trees. The provision of ES globally is in decline because of a lack of awareness of the total economic value of ES in the public, policy and political fora.
2. Providing a scientific understanding of the relationships among ecosystem structure, function and provision of ES, plus determining actual economic value of ES, is the central challenge to environmental scientists (including triple bottom-line economists).
3. Some ES are widely dispersed throughout many different ecosystems. Carbon accumulation in trees and the contribution of biodiversity to ES provision, are two examples of highly dispersed attributes common to many ecosystems. In contrast, other ES are best considered within the context of a single defined ecosystem (although they may occur in other ecosystems too). Mangroves as “nursery” sites for juvenile fish is one example.
4. Examples of catchment-scale and local-scale provision of ES are discussed, along with future research issues for the nexus between ES and environmental sciences.

2.0 Introduction

Student numbers in Business and IT degrees are increasing as students pursue degrees with obvious economic links. In contrast, student numbers in science, including biology and ecology, are falling, partly because of the lack of perceived economic value of these topics. Ironic it is, then, to see that ecosystem services have been valued at between US\$16 – 54 trillion per year (with an average of \$33 trillion per year), more than the global gross national product (Costanza *et al.* 1997). It is doubly unfortunate that the study of ecology and ecophysiology are not perceived as contributing directly to national economies and policy development. Doubly unfortunate because not only is the study and funding of botanical research suffering, but also because the lack of understanding of the economic value of ecosystem services to economic health is causing long-term impoverishment of both the economy and ecology of developed and developing countries alike.

We present this review in 4 stages (sections 3 to 6). We begin by a) defining ecosystem services and b) considering issues pertinent to valuing ecosystem services in the marketplace. In doing so we aim to establish the importance of ecosystem services as a valuable way of thinking and to establishing a common currency among policymakers, managers, researchers and the public as to the value of natural systems. To highlight the broad applicability of this way of thinking, we provide case studies that cover a range of different ecosystem types and consider ecosystem services at both c) catchment (across several ecosystems) and d) individual ecosystem scales. These will provide examples of ecosystem services and illustrate how basic science in ecology and ecophysiology has illuminated our understanding of ecosystem services.

Our catchment scale (terrestrial) case studies have a distinctly Australian focus while our studies of particular ecosystems, which are mostly aquatic, have a more international flavour. We have taken this approach because there have been far fewer studies of aquatic ecosystem services in Australia compared to terrestrial ecosystem services and we argue that aquatic ecosystems are more universal across continents than terrestrial ecosystems. In the Australian context, terrestrial ecosystems are strongly influenced by the combination of low rainfall and low soil nutrients on a continental scale, making them highly unique (Eamus 2003). Freshwater ecosystems are influenced by these conditions to some degree (particularly if the water-body is ephemeral) but the elements of ecosystem structure and function are more similar between continents than those for terrestrial ecosystems, due to convergent evolution. Marine ecosystems are the most similar of ecosystems on a global scale because the lack of barriers allows dispersal of plants and animals over long distances (May 1992).

3.0 Defining ecosystem services

Ecologists use the phrases “ecosystem structure” and “ecosystem function”. Ecosystem structure refers variously to the aggregate of species composition, population and community structure and inter-relationships, climate, soils and plant form (or habit). Ecosystem function refers to system properties or processes occurring within and between ecosystems, such as nutrient recycling (Costanza *et al.* 1997). However, the concept of ecosystem services (or ecosystem goods and services) is a more recent development. Ecosystem goods and services (hereafter the two are deemed to be contained within the phrase ecosystem services (ES)) are those processes and attributes of an ecosystem (or part of an ecosystem) that benefit humans (Costanza *et al.* 1997). Alternatively, ES are transformations of natural assets (including molecules such as CO₂, timber, or

biodiversity) into products that have human-centred value (Cork *et al.* 2001). We shall not debate whether such an anthropocentric definition is sufficient or whether non-anthropocentric values (inherent values; Turner *et al.* 2003) should be included. In the absence of humankind, this debate would not occur and therefore it is the presence and activities of humans that generates the need for such a valuation.

Ecosystems undoubtedly produce ES. The list of ES that can be recognised is longer than might be anticipated and includes:

- (1) soil formation;
- (2) erosion control;
- (3) regulation of water flow (surface, sub-surface and groundwater recharge);
- (4) water purification;
- (5) regional climate regulation (temperature and rainfall);
- (6) carbon sequestration and global climate effects;
- (7) recreation;
- (8) pollination;
- (9) waste disposal and treatment;
- (10) food, timber, textiles and other resource production;
- (11) genetic resources;
- (12) cultural;
- (13) nutrient recycling;
- (14) pollution interception.

An easy way to think about an ES is to ponder the question: what would happen if a process did not occur across vast areas of the landscape? For example, what would happen if soil erosion went unchecked across 90% of the landscape? What would happen if nutrient recycling stopped for 100 years, globally? What would happen if woodlands and forests ceased transpiring water and absorbing carbon dioxide? Any attempt to address ES issues holistically will require integration of many disparate disciplines, including ecology, sociology, economics and others (Fig. 1).

Furthermore, it is apparent that the services provided by one ecosystem can not be viewed in isolation from other ecosystems. Thus, the concept of metacommunities (Leibold *et al.* 2004) may be expanded upon to incorporate “metaecosystems”, considering the fundamental links among, and the non-independent functioning of, ecosystems (see section 6 for examples).

3.1 *Some issues pertaining to ES*

3.1.1 Should we attempt to put an economic value on ES?

Economies based on money dominate the means of exchange of goods and services between people and entities and consequently, to influence these economies requires monetary values to be assigned. The tragedy of the commons is the failure of common ownership of goods and services (often land and water) to manage these resources sustainably; oceanic fisheries are a classic example. Commonly owned resources are invariably degraded over time, and are a clear reason why we should put an economic value on ES. Furthermore, a lack of an economic value for ES partially explains why ES are in decline globally. But there are many other reasons why globally, the provision of ES are in decline and many reasons why we should put an economic value on ES. These are now discussed.

Why are ES in decline globally? Several reasons exist, including (Cork *et al.* 2001):

- 1) poor education levels of the public, managers and policy makers, about the link between ecology and economy, including:
 - (i) an assumption that ES are infinite (for example, dumping of waste in the sea or the atmosphere because of its perceived ability to store and treat waste materials indefinitely);
 - (ii) no understanding of the links between ecosystem structure, function and services;
- 2) the long-lead time between unacceptable behaviour by humans (for example, waste dumping or forest clearing) and ecosystem dysfunction (that is, loss of ES);
- 3) the belief that technology can remediate/compensate/overcome declines in the provision of ES;
- 4) few incentives in classic economic structures to invest in ES.

Why should we put an economic value on ES? There are four reasons: first, because results of classical ecological studies do not engage economic markets using a language that is able to cause change in that market. Whilst environmental sciences and ecology have convinced many of the “intrinsic value” of various attributes of ecosystems (usually the photogenic or cuddly ones), they have not caused sufficient responses from market economies for sufficient changes in practice to occur. Changes have been too slow, too localized and too poorly coordinated to effect the changes required for large-scale sustainable development of ecosystem resources. Second, by placing a

value on ES, we can engage in cost-benefit analyses of current and future activities and attempt to answer the question: if an ES is lost or seriously degraded, do the economic benefits justify the economic cost to the ES? Third, it can assist in deciding how to allocate finite resources (time, money) to competing demands within funding agencies, resource management agencies and others. Finally, Lawton (1999) has argued that ecology has yet to develop many laws that are universally applicable and that the laws, rules and mechanisms that underpin these patterns in ecology depend on the species complement and the specific environment in which those species occur. We tentatively suggest that applying an ES framework to studies of ecology may enhance our ability to formulate more widely applicable rules and may act as a catalyst to asking new questions and adopting new approaches to ecology. As an example of this we refer to the developing realisation that, from the perspective of vegetation water flux at catchment scales, a tree is a tree is a tree and consideration of species becomes superfluous (see below). We doubt that such a realisation would have developed from a purely ecological approach.

3.2 *Some questions for ES research*

If ES is accepted as an overarching philosophy within ecology, it raises new questions for research, including:

1. Which ecosystem(s)/component(s) is/are best at providing which ES?
2. What are the impacts of human activities on ES at local, regional and global scales?
3. What is the relationship between ES and ecosystem condition?
4. What is required to restore ES in degraded systems and how would we know when this has been achieved?
5. How interdependent are ES within an ecosystem and across ecosystems?
6. How much of ecosystem structure and function can be lost before ES are irretrievably lost?

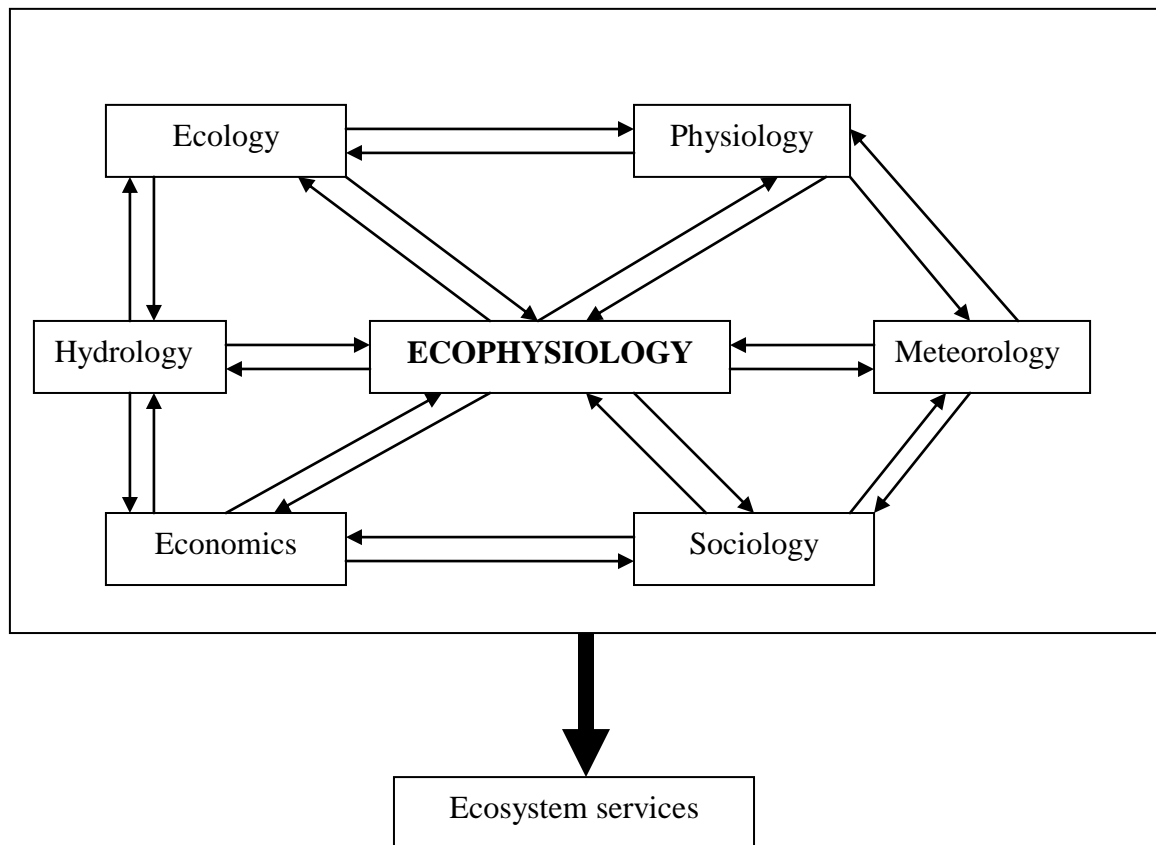


Figure 1. Projects that attempt to address ES issues should integrate information from many disciplines, as shown here.

3.3 Estimates of ES

It is clearly very difficult to value ES. However, many attempts have been undertaken in the past 10 years (e.g. Costanza *et al.* 1997; Jansson *et al.* 1999; Turner *et al.* 2003). Costanza *et al.* (1997) divide the world into 6 oceanic, coastal and estuarine ecosystems and 10 terrestrial ecosystems and identified 17 ES. For each ecosystem they assigned a dollar value for every relevant ES (no single ecosystem provides all 17 ES). The vexing question of how to assign the dollar value is not discussed further here, except to note that many methods for estimating values have been used in the past, including:

- 1) willingness-to-pay, whereby valuations are deduced from surveys of the public or through expert assessments of business or public's imputed willingness to pay;
- 2) valuations of known ES that already have a market value (timber, for example);

- 3) the cost of a human-made substitutable good (for example the cost of providing clean water through desalination stations or sewage treatment plants at locations where potable water supplies are depleted/degraded);
- 4) implicit value; This is similar to (3) above. For example, forested catchments dampen flash floods and retain water for a long time (months), releasing it slowly into streams and rivers and as recharge to groundwater. In the absence of these forests, concrete flood drains, water storage facilities and sediment traps are required to protect down-stream sites. It is the value of the structures not built if the ES is maintained, that is assigned as the value of the ES.
- 5) willingness-to-accept compensation for loss of an ES;
- 6) valuation of the loss of economic activity directly arising from the loss of an ES (for example, the lost value of agricultural productivity where saline landscapes prevent agriculture productivity).

Costanza *et al.* (1997) produced global estimates of 17 ES. For example, atmospheric gas regulation was estimated to be valued at US\$1.3 trillion per year, waste treatment was valued at US\$2.3 trillion per year and nutrient cycling at US\$17 trillion per year. It should be noted that the dollar value *per se* is not the most important feature, but it is the realization that the absence of such ES that will have a massive economic impact and that human welfare is inextricably linked to ecosystem health. Furthermore, the principle aim is not to provide a price tag on ES but to express the effect of a marginal change in the provision of the ES in terms of a rate of trade-off against other commodities (Turner *et al.* 2003). An interesting point to note is that as ES become more and more scarce, their value in classic economic theory will increase, leading to the erroneous but logical conclusion that maintaining ES at their best and most pervasive is less desirable than allowing them to decline, as this increases their economic value. Similarly, the willingness-to-pay concept also fails. For example, most people would be willing to forfeit all of their savings to maintain the supply of oxygen when asked: how much would you pay to maintain the oxygen producing capacity of all the chloroplasts in the world? Despite these logical and methodological frailties, we are in no doubt as to the importance and validity of the ES approach to guiding science, funding and decision making in the future.

Some ES are more dispersed across a range of ecosystems than others. We consider (section C) biodiversity to be a structural attribute underpinning many ES, while carbon sequestration, and regulation of groundwater levels are ES provided by many diverse ecosystems. Alternatively, we

may consider ES at the individual ecosystem scale and do so briefly in case studies (wetlands, riparian, seagrasses and mangroves) in section D.

4.0 Biodiversity, carbon flux and water flux as broad-scale ES across all terrestrial ecosystems

4.1 How ecosystem structure and function relate to ES

The goods and services (ES) we acquire from ecosystems are a product of natural functions and processes occurring within ecosystems (Daily *et al.* 1997). However, links between ecosystem function and ES are not necessarily straightforward. In some cases, several ecosystem functions are required for a particular ES; in other cases, a single ecosystem function contributes to more than one ES (Fig. 2). Ecosystem functions are carried out by the species inhabiting ecosystems. Thus, understanding how ecosystems are structured in terms of species richness and composition (i.e. species identity and abundance) is central to a comprehensive understanding of ES (Fig. 2). In particular, a question of increasing importance is: how does human-induced change in ecosystem structure impact on the ES upon which we depend? This research question is currently the focus of much speculation and interest among biologists, because there is considerable concern that changes to ecosystem structure due to habitat clearing, fragmentation and the introduction of alien species lead to the disruption of vital ES (Costanza *et al.* 1997).

Links between ecosystem structure and function have been well researched (see Tilman 1997; Chapin *et al.* 1998; Loreau *et al.* 2001; Engelhardt and Ritchie 2002; Naeem 2002; LeVeque and Mounolou 2003; Gaston and Spicer 2004; Stanzner and Moss 2004). For convenience, ecosystem structure is usually represented as species richness (Tilman 1997). Species richness is a common measure of biodiversity because it is easily quantified, there is a lot of existing information on richness, it is a good surrogate for many other kinds of variation in biodiversity (e.g. genetic, organismal and ecological diversity), and it is a unit of practical management for legislation (Gaston and Spicer 2004).

A surprising amount of controversy and heated debate has been generated by studies exploring links between biodiversity and ecosystem function. This only emphasizes the importance and contemporary relevance of understanding these links for scientific, economic and social purposes (see Naeem 2002 for discussion). Overwhelmingly, it has proven very difficult to find unequivocal

support for any one of the proposed theoretical models linking changes in ecosystem function to changes in biodiversity over the others (Chapin *et al.* 1998; Loreau *et al.* 2001). Such models include the “diversity-stability” hypothesis; the “rivet” hypothesis; the “drivers-passengers” hypothesis and the “idiosyncratic” hypothesis. See LeVeque and Mounolou (2003) for a discussion of these. In general, however, Schwartz *et al.* (2000) found that much experimental work supports the notion that high species richness is required to maintain a high degree of ecosystem functioning. For example, the work of Tilman *et al.* (1996) in the Cedar Creek grasslands (North America) showed convincingly that plant biomass (productivity) increases with species richness. Consistent with this, Hector *et al.* (1999) demonstrated that decreased species richness was associated with low productivity in European grasslands. The advantage of these experimental manipulations is that confounding factors can be controlled for. Thus, despite other outcomes having been reported, there is rigorous experimental evidence for the importance of increased levels of biodiversity for ecosystem functioning (Gaston and Spicer 2004).

Apparent contradictions in the findings of different studies are probably due to issues such as experimental design and differences in spatial scales. These can be addressed appropriately in future work. For example, the design of some synthetic communities used in experiments testing links between ecosystem function and biodiversity has not incorporated randomly chosen taxa from the available species pool, a feature that can bias the outcomes of such studies (Chapin *et al.* 1998). In relation to spatial scale, the findings of observational studies contradict those of experimental studies because observational studies look at patterns across multiple sites while experimental studies examine patterns within a site (Naeem 2002). Publication bias might also be influencing our understanding of biodiversity and ES, with studies showing the importance of high levels of biodiversity being preferentially published (Kaiser 2000).

Despite controversy, important generalizations are emerging, namely:

(1) There is consensus that at least some minimum number of species (i.e. minimum level of biodiversity) is essential for ecosystem functioning and the provision of ES under conditions where the environment is not changing (Loreau *et al.* 2001). In some cases, a few dominant species may be enough to provide for a substantial level of ecosystem functioning, e.g. NPP in grassland ecosystems (Sala *et al.* 1995; Chapin *et al.* 1998). For instance, a seagrass meadow dominated by one species may have equal ecosystem function to a mixed-species meadow (Duarte 2000).

(2) High species richness can minimize large reductions in ecosystem functioning by acting as a buffer against variation in environmental conditions. This is because species whose effects on ecosystem functions are similar may be differentially susceptible to extinction from the community under changing conditions in the environment. Hence, differential loss of species does not impact negatively on ecosystem services because loss of particular species is buffered by other species in the ecosystem (Chapin *et al.* 1998). However, recent theoretical work is showing that this “compensation effect” will vary depending on whether species go extinct randomly or in order of their sensitivity to a stress that intensifies over time (e.g. climate change) (Ives and Cardinale 2004). Mathematical simulations of food web structure indicate that when extinction is ordered, there tends to be greater resilience in the web (and hence compensation) because surviving species have greater average resistance to the stress (Ives and Cardinale 2004).

(3) The various functions performed and services provided by ecosystems exhibit a ceiling level set by abiotic conditions and the maximum amount of biodiversity (Naeem 2002).

(4) There are two contrasting views on how the identity of species in an ecosystem contributes to ecosystem functioning and ES. Species may be functionally equivalent to one another (redundant) or their function might be unique (Walker 1992; Naeem 1998). The maintenance of natural ecosystem functioning is probably reliant on a mix of a certain amount of redundancy (see point 2 above), and uniqueness among species.

(5) The effects of species on ecosystem function and ES may be multiplicative through their interactions with other species, or the effects of species may be additive (Power *et al.* 1996; Sala *et al.* 2000).

(6) Experimental studies have shown that high levels of biodiversity are important for ecosystem functioning. While there is much work yet to be done in translating these results to larger (landscape) scales, an appropriate management strategy would be to adopt the Precautionary Principle to conserve as much biodiversity as possible (Loreau *et al.* 2001). In this way, we will not inadvertently lose ES through loss of biodiversity.

4.1.1 Future research questions

While it is clear that a minimum number of species and hence ecosystem structure is important for ES, we are still far from a comprehensive understanding of the influence of ecosystem structure and loss of species on ecosystem function and hence ES. Because ecosystem functions can be involved in more than one ES, and because one ES may rely on several separate functions of an ecosystem (Fig. 2), there needs to be a concerted effort among biologists to understand better the links between ecosystem structure, ecosystem function and ES. Considering that the economic and social values of ES are increasingly being assessed (e.g. IACSEA 1998), it is likely that biologists will be required more and more to relate their ecosystem research to market-driven forces and social expectations. In addition, there needs to be recognition that:

(a) Ecosystem function (and hence ES) is not just a function of species richness. There is considerable diversity among the populations of individual species, which can be important for ES. Luck *et al.* (2003) have suggested that a focus of future work should be on “service-providing units” (SPUs). These SPUs provide a recognized ES at some temporal or spatial scale. For example, the entire population of a tree species sequesters carbon globally; regional populations of the species in agricultural areas utilise groundwater recharge thus ameliorating dryland salinity; and local populations provide food for livestock. However, the current suggestion from biologists tackling the issue of the link between biodiversity and ecosystem services is not to abandon traditional species-based approaches when assessing biodiversity decline, but rather, to give more attention to the role of population diversity and genetic differentiation among populations, and to consider the usefulness of the SPU concept (Luck *et al.* 2003).

(b) Organisms provide different ecosystem functions and services at different life history stages. For example, see discussion of forest regrowth and transpiration below.

(c) Contrary to expectation, human activities can result in both decreases and increases in species richness (Sax and Gaines 2003). Biodiversity is decreasing globally due to habitat destruction and the introduction of exotic species. For example, invasion by the exotic shrub Tamarisk (*Tamarix* sp.) reduced biodiversity of riparian habitats and the services those habitats provide (Zavaleta 2000).

At local and regional scales, losses of native species can be offset by the establishment of exotics, which can result in an increase in biodiversity at these scales. Thus, the complex nature of the link between biodiversity and ES becomes more complex, given that we now have to consider how

increases in biodiversity at local and regional spatial scales due to invading species will impact on the ES upon which we depend.

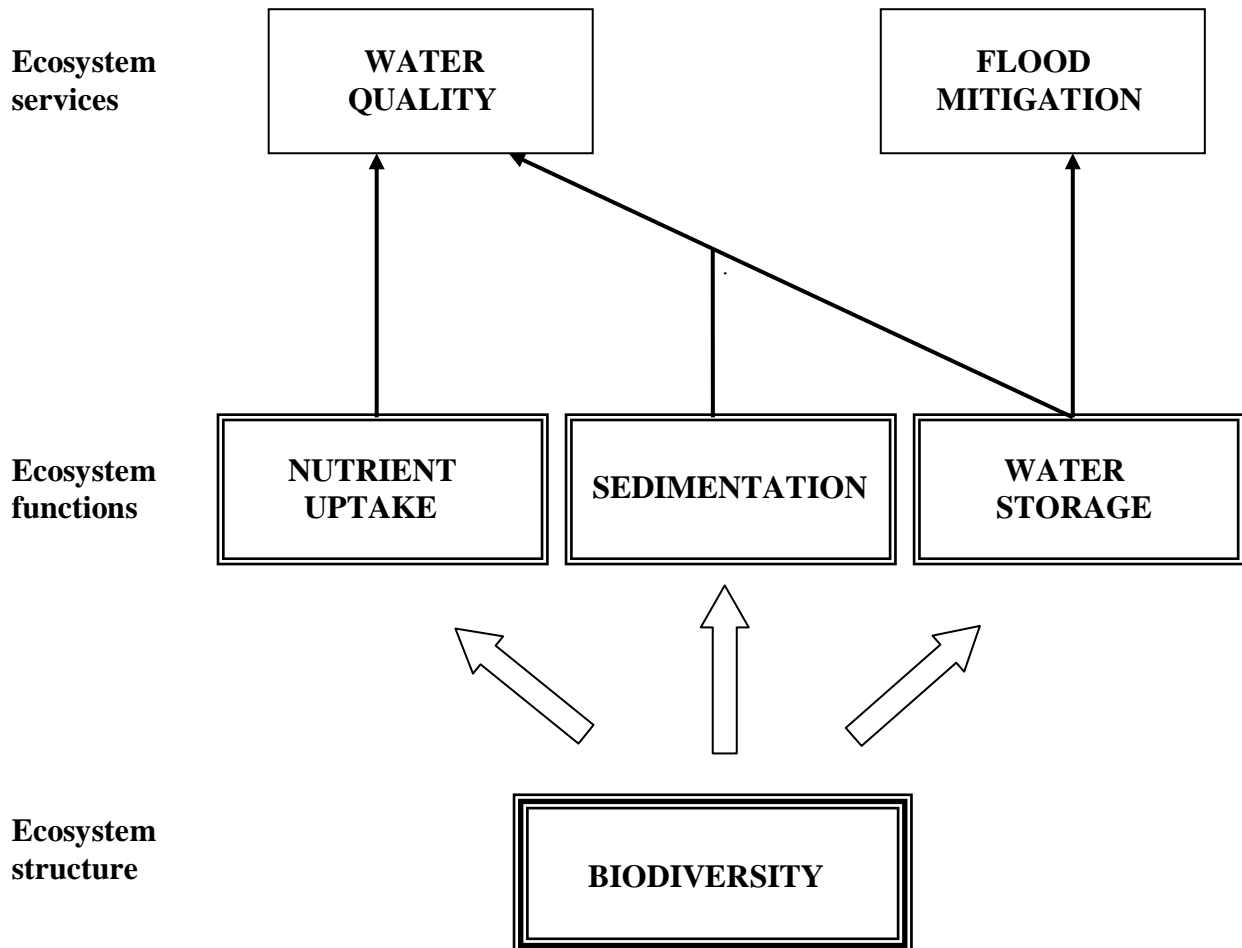


Figure 2. A simple illustration of how more than one ecosystem function is required to produce a particular ES, while a single ecosystem function can contribute to more than one ES. In this example of a wetland ecosystem, the ES of water quality is provided by three functions of the ecosystem operating in tandem (nutrient uptake, sedimentation, and water storage). The function of water storage is also required for the ES of flood mitigation. The link between ecosystem structure/biodiversity and ecosystem functioning is currently under much scrutiny from biologists.

4.2 Carbon sequestration by woodlands and forests

4.2.1 Introduction

Carbon fixation by vegetation fulfils three distinct ES. These are (a) it is the basis for crop and forest yield; (b) it is involved in climate regulation; and (c) it is the foundation of all other ES. The

first requires no further explanation. For the second, we accept, *a priori*, that large increases in atmospheric carbon dioxide concentration result in changes in global and regional climate and that maintaining a stable climate is a significant ES. Extremes in weather generate losses to agricultural production and increase insurance and other costs to human welfare; long-term changes in climate require adjustments in infrastructure and industry. For the third ES, we argue that understanding Net Primary Productivity (NPP) or Net Ecosystem Exchange (see Kirschbaum *et al.* 2001 for a discussion of productivity terms) is the foundation for all other terrestrial ES. In the absence of carbon fixation, all ES (and all terrestrial, freshwater and coastal ecology) grinds to a halt. Therefore, a discussion of carbon budgets and NPP is central to any basic understanding of all ES.

In order to contribute to research on ES, it is necessary to quantify net carbon gain (NPP). To-date, NPP has been modeled at global, continental and regional scales, while measurements are made at local scales. This section principally addresses the question: how big is the NPP of Australia, at continental, regional and local scales? It is important to note that because of the long residence time for carbon in terrestrial systems, small increases in NPP result in large increases in the sequestration of C in biomass and soils. Consequently, precise estimates of NPP are needed for carbon accounting purposes. Global estimates of C turnover are generally 20 – 60 y (Schimel *et al.* 1994) but a recent analysis by Barrett (2002) concludes Australian terrestrial C has a turnover time of 78 y. Low soil water content, frequent fires (and so the formation of non-labile charcoal) and high C absorption capacity of Australia soils probably explain this (Barrett 2002).

Biology determines the global carbon cycle through production and turnover of organic matter (Field 1998). Production is via photosynthesis, turnover is through respiration and decay. NPP is the principle regulator of all ecological processes, both within and between trophic levels and ecosystems. NPP for terrestrial systems is theoretically simple to determine, but in practice is difficult, time consuming and expensive, especially for woody ecosystems, because of problems dealing with below-ground processes, long time-scales and considerable spatial and temporal variability in NPP. Consequently, modeling is often used to estimate regional or continental NPP (Cao and Woodward 1998).

4.2.2 Global, continental and regional estimates of NPP

Mean global estimates of NPP range from 44 to 66 Gt C yr⁻¹ (Cramer *et al.* 1999; Field *et al.* 1995). Using a simple modeling approach, and including discounts for water and temperature stress, Field *et al.* (1998) calculate an average NPP of land without permanent ice cover as 426 g of C m⁻² y⁻¹.

Multiplying this value by the area of Australia, yields a continental estimate of 3.24 Gt C y⁻¹. This is an overestimate since much of Australia is desert with extremely low NPP. Cao and Woodward (1998) estimate an average NPP to be 422 g m⁻² y⁻¹, which yields an average Australian NPP of 3.21 Gt C y⁻¹ which is a similarly overestimated value. De Fries (1999) estimates the NPP of Australian native vegetation to be 2 Gt C y⁻¹.

Global models of terrestrial NPP show maxima at two latitudinal peaks: approximately 40 – 70 ° N and 10 ° N to 15 ° S, with peak values of about 0.3 Pg C per degree of latitude (Field *et al.* 1998; Cao and Woodward 1998). These spatial patterns reflect the combined distributional effects of rainfall, forest cover and deserts. Seasonal patterns of NPP are consistent with seasonal changes in temperature, rainfall and net radiation (Cao and Woodward 1998) and can be found in estimates of NPP for different regions of Australia.

Within these global models, values of NPP within Australia range from about 50 g C m⁻² y⁻¹ for central Australia, to about 850 – 900 g C m⁻² y⁻¹ for east coast regions and far north tropical Australia (Field *et al.* 1998) or up to 1000 – 1100 g C m⁻² y⁻¹ (Cao and Woodward 1998).

How do the global estimates (Cao and Woodward 1998; Field *et al.* 1998; DeFries 1999) compare with Australian models? Roderick *et al.* (2001) estimate Australian NPP to be about 3.2 Gt C y⁻¹ (1 Gt = 1 Pg = 10¹⁵ g), and cite 3 other estimates ranging from 1.6 to 2.8 Gt C y⁻¹. As argued above, estimates around 3 Gt C y⁻¹ are likely to be overestimates. Wang and Barrett (2003) cite estimates of Australian NPP ranging between 1 and 3 Gt C y⁻¹ whilst themselves estimating NPP at between 0.79 and 1.1 Gt C y⁻¹ with a bimodal distribution in time. Thus, in northern Australia, NPP increases during the summer wet season and decreased in the winter dry season but in temperate Australia the peak is in October. A key finding from Roderick *et al.* (2001) is that productivity of vegetation increases substantially when the diffuse fraction of solar radiation increase due to cloud or pollution and the volume of shade within a canopy declines. Interestingly, in a comparative review of four approaches to modeling C gain by canopies, a sun-shade model performed the best at all spatial scales (Medlyn *et al.* 2003).

Can any of these model estimates be compared to field-based estimates for Australian ecosystems? This is difficult to achieve because (a) continental-scale estimates of NPP have relatively poor spatial resolution and assign average vegetation attributes across large areas; (b) field estimates provide only point (local) estimates of NPP and the resources required to provide far more field estimates are not readily available; and (c) there are only two comprehensive and detailed point estimates of NPP in Australia. Esser (1998) summarises about 12 estimates for Australian pastures,

eucalypt forest, mangrove, saltbush and desert shrubland. Values range from 30 - 40 g C m⁻² y⁻¹ (desert shrub and Banksia and Xanthorhea woodland) to 1100 – 1200 g C m⁻² y⁻¹ for pasture and eucalypt forest to 2915 g C m⁻² y⁻¹ for wetland and heathland. However, almost all studies cited (from the 1960s – 1970s) did not include below-ground processes and the assumption was made that below-ground NPP equaled above-ground NPP. Therefore these values should be viewed with caution.

The estimate of NPP (2.08 t C ha⁻¹ y⁻¹) for region H (monsoonal Australia excluding Queensland) of Wang and Barrett (2003) could be taken as an estimate for the NPP for north Australian savannas (Chen *et al.* 2003). Similarly, Wang and Barrett's estimate of NPP for region D (south-eastern Australia) was 2.05 t C ha⁻¹ y⁻¹ may approximate to a broadleaved forest around Canberra (Keith *et al.* 1997). Alternatively, Cao and Woodward (1998) calculate NPP for tropical savannas to be 6.6 tC ha⁻¹ y⁻¹ and NPP for temperate evergreen forest was calculated to be 6.98 tC ha⁻¹ y⁻¹. Do these values approximate field studies of NPP in Australia?

Surprisingly, there are only two comprehensive published studies of NPP in Australia, in tropical savannas (Chen *et al.* 2003) and temperate snowgum forest (Keith *et al.* 1997). NPP of the savanna was about 11 t C ha⁻¹ of which 8 ton C ha⁻¹ was below-ground productivity. Most of the fluxes occurred in the wet season, except for fluxes associated with fires, which occurred in the dry season. All measures of productivity (GPP, NPP and NEP) showed that C fluxes of north Australian savannas are tightly coupled to seasonal patterns of rainfall and soil moisture, a result in agreement with leaf (Prior *et al.* 1997; Eamus *et al.* 1999), tree (O'Grady *et al.* 1999; Eamus *et al.* 2000) and canopy (Eamus *et al.* 2001; Hutley *et al.* 2000) scale measurements. NEP in Chen *et al.* (2003) was estimated as 3.8 ton C ha⁻¹ y⁻¹. Using eddy covariance data at a single savanna site, Eamus *et al.* (2001) estimated NEP at 2.8 ton C ha⁻¹ y⁻¹. NEP is the difference between NPP and soil respiration (Wang and Barrett 2003). There are exceedingly few estimates of NEP in Australia (Wang and Barrett 2003).

Keith *et al.* (1997) showed that for a mature snowgum (*Eucalyptus pauciflora*) forest 50 km west of Canberra, Australia, NPP was 7.65 t C ha⁻¹ y⁻¹. Peak basal area increment occurred between November to January and again in March and April. In contrast to the savanna site, 25% of the standing biomass was located below-ground (compared with 40% in savannas), a result not expected from consideration of the much larger annual rainfall at the savanna site. If we exclude heathland and mangroves, the root to shoot biomass ratio for Australian ecosystems is 0.2 to 0.4

(Snowdon *et al.* 2000), and rainfall is a poor predictor of root biomass (Snowdon *et al.* 2000), although root depth may be inversely correlated to site aridity (Eamus and Prior 2001).

Several conclusions are apparent from comparing modeled regional estimates of NPP with field measurements. These are:

1. There are surprisingly few (two) estimates of NPP for Australian ecosystems.
2. Seasonality of changes in NPP observed in field data is adequately captured in the models. Similarly, the change from summer peaks in NPP in tropical Australia to spring and autumn for temperate forest, is also captured in the models.
3. Allocation between above- and below-ground processes varies between sites but this difference is not immediately explained by differences in annual rainfall.
4. For both the savanna and snowgum forest, field measurements of NPP greatly exceed NPP calculated by the models. Two reasons may be proposed for this. First, the field studies may not have been carried out in the same type (structure) of ecosystems that were assumed to be representative of the entire region by the modelers. Second, the climate for the large-scale regions used by modelers may not accurately represent the actual climate of the field sites and if conditions at the field site were better (less restricted by water and temperature) than average large-scale climate assumed by the modelers, then actual NPP will exceed modeled NPP. Both probably apply.

Carbon uptake by terrestrial ecosystems is an ES because it contributes to stabilization of atmospheric composition and hence climate regulation and through production of timber and crop yield. Confusingly, Costanza *et al.* (1997) list stabilization of atmospheric composition and climate regulation as separate ES and provide a dollar value for each. Thus, forests (tropical and temperate) are estimated to provide climate regulation services valued at more than US\$300 per hectare per yr and grasslands, rangelands and wetlands provide gas regulation services valued at more than US\$400 per hectare per year (Costanza *et al.* 1997). It is clear, however, that ecology and related disciplines need to provide far more information about ecosystem structure, function, allocation patterns and light conversion efficiencies before the real supply of ES through C uptake can be accurately estimated at local, regional or continental scales.

Carbon trading on the stock market will soon start, with an estimated price of \$10 – 30 per tonne of carbon. If the NPP of a site is $500 \text{ g C m}^{-2} \text{ y}^{-1}$ ($= 5 \text{ t C ha}^{-1}$) then this puts a C trading value of \$50

to \$150 per hectare. From knowledge of NPP for disparate ecosystems and the trading price on the market for C, we can start to answer such questions as: which ecosystem is best at providing climate regulation and gas regulation? What is the cost : benefit ratio of degrading different ecosystems? How much degradation (loss of NPP) should be allowed before the lost value in C trading is too much? To-date, however, estimates of regional or continental-scale NPP differ by factors of 3, and plot-scale estimates differ significantly from model estimates, suggesting that our understanding of factors that regulate NPP at regional scales is still incomplete.

4.2.3 Future research

In relation to NPP and ES, the following research topics are suggested:

1. Can we define allocation rules for C within plants in different ecosystems? Friedlingstein *et al.* (1999) show how changes in the percentage allocation of NPP to below ground processes influences biomass accumulation and stress responses, but we do not have a convincing mechanistic understanding of allocation rules for trees in the field (Eamus 1996)
2. Using field data, what are the seasonal and annual NPPs for all the major biomes in Australia?
3. What mechanisms link variation in climate and soils to variation in NPP?
4. How can we reliably quantify the C storage of natural ecosystems of Australia?

The next section deals with the role of trees in catchment water balance and the ES associated with water fluxes through trees.

4.3 *Trees and forests as regulators of water tables*

Woodlands and forests, native and plantation, provide a major discharge path for water and therefore, have a major role in determining the hydrological balance of catchments. By acting as wicks and transporting water from soil/groundwater back into the atmosphere, they minimise groundwater recharge, thereby preventing or ameliorating the development of dryland salinity. Furthermore, forested catchments provide a more stable and cleaner water supply than water collected from urban or industrial catchments, therefore, the water requires far less treatment to make it suitable for human use. Forests also dampen the flow of water into rivers and streams and

thereby reduce the impact of floods, reduce soil erosion and sediment accumulation in streams and rivers and reduce nutrient input to these water bodies (see Riparian ES case study below). Therefore, trees provide at least three ecosystem services; the prevention or amelioration of dryland salinity; the stable provision of clean water; and mitigation of floods and soil and nutrient loss through surface flows.

4.3.1 Supply of potable water

2.2 million deaths, or 4% of all fatalities worldwide, are attributed to insufficient supplies of clean water and sanitation (Dudley and Stolton, 2003). Well-managed, forested catchments provide ES by supplying potable water. These catchments supply water that contains fewer pollutants, sediments and nutrients, and that requires significantly less treatment than water derived from catchments that are urbanised/industrialised, cleared or contain poorly managed forests (Dudley and Stolton, 2003).

Changes in forest cover affect the water yield of a catchment (Jones and Post, 2004; Lu *et al.* 2004). For example, increases in forest cover due to regrowth after clearing decreases the water yield of a catchment, as younger trees transpire more than mature forests. As the trees mature, water yield increases (Fig. 3) (Vertessy *et al.* 1995; 2001). Cleared forests allow more water to run off but water quality is significantly reduced because of suspended sediment, nutrients and debris.

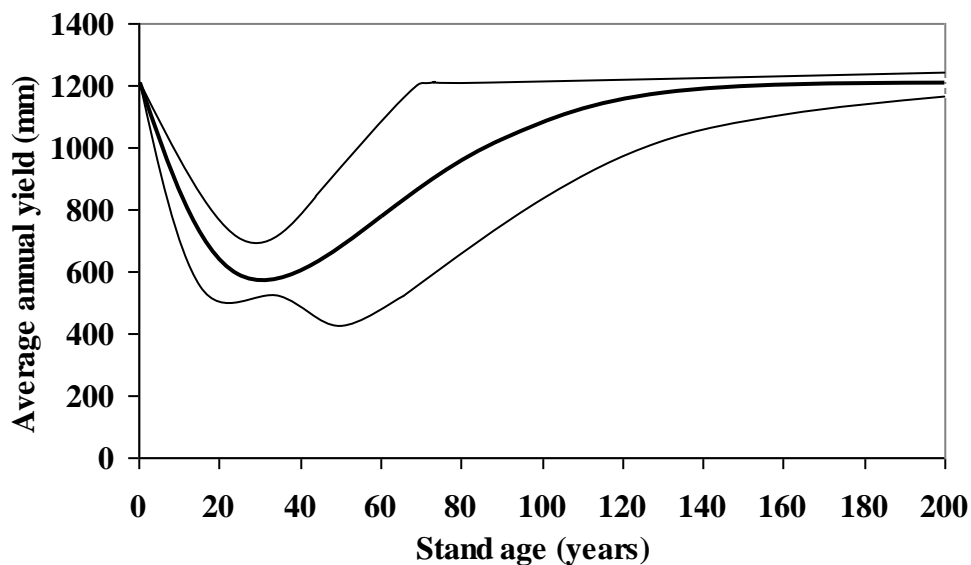


Figure 3. Relationship between mean annual runoff and stand age from mountain ash forest catchments (after Kuczera 1985).

4.3.2. What do we need to know to manage and maintain supplies of clean drinking water from forested catchments?

To manage forests to provide potable water, it is necessary to understand interactions between climate, soils, disturbance and vegetation as these determine the quantity of water transpired and hence catchment water yield (Vertessy *et al.* 1995; Cornish and Vertessy 2001). Indeed, understanding the control of forest water use is central to determining the water balance of a site (Wullschleger *et al.* 1998) and the development of a mechanistic understanding of the regulation of tree water use has allowed calculations of tree water use to be scaled temporally and spatially, to estimate the water use of stands of trees, forests and catchments (Wullschleger *et al.* 1998). Scalars that have been successfully used to scale from individual tree to whole stands and forests include basal area, (O'Grady, 2000), stem diameter at breast height (Vertessy *et al.* 1995, 1997), and leaf area (Hatton *et al.* 1995).

The relationship between forest age and water yield is complex and determined by several interacting factors including leaf area index (LAI; Fig. 4a), transpiration rates of tree and understorey vegetation, sapwood area (Fig. 4b), soil and litter evaporation and tree interception. From knowledge of these factors an estimate of the water yield from a forest can be determined. Topography and climate also influence water use and must be examined when comparing different catchments (Barrett *et al.* 1996).

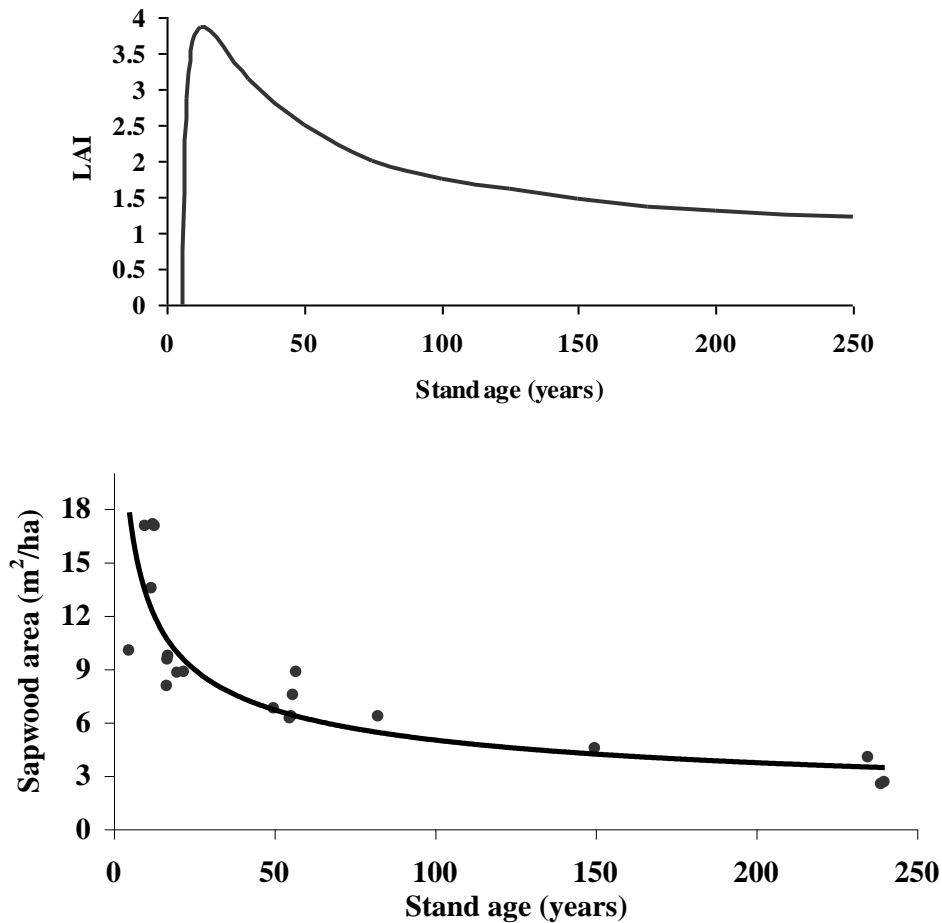


Figure 4. (a) Relationship between mountain ash stand age and leaf area index (LAI) and (b) stand age and sapwood area) (after Watson and Vertessy 1996).

The Maroondah catchment (Victoria, Australia) supplies drinking water for Melbourne. The catchment is forested with Mountain Ash (Vertessy *et al.* 1995) and yields high quality water that requires minimal treatment. The Mountain Ash forest yields about 80% of the total water derived from the catchment runoff, and therefore understanding how forest water use varies with climate and forest age allows catchment managers to predict supply into the future. Figure 5 shows a catchment water balance for the Maroondah water supply catchment showing how runoff (water yield) varies with the age of the stand.

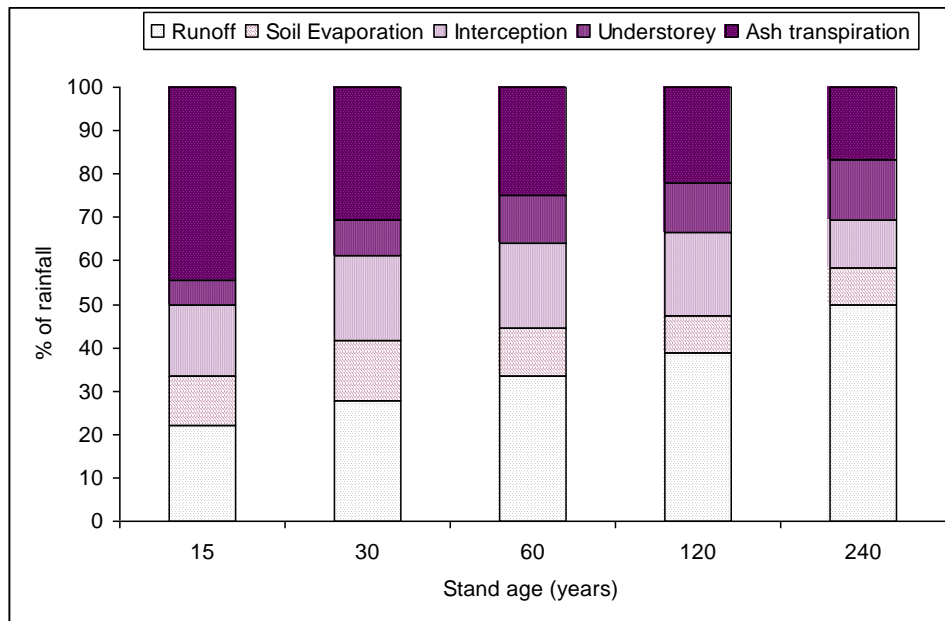


Figure 5. The proportion of run-off, tree transpiration, understorey transpiration and soil evaporation changes as a stand of mountain ash ages. Data from Vertessy *et al.* (1995).

The importance of forested catchments in the provision of this ES is demonstrated in New York, one of the most densely populated cities on the planet. The Catskill/Delaware catchment, provides the nine million residents of New York with 90% of their drinking water, approximately 1.3 billion gallons of water per day (Dudley and Stolton, 2003). It has been estimated that the cost of a plant to treat water (US\$6-8 billion; annual running cost \$300 million) to potable quality would be 7 times greater than protecting the forest. In contrast, the protection of the catchment will cost US\$1 – 1.5 billion over ten years (Dudley and Stolton, 2003).

4.3.3 Prevention and amelioration of dryland salinity

Dryland salinity is a major environmental problem for Australia (SCSI, 2004). In 2001 there were 5.7 million ha of land at risk or affected by dryland salinity (NLWRA, 2001). The significance of the problem is demonstrated by the commitment of the federal government to spend \$1.7 billion over seven years in the National Action Plan for Salinity and Water Quality (Standing Committee on Science and Innovation, 2004). Dryland salinity has significant negative impacts on agricultural land, roads and buildings, and biodiversity (NLWRA, 2001, Littleboy *et al.* 2001; Zeppel *et al.* 2003). Dryland salinity is estimated to cause \$300 million of lost agricultural production in the

Murray Darling Basin alone whilst damage to NSW roads costs \$9 m per year for classified roads (NLWRA, 2001). The loss in profits for the agricultural sector in WA, due to dryland salinity, is estimated at between \$80 and \$260 million per year. In Wagga Wagga, the local Council estimate the damage to infrastructure in the town would amount to \$180 million over 30 years, with some residents already spending up to \$20,000 to repair their homes (SCSI 2004).

The removal of deep-rooted, perennial native vegetation and its replacement with shallow rooted, annual crops has altered the hydrological balance away from neutrality (groundwater levels remain in equilibrium, neither rising nor falling over the medium term) to significant groundwater recharge. Forests therefore contribute to the management and prevention of dryland salinity by minimising groundwater recharge by transpiring almost all of the annual rainfall (Clarke *et al.* 2002; Kington and Pannell, 2003) or the lateral flow of water through landscapes (Timms *et al.*, 2001). Returning trees to the landscape may be part of the solution to dryland salinity (George *et al.*, 2001; Stirzaker *et al.* 2002; Walker *et al.* 2002).

4.3.4 What do we need to know to manage and maintain areas at risk or affected by dryland salinity?

To manage and maintain biodiversity and productivity of agricultural land in areas at risk or affected by salinity, we need to know the best locations to plant trees (Farrington and Salama, 1996; McJannet *et al.* 2000), and the effects of reforestation or clearing on local and regional patterns of groundwater recharge (Schofield, 1990). When replanting on hillslopes to ameliorate dryland salinity, it is important to consider where to place the trees in relation to zones of discharge and recharge, the spacing between trees, and what configurations to use, for example block plantings, tree belts or alley cropping (Stirzaker *et al.* 2002). Groundwater depth and salinity are also important inputs to determining where to plant trees to reduce recharge.

Managing dryland salinity requires knowledge of the effects of temperature, rainfall and soil conditions (especially waterlogging and salinity) on the growth, water use and survival of different tree species (Bell, 1999; Marcar *et al.* 1995; Thorburn, 1996; Stirzaker, 2002). The amount of water transpired by trees, and hence diverted from groundwater recharge, is affected by root distribution, rainfall interception, and leaf area index of trees. Indeed, Hatton and Nulsen (1999) argue that effective control of catchment water balance will only be achieved by revegetation that

generates a leaf area index approximating that of the natural, pre-cleared state, and revegetation with either trees or plants with similar ecohydrological characteristics as trees is required.

Reforestation has successfully lowered water tables in saline areas in Queensland (Walsh *et al.* 1995), and Western Australia (Silberstein *et al.*, 2002). Thus, a reforested valley in Western Australia had a substantially lowered saline groundwater table across the site, as well as a reduced average salinity of the groundwater (Bari and Schofield, 1992). However these examples are of relatively small-scale local areas, and additional methods may be required to reclaim large-scale regional aquifers (Silberstein *et al.* 2002). In addition, the amount of area within a catchment that needs to be forested may be up to 70-80% of the catchment (George *et al.*, 1999; Hatton *et al.* 2002) so it is important to remember that the solutions for dryland salinity are not fast and simple (Hobbs *et al.* 2003; Kington and Pannell, 2003).

4.3.5 Future Research

Research needs to be focussed on examining new sustainable land and water use systems (SCSI, 2004). Further research is required examining the effects of different forests, plantations and crops on groundwater recharge and discharge. Currently, revegetation strategies mean that agricultural land must be transferred from crops to planted trees, so preferably these trees would allow some profit for the landholder. Further research needs to be conducted addressing which tree species will be economically viable, in addition to being able to grow, transpire and survive under different climatic conditions while lowering groundwater. Finally, there has been no consistent field based approach to assessing the impact of rising water tables, water logging and salinity on native vegetation (Cramer and Hobbs, 2002). Cramer and Hobbs provide suggestions for addressing this in Western Australia, yet there is a paucity of research on the impacts of salinity on native vegetation in eastern Australia (but see Briggs and Taws 2003). There is a lack of reliable, quantitative field data examining the effects of dryland salinity on terrestrial vegetation in eastern Australia (Briggs and Taws, 2003).

5.0 Ecosystem-specific examples of ES

In the sections above we considered ES that are provided by a range of ecosystems. However, other equally important ES may be specific to particular ecosystems. Here we consider some of the services provided by vegetative components of particular ecosystems and illustrate how basic

ecology and plant ecophysiology has contributed to our understanding and valuation of ecosystem services.

5.1 *Riparian ecosystems*

The riparian zone is the interface or ecotone between aquatic habitats and their terrestrial catchments (Boulton and Brock 1999). Riparian areas are adjacent to perennial, intermittent, and ephemeral streams, lakes and estuarine-marine shorelines, although are most commonly thought of as those areas adjacent to freshwater habitats such as rivers and wetlands (Committee on Riparian Zone Functioning and Strategies for Management *et al.* 2002) and are considered in that context here. Riparian zones are under threat, as vegetation is often cleared to improve access for stock to water, for logging, to reduce local flooding by improving channel carrying capacity, or to maximise available cropping space (Tockner and Stanford 2002). In parts of Europe and Asia, between 60 and 99% of the riparian corridor has been developed (Ravenga *et al.* 1998).

To survive in riparian zones, vegetation must adapt to the rise and fall of water levels, unstable substrata, flooding and anoxia (Naiman and Decamps 1997). Adaptations to these conditions include adventitious roots, stem buttressing and root flexibility. Plants may also possess air spaces (aerenchyma) in the roots and stems to survive anaerobic conditions (e.g. Cyperaceae and Juncaceae). Having strong and/or flexible roots and stems allows plants to cope with the shear stresses of high flows (Naiman and Decamps 1997).

The ES these ecosystems provide are many. Most notably, they provide services to:

- 1) maintain water quality by filtering or ‘buffering’ the input of sediment, nutrients and toxicants from the catchment;
- 2) stabilise banks from erosion, and
- 3) provide habitat and contribute organic matter to maintain aquatic ecosystems.

5.1.1 Filtering

The importance of riparian vegetation in filtering runoff has long been recognised (Muscutt *et al.* 1993; Hook 2003) and they are now key components of many agricultural best management practices as a means of managing non-point source pollution. Riparian buffer strips (also known as filter strips or vegetative filter strips) filter runoff entering adjacent water ways by increasing

infiltration of water to the soil, and decreasing the turbulence of runoff water, thus enhancing pollutant removal by sedimentation (Abu-Zreig *et al.* 2003). Because many pollutants (nutrients, pesticides, metals) are adsorbed to sediment/soil particles, riparian strips also effectively reduce the pollutants reaching aquatic environments. However, riparian buffer strips can also remove soluble nutrients (e.g. Patty *et al.* 1997). The efficiency of riparian buffer strips depends on numerous factors, but most notably, vegetation type and species, and buffer strip width.

The effectiveness of different plant species and type in removing nutrients and sediment has been determined. Lee *et al.* (2000) showed that a combination of grass and woody species removed larger amounts of nutrients and retained larger amounts of sediment than did grass strips alone. They suggest that deep-rooted woody species increase the infiltration capacity of the strip, however, the comparison of vegetation types in that study was confounded by differences in strip width.

Hook (2003) showed significant effects of vegetation type in sediment retention, but differences were dependent on the width of the buffer strip. For narrow strips, retention was significantly less in dry upland plots compared to either transitional or wetland plots, but for wider strips (6 m) there was no significant difference in the effectiveness of the vegetation types. The upland plots had a much lower vegetative biomass and density than the other 2 vegetation types; prompting the authors' conclusion that vegetation density was a significant factor determining buffer strip efficiency.

Both forested and grass riparian buffer strips reduced (by up to 90%) nitrate-N concentrations in groundwater reaching an adjacent stream (Osborne and Kovacic 1993). However, on an annual basis, forested strips were more effective at reducing concentrations of nitrate-N than were grass strips, but were less efficient at retaining total and dissolved P (Osborne and Kovacic 1993). In their review, Lyons *et al.* (2000) concluded that grassy riparian zones might be better than wooded areas in filtering runoff and reducing bank erosion, but that woody species provided greater bank stabilisation. However, this is somewhat dependent on bank morphology and local hydrology. Indeed, maintaining the grassy riparian zones requires on-going management because successional processes will tend ultimately to favour woody species (Lyons *et al.* 2000). Deep-rooted woody species may also provide other benefits such as lowering groundwater tables (see above).

The inclusion of tall woody riparian zones provides for other ES not provided by grassy species. In particular, woody species provide stream shading, which may be useful for limiting microphyte weed growth (e.g. Bunn *et al.* 1998) and buffering stream temperature fluctuations (Castelle *et al.* 1994). The presence of tall riparian buffer strips can also reduce contamination of waterways by intercepting aerial drift from agricultural spraying (e.g. Ucar and Hall 2001; Felsot *et al.* 2003).

Increasing width of the buffer strip increases the removal of sediment and nutrients. Thus, Abu-Zreig *et al.* (2003) showed that buffer strip width was the critical factor affecting phosphorus removal from agricultural runoff. In that study, a 15 m wide strip removed 89% of the P.

Increasing the width beyond 15 m was unlikely to improve sediment retention, but was likely to increase P removal (Abu-Zreig *et al.* 2003). Mickelson *et al.* (2003) showed an 87% reduction in sediment removal for 9.1 m strips, 16 % more than for 4.6 m strips. Patty *et al.* (1997) also report 89% removal of P, but 100% removal of sediment over a grassy 18 m strip; smaller strips were much less efficient. Hook (2003) suggest that riparian buffer strips in rangelands should be at least 6 m wide. This suggestion is consistent with other studies, but generally, widths greater than 15 m are most effective (Castelle *et al.* 1994).

5.1.2 Erosion control

By limiting sediment influx and reducing bank erosion, riparian ecosystems provide a critical service in maintaining aquatic ecosystem health. High volumes of sediment entering streams can cause a loss of aquatic habitat and biodiversity, a decline in water quality, increased flooding in silted streams, and decreased water storage capacity, thereby reducing the availability of water resources.

Zaimes *et al.* (2004) demonstrated that intact riparian zones had significantly lower rates of stream bank erosion than grazed or cropped areas. Generally, the presence, density and type of stream bank vegetation influences bank erosion (Beeson and Doyle 1995; Harmel *et al.* 1999) with forested riparian zones subject to less erosion than grassed riparian zones (Harmel *et al.* 1999). Interestingly, there is some evidence to suggest forest age also influences erodability, with older forest less prone to erosion (Odegaard 1987, Zaimes *et al.* 2004). Considering the reduction in stream sedimentation by riparian zones due to both the interception of runoff and bank stability, the total stream sediment load could be reduced by approximately 80% by forested riparian buffers (Zaime *et al.* 2004).

Riparian zones provide other valuable ES, such as habitat for fish and aquatic invertebrates (Boulton and Brock 1999; Pusey and Arthington 2003). Riparian zones themselves are significant components of biodiversity at local and regional scales because riparian zones are often disproportionately species-rich compared to surrounding ecosystems (Nilsson and Svedmark 2002) and also serve as wildlife corridors (Mitsch and Gosselink 2000b). Riparian vegetation provides habitat for more bird species than any other vegetation association (Tockner and Stanford 2002). Riparian buffers also enhance the in-stream processing of both non-point and point source pollutants, thereby reducing the impact on downstream rivers and estuaries, but studies have yet to assess the extent and magnitude of the benefits this provides (Dosskey 2001).

Considering these ecosystem services provided by buffer strips in agricultural areas (not just as riparian zones), Rein (1999) showed the economic value of implementing 1 ha of buffer strip at around US\$15000 over 5 years (based on buffers strip of 1 ha per 35 ha of cultivated land). Assuming that existing riparian zones do not incur the costs of planting or maintenance, the financial benefits they provide may be even greater than suggested above. However, as discussed above, considerations of buffer width and vegetative cover will greatly influence their effectiveness and the financial benefits they return. Zavaleta (2000) also valued riparian ecosystems of the US in response to invasion by the exotic shrub, Tamarisk (*Tamarix* sp.). Tamarisk consumes more water than native riparian species and contributes to increased stream sedimentation and, consequently, increased frequency and severity of flooding (Zavaleta 2000). Conservative estimates of Tamarisk impact are US\$280-450 per ha which represents that portion of the value of riparian ecosystem services that has been lost. Clearly, the economic value of intact riparian ecosystems would be far greater than this.

5.2 *Freshwater and wetland ecosystems*

Like riparian ecosystems, wetlands span the divide between wholly aquatic and wholly terrestrial ecosystems and provide many similar ES. In contrast to riparian zones, however, wetlands have soils that are saturated during part of the vegetation-growing season, and support plants that are typical of saturated soils. Wetland ecosystems vary greatly in type, ecological function, and the ecosystem services they provide (Mitsch and Gosselink 2000a). Wetlands can be both marine and freshwater dominated, and include tidal marshes, fens and bogs, swamps and riverine macrophyte beds. Wetlands associated with riverine ecosystems are the focus of this case study (but see seagrass case study for marine-dominated example).

The ecological functions of wetlands include water storage, maintenance of surface and groundwater flows, biochemical cycling, retention of sediment and dissolved materials and provision of habitat (Mitsch and Gosselink 2000a). Aside from recreation and aesthetics, perhaps the most widely exploited services of wetland ecosystems are the ability to treat and improve water quality, and water storage/flood mitigation.

The ability of wetlands to remove nutrients, metals and other toxicants, and trap sediment (Johnston 1991), underlies their extensive use in water treatment facilities. Because nitrogen is important to eutrophication and health effects in drinking water, its removal from water by wetlands has been extensively studied. Three processes contribute to nitrogen retention by wetlands: denitrification, sedimentation and uptake by plants (Johnston 1991; Saunders and Kalff 2001). Denitrification involves anaerobic bacteria that release N to the atmosphere. Aquatic plants may take up and store N in their shoots and roots during the growing season, and by altering and reducing stream flow (see below), aquatic plants facilitate sedimentation and the incorporation of N in the sediment (Saunders and Kalff 2001).

Jansson *et al.* (1998) estimated that the potential nitrogen retention of existing wetlands in the Baltic Sea catchment could retain about 5-13% of the total annual N load. This represents a substantial N removal and reduces the eutrophication of the Baltic Sea. In the USA, Mitsch *et al.* (1999, cited in Mitsch and Gosselink 2000b) found that 3.4-8.8% of the Mississippi River Basin must be converted to wetlands or riparian forest in order to achieve a 50% reduction in the nitrogen loads entering the Gulf of Mexico by 50%.

At a smaller scale, Casey and Klaine (2001) demonstrated that wetlands were able to remove nitrogen and phosphorus from terrestrial runoff during storm events. Wetland sediments are important sinks for phosphorus (Casey *et al.* 2001), although the vegetation of the wetland can have significant effects on phosphorus dynamics by altering the redox potential of the sediment (Aldridge and Ganf 2003). The ability of plants to alter sediment conditions varies widely among species (e.g. Aldridge and Ganf 2003).

The physical presence of wetlands alters the flow and sediment dynamics of a water body. Macrophyte beds reduce current velocities both within and adjacent to beds, resulting in increased sedimentation and reduced turbidity (Madsen *et al.* 2001). The presence of macrophytes also

reduces the likelihood of sediment resuspension. Increased sedimentation and reduced turbidity provide ideal sediment and water clarity conditions to promote further macrophyte growth.

At a broader scale, wetlands capture floodwater and sediments and slowly release the water back to the river after flood passes. The role of macrophytes here is to slow down currents, increase transpiration and shade water (Mitsch and Gosselink 2000b). The economic value of wetlands in terms of flood mitigation alone was estimated at approximately US\$1000 per ha (in 1990 \$ values, Woodward and Wui 2001). However, the placement of wetlands within a catchment to maximise the benefits to flood control is subject to debate (see Mitsch and Gosselink 2000b), but provision of this service is largely restricted to floodplain wetlands (Bullock and Acreman 2003).

Wetlands also play important roles as habitat, nursery areas and refugia for aquatic life. For example, macrophytes reduce the impacts of pesticide contamination on aquatic systems, by either providing a refuge for fish (e.g. Napier 1992) or adsorbing toxicants from the water column (e.g. Brock *et al.* 1992). Wetlands also have their own intrinsic biodiversity value, which may ultimately influence their ability to provide key ecosystem services (e.g. Engelhardt and Richie 2002, but see the biodiversity discussion above for more detail).

Costanza *et al.* (1997) provided a global annual estimate of wetland services at US\$4.9 trillion, which equates to approximately \$14, 785 ha/yr. Wetlands are behind only estuaries, seagrass beds and floodplains in their per hectare value. Interestingly, analysis by Woodward and Wui (2001) suggests that the per-hectare value of wetlands varies little with wetland size. They also recognised that any given wetland will not provide all the services attributable to wetlands, yet even those that might provide only a single service are valuable. For example, those which provide water quality improvements alone may be valued at over US\$1000 ha/yr (in 1990 dollar values; Woodward and Wui 2001).

5.3 *Future research needs*

The ecosystem services described here for wetland and riparian ecosystems are those that are already identified and well described in the literature. The future for research in these systems is to identify and quantify the value of other services such as nutrient cycling, and the relative roles of various wetland types within a catchment. In the management of any ecosystem(s) we risk mismanaging the resource if we fail to acknowledge the interconnectedness of ecosystems and ES.

This is no more apparent than for riparian and wetland systems. So, for example, is the value of ES provided by a wetland made greater or does the system become more efficient in providing a service when adjoined by a functioning riparian zone? Which prompts the question, is the value of ES by adjoining ecosystems additive or multiplicative?

6.0 Seagrasses and mangroves

Seagrass and mangrove ecosystems occur throughout the world in coastal and estuarine zones. Seagrasses, by definition, live fully submerged in seawater, have an anchoring system, have hydrophilous pollination and are able to cope with high salinity (den Hartog 1970; Kuo 1982). The term mangrove refers to woody halophytes living at the interface of land and sea (Moberg and Rönnbäck 2003). Specialist morphological and physiological adaptations of mangroves include aerial roots, tidal dispersion of propagules, highly efficient nutrient retention mechanisms and the ability to also cope with high levels of salt (Duke *et al.* 1998; Alongi 2002). Seagrass meadows and mangrove forests are intimately linked, physically and functionally (Fortes, 1991) and both play an integral role in marine food chains (Kuo 1982; Alongi 2002).

Seagrasses are a highly productive component of the benthic ecosystem (West and Larkum 1982; Beer and Koch 1996). Their productivity is on a par with that of a marsh or coniferous forest (McComb *et al.* 1981; Beer and Koch 1996). Seagrass meadows act as estuarine filters, removing sediments and nutrients from coastal waters (Short and Short 1984; Short and Wyllie-Echeverria 1996), and provide shelter for juvenile fish species (Pollard, 1984; Burchmore *et al.* 1993; Carruthers and Walker 1997), and substrate for sessile plants and animals through substrate extension (den Hartog 1979; McComb *et al.* 1981). Seagrasses are used as a direct and indirect food source by crustaceans and other invertebrates, fish, turtles and dugongs (West and Larkum 1982; Montgomery and Targett 1992). Similarly, mangroves provide breeding areas and support food webs for birds, fish, crustaceans, shellfish, reptiles and mammals (Loneragan *et al.* 1997; Alongi 2002; Lal 2003). Mangroves are a renewable source of wood, produce oxygen, act as a carbon dioxide sink, trap sediments, pollutants and nutrients and protect the coast against erosion (Alongi 2002; Moberg and Rönnbäck 2003).

The global economic value of seagrass/algae beds is estimated to be \$ 3,801 x 10⁹ yr⁻¹, while that for tidal marsh and mangroves is \$1,648 x 10⁹ yr⁻¹ (Costanza *et al.* 1997). These values do not take into account a number of well-known ecosystem services for these biomes. For seagrasses, gas regulation, disturbance regulation, erosion control, waste treatment, habitat, food production and

recreation should all be assigned an economic value (Short *et al.* 2000; Duarte 2002). For mangroves, unvalued services include gas regulation, water regulation, erosion control, soil formation, nutrient cycling and cultural uses (Lal 2003; Moberg and Rönnbäck 2003). Therefore the estimates provided by Costanza *et al.* (1997) are highly conservative. Despite the value of seagrasses and mangroves, destruction of habitat, particularly close to human population has been increasing over the last 30 years (Fortes 1991; Alongi 2003; Duarte 2002), largely due to resource exploitation and pollution.

Seagrass meadows improve water quality and cycle nutrients

Physiological studies have been vital in defining the role of seagrass meadows as estuarine filter systems. Seagrass communities alter current velocities, most significantly by creating a zone of reduced flow within the leaf canopy (Fonseca *et al.* 1983; Leadbitter 1986). This removes sediments and nutrients from coastal waters (Short and Short 1984; Short and Wyllie-Echeverria 1996) by encouraging the settling of fine particles (such as organic material) and prevents already settled particles from being resuspended and carried away (Leadbitter 1986). Furthermore, both nitrogen and phosphorus are taken up by leaves from the surrounding water, increasing nutrient removal and cycling (Short and Short 1984). Seagrass roots and rhizomes resist sediment erosion, promoting a tightly bound substrate (Zieman 1975; Leadbitter 1986). Vegetative reproduction and rhizome extension promote the physical stability and resilience of meadows (Procaccini *et al.* 1996).

Besides filtering nutrients from the water column, seagrass meadows aid in the return of nutrients to the food web. Aquatic angiosperms are unique, in that nutrients are absorbed through the roots (as in terrestrial plants) as well as through the leaves (as in macroalgae) and translocation of nutrients between the roots and leaves occurs depending on the site of uptake and the concentration of nutrients (Cambridge and Hocking 1997). In this way, *Thalassia* sp. accounts for much of the movement of cations, including Fe, Pb and Cd (Schroeder and Thorhaug 1980).

Nutrients are lost from seagrass meadows through leaching, the export of sloughed leaves and leaf fragments, nutrient transfer by foraging animals, denitrification and diffusion from the sediment. The mechanisms of nutrient gain include nitrogen fixation, sedimentation and nutrient uptake by leaves (Hemminga *et al.* 1991; Herbert 1999).

The true value of seagrasses as estuarine filters has been fully appreciated through physiological studies to find reasons for decline, particularly because seagrass loss is a compounding process. Once die-off begins, secondary effects such as resuspension of sediments, increased turbidity and reduced light penetration exacerbate the situation (Thayer *et al.* 1994), sometimes leading to autocatalytic decline (Larkum and West 1982).

Coastal eutrophication is one of the major factors leading the global declines in seagrasses (Short and Wyllie-Echeverria 1996; Duarte 2002). Excess nutrients stimulate growth of phytoplankton which reduces light penetration and promotes epiphytic macroalgae growth, which shades and suffocates seagrasses (Duarte 2002). Light availability has long been recognised as the major environmental factor in controlling distribution, growth and survival of seagrasses (Dennison 1987; Batuik *et al.* 1992). Minimum light requirements for seagrasses are higher than those for phytoplankton and macroalgae (Abal *et al.* 1994) due to physiological demand of living in anoxic sediments and the respiratory demand of roots (Goodman *et al.* 1995) and thus, higher concentrations of chlorophyll *a*, total suspended solids, dissolved nutrients and light attenuation coefficients were associated with shallower depth limits in Moreton Bay (Abal and Dennison 1996).

Reduction in the distribution of seagrasses reduces ecosystem services by reducing the area available for foodwebs and habitat. Areas without seagrass cover become highly turbid as sediments become suspended in the watercolumn and poor water quality leads to further decline in remaining seagrasses, further reducing their distribution and therefore value. Furthermore, morphological characteristics of seagrasses growing under low light can be altered, reducing their value as habitat. Seagrasses grown in low light have thinner leaves, lower rates of productivity (and therefore biomass), larger shoots (Abal *et al.* 1994) and lower shoot densities (Olesen 1996).

6.1 *Productivity in mangroves and seagrasses*

Rates of primary production in seagrasses and mangroves influence their ecosystem services. Generally, higher productivities enhance goods production by stimulating foodwebs and nutrient turnover (Lal 2003; Moberg and Rönnbäck 2003).

Seagrasses are highly productive ecosystems, even though they occur under low nutrient conditions (den Hartog 1979; Cambridge and Hocking 1997). Daily productivities are $8 \text{ g C m}^{-2} \text{ day}^{-1}$ in

Zostera sp. and $16 \text{ g C m}^{-2} \text{ day}^{-1}$ in *Thalassia* sp. (Jørgensen *et al.* 1981). The bulk of seagrass biomass is mineralised through detrital food chains (50%) and usually less than 20% is directly consumed by herbivores (Duarte and Cebrián 1996). Sediment storage accounts for 16 % of the fixed carbon, while 34% is exported as dissolved organic matter, a vital nutrient source in coastal systems (de Boer *et al.* 2000). The organic matter provided by seagrasses initiates sulfate reduction and therefore maintains an active sulfur cycle in estuarine sediments (Zieman 1975; Lee and Dunton 2000). Dissolved free amino acids (DFAA) are also derived from seagrasses. Above a seagrass community, concentrations of DFAA were generally 2 to 5 times higher than those measured over deep-ocean areas and they were similar to values obtained for other highly productive marine environments (Jørgensen *et al.* 1981). These organic nutrients eventually feed prawns and other commercial fishes (Loneragan *et al.* 1997). Seagrasses also contributed DFAA to the sediment pore-water, thereby assisting the benthic infauna (Jørgensen *et al.* 1981).

Mangroves fix and store significant amounts of carbon and therefore make a vital contribution to global carbon budgets (Alongi 2002). Mangroves also make a significant contribution to coastal foodwebs (and therefore fisheries, Mumby *et al.* 2003). Earlier reported values of mangrove productivity were derived from measurements of light attenuation under the canopy but these rates are underestimates as they do not account for accumulation of biomass above ground (Alongi 2002). So productivities such as $1.4 \text{ g C m}^{-2} \text{ day}^{-1}$, reported by Upadhyay *et al.* (2002) may be only 10% of the actual photosynthetic production (Alongi 2002). A more accurate measure of mangrove productivity involves measuring light transmission and leaf photosynthesis (Ross *et al.* 2001; Alongi 2002). Therefore, best estimates of mangrove productivities suggest they can be as productive as seagrasses ($15.5 \text{ g C m}^{-2} \text{ day}^{-1}$, Alongi 2002; $7.2 \text{ g C m}^{-2} \text{ day}^{-1}$, Ross *et al.* 2001).

Carbon fixed in mangrove ecosystems is budgeted in the following manner: decomposed within the system (40%), exported (30%), stored in sediments (10%) and consumed by herbivores (9%) (Duarte and Cebrián 1996). More recent studies suggest these values may underestimate the carbon stored in wood and eventually decomposed and the carbon stored in sediments or exported (Alongi 2002). None-the-less, these values indicate the contribution to detrital foodwebs which support higher-order consumers. Hence, mangroves adjacent to coral reefs in the Caribbean influence the fish community structure by enhancing the survivorship of juvenile fish and doubling the biomass of some commercially important fish species (Mumby *et al.* 2003).

A number of factors influence mangrove productivity. For instance, a fringe forest was more productive than a dwarf forest (Ross *et al.* 2001), productivity increases with increasing stand age (Alongi 2002) and productivity was higher in the lower estuary than the higher estuary (Chen and Twilley 1999). These physiological characteristics demonstrate the enhanced value of mature forests over juvenile forests and may indicate the influence of nutrient inputs from the mouth of an estuary over land-derived nutrients (Chen and Twilley 1999). Furthermore, a relatively pristine mangrove forest was more efficient in carbon processing than a disturbed one (Alongi 2002). These natural and human-induced associations demonstrate the need to manage mangrove forests for their carbon budgets and perhaps prioritise conservation of more productive systems.

If ES rely on the interactions between seagrasses and mangroves (Fortes 1991), the loss of ecosystem interactions can lead to the loss of ecosystem services derived from the connected ecosystems in the seascape (Moberg and Rönnbäck 2003). Therefore effective management of mangrove and seagrass ecosystems relies on a detailed understanding of the ecophysiological requirements of both ecosystems.

6.2 *Future research questions*

For the most effective management and conservation of coastal ecosystems, associations between mangrove and seagrass ecosystem services need to be quantified. For instance, do seagrasses adjacent to highly productive mangroves have higher productivities and more efficient nutrient cycling and do seagrass meadows adjacent to highly productive mangroves have different carbon allocation budgets to those adjacent to less productive mangroves? More broadly, linkages amongst interacting ecosystems (metaecosystems) require investigation to quantify ES provision (Fig. 6).

7.0 **Conclusion**

In this review, we have (1) defined and described ecosystem services, (2) argued that it is vitally important that we overcome inertia among environmental scientists to place economic values on ecosystem services, (3) discussed the important links between ecosystem structure, function and services, and (4) provided empirical examples of how ecophysiology has contributed substantially to our understanding of ecosystem services. We have also presented a set of research questions that need answering in order to provide a comprehensive understanding of ecosystem services. In doing so it has become apparent that the services provided by one ecosystem can not be viewed in isolation from other ecosystems. In this sense, the concept of metacommunities (Leibold *et al.*

2004) may be expanded upon to incorporate “metaecosystems”, considering the fundamental links among, and the non-independent functioning of, ecosystems.

It is our contention that the concept of ecosystem services provides a unifying language and approach for dialogue between environmental scientists, industry, economists, the public, policy makers and politicians. Given the current and impending ecological crises facing the globe, and the general degradation of the goods and services provided by natural ecosystems, we believe the unification of environmental, economic and social needs in the concept of ecosystem services provides an engaging approach to ensure an environmentally sustainable future. Until recently, there has been an unfortunate absence of a common language for communication between scientists and other stakeholders, which has mitigated against environmental sciences penetrating the minds of those that have their hands on the levers of industry, policy and management. It is imperative that transparent discussion among stakeholders takes place with a common language, and the language of ecosystem services offers a practical, yet scientifically based, way forward.

8.0 References

- Abal EG, Dennison WC (1996) Seagrass depth range and water quality in southern Moreton Bay, Queensland, Australia. *Marine and Freshwater Research* **47**, 763-771.
- Abal EG, Loneragan N, Bowen P, Perry CJ, Udy JW, Dennison WC (1994) Physiological and morphological responses of the seagrass *Zostera capricorni* Aschers. to light intensity. *Journal of Experimental Marine Biology and Ecology* **178**, 113-129.
- Abu-Zreig M, Rudra RP, Whiteley HR, Lalonde MN, Kaushik NK (2003) Phosphorus removal in vegetated filter strips. *Journal of Environmental Quality* **32**, 613-619
- Aldridge KT, Ganf GG (2003) Modification of sediment redox potential by three contrasting macrophytes: implications for phosphorus adsorption/desorption. *Marine and Freshwater Research* **54**, 87-94
- Alongi DM (2002) Present state and future of the world's mangrove forests. *Environmental Conservation* **29**, 331-349.
- Bari MA, Schofield NJ (1992) Lowering of a shallow, saline water table by extensive eucalypt reforestation. *Journal of Hydrology* **133**, 273-291.
- Barret DJ (2002) Steady State turnover time of carbon in the Australian terrestrial biosphere. *Global Biogeochemical Cycles* **16**, 55-1 to 55-21.
- Barrett DJ., Hatton TJ, Ash JE, Ball MC (1996) Transpiration by trees from contrasting forest types. *Australian Journal of Botany* **44**, 249-263.
- Batuik RA, Orth RJ, Moore KA, Dennison WC, Stevenson JC, Staver L, Carter V, Rybicki N, Hickman RE, Kollar S, Bieber S, Heasley P, Bergstrom P (1992) 'Chesapeake Bay Submerged Aquatic Vegetation Habitat Requirements and Restoration Targets: a Technical Synthesis.' United States Environmental Protection Agency, Annapolis, Maryland.
- Beer S, Koch E (1996) Photosynthesis of marine macroalgae and seagrasses in globally changing CO₂ environments. *Marine Ecology Progress Series* **141**, 199-204.
- Beeson CE, Doyle PF (1995) Comparison of bank erosion at vegetated and non-vegetated channel bends. *Water Resources Bulletin* **31**, 983-990
- Bell DT (1999) Australian Trees for the Rehabilitation of Waterlogged and Salinity-damaged Landscapes. *Australian Journal of Botany* **47**, 697-716.

- Boulton AJ, Brock MA (1999) 'Australian freshwater ecology: processes and management.' (Gleneagles Publishing: Glen Osmond, SA)
- Briggs SV, Taws N (2003) Impacts of salinity on biodiversity - clear understanding or muddy confusion. *Australian Journal of Botany* **51**, 609-617.
- Brock TCM, Crum SJH, van Wijngaarden R, Budde BJ, Tijink J, Zuppelli A, Leeuwangh P (1992) Fate and effects of the insecticide Dursban 4E in indoor Elodea-dominated and macrophyte free freshwater model ecosystems: I. Fate and primary effects of the active ingredient chlorpyrifos. *Archives of Environmental Contamination and Toxicology* **23**, 69-84.
- Bullock A, Acreman M (2003) The role of wetlands in the hydrological cycle. *Hydrology and Earth System Sciences* **7**, 358-389
- Bunn SE, Davies PM, Kellaway DM, Prosser IP (1998) Influence of invasive macrophytes on channel morphology and hydrology in an open tropical lowland stream, and potential control by riparian shading. *Freshwater Biology* **39**, 171-178
- Burchmore JJ, Pollard DA, Middleton MJ, Williams RJ (1993) 'Estuarine Habitat Management Guidelines.' New South Wales Fisheries, Sydney, NSW.
- Cambridge ML, Hocking PJ (1997) Annual primary production and nutrient dynamics of the seagrasses *Posidonia sinuosa* and *Posidonia australis* in south-western Australia. *Aquatic Botany* **59**, 277-295.
- Cao M, Woodward IF (1998) Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. *Global Change Biology* **4**, 185-198.
- Carruthers TJB, Walker DI (1997) Light climate and energy flow in the seagrass canopy of *Amphibolis griffithii* (J.M. Black) den Hartog. *Oecologia* **1109**, 335-341.
- Casey RE, Klaine SJ (2001) Nutrient attenuation by a riparian wetland during natural and artificial runoff events. *Journal of Environmental Quality* **30**, 1720-1731
- Casey RE, Taylor MD, Klaine SJ (2001) Mechanisms of nutrient attenuation in a subsurface flow riparian wetland. *Journal of Environmental Quality* **30**, 1732-1737
- Castelle AJ, Johnson AW, Conolly C (1994) Wetland and stream buffer size requirements - a Review. *Journal of Environmental Quality* **23**, 878-882

Chapin FS, Sala OE, Burke IC, Grime JP, Hooper DU, Lauenroth WK, Lombard A, Mooney HA, Mosier AR, Naeem S, Pacala SW, Roy J, Steffan WL & Tilman D (1998) Ecosystem consequences of changing biodiversity. *Bioscience* **48**: 45-52.

Chen R, Twilley RR (1999) Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* **22**, 955-970.

Chen X, Hutley, L, Eamus, D (2003) Carbon balance of a tropical savanna of Northern Australia. *Oecologia* **137**, 405-416.

Clarke CJ, George RJ, Bell RW, Hatton TJ (2002) Dryland salinity in south-western Australia: its origins, remedies, and future research directions. *Australian Journal of Soil Research* **40**, 93-113.

Committee on Riparian Zone Functioning and Strategies for Management, Water Science and Technology Board, Board on Environmental Studies and Toxicology, Division on Earth and Life Studies, National Research Council (2002) Riparian areas: functions and strategies for management. National Academy Press, Washington, DC.

Cork S, Shelton, D, Binning, C, Parry, R (2001) A framework for applying the concept of ecosystem services to natural resource management in Australia. In 'Third Australian Stream Management Conference'. Brisbane. (Ed. I Rutherford, Sheldon, F., Brierley, G., and Kenyon, C.) pp. 157-162. (CSIRO Sustainable Ecosystems)

Cornish PM, Vertessy RA (2001) Forest age-induced changes in evapotranspiration and water yield in a eucalypt forest. *Journal of Hydrology* **242**, 43-63.

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The values of the world's ecosystem services and natural capital. *Nature* **387**, 253-260.

Cramer VA, Hobbs RJ (2002) Ecological consequences of altered hydrological regimes in fragmented ecosystems in southern Australia: Impacts and possible management responses. *Austral Ecology* **27**, 546-564.

Cramer W, Kicklighter DW, Bondeau A *et al.* (1999) Comparing global models of terrestrial net primary productivity:overview and key results. *Global Change Biology* **5**, 1-15.

Daily GC, Alexander S, Ehrlich PR, Goulder L, Lubchenco J, Matson PA, Mooney HA, Postel S, Schneider SH, Tilman D & Woodwell GM (1997) Ecosystem services: benefits supplied to human societies by natural ecosystems. *Issues in Ecology* **2**: 1-16.

de Boer WF (2000) Biomass dynamics of seagrasses and the role of mangrove and seagrass vegetation as different nutrient sources for an intertidal ecosystem. *Aquatic Botany* **66**, 225-239.

DeFries R, Field C, Fung I, Collatz G, Bounoua L (1999) Combining satellite data and biogeochemical models to estimate global effects of human-induced land cover change on carbon emissions and primary productivity. *Global Biogeochemical Cycles* **13**, 803-815.

den Hartog C (1970) *Seagrasses of the World*, North-Holland Publishing Co., Amsterdam.

den Hartog C (1979) Seagrasses and seagrass ecosystems, an appraisal of the research approach. *Aquatic Botany* **6**, 105-117.

Dennison WC (1987) Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany* **27**, 15-26.

Dosskey MG (2001) Toward quantifying water pollution abatement in response to installing buffers on crop land. *Environmental Management* **28**, 577-598.

Duarte CM (2002) The future of seagrass meadows. *Environmental Conservation* **29**, 192-206.

Duarte CM, Cebrián J (1996) The fate of marine autotrophic production. *Limnology and Oceanography* **41**, 1758-1766.

Dudley N, Stolton S (2003) 'Running pure: the importance of forest protected areas to drinking water. A research report for the World Bank/Alliance for Forest Conservation and Sustainable Use.' WWF.

Duke NC, Ball MC, Ellison JC (1998) Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters* **7**, 27-47.

Eamus D (1996) CO₂ and temperature interactions, biomass allocation and stand scale modelling in the study of tree responses to CO₂ enrichment. *Tree Physiology*, **16**, 47-52

Eamus D (2003). How does ecosystem water balance affect net primary productivity of woody ecosystems? *Functional Plant Biology* **30**, 187-205.

Eamus D, Myers, B, Duff, G, Williams, RJ (1999) Seasonal changes in photosynthesis of eight savanna tree species. *Tree Physiology* **19**, 665-671.

Eamus D, Hutley LB, O'Grady AP (2001) Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna. *Tree Physiology* **21**, 977-988.

Eamus D, O'Grady AP, Hutley LB (2000) Dry season conditions determine wet season water use in the wet-dry tropical savannas of northern Australia. *Tree Physiology* **20**, 1219-1226.

Eamus D and Prior L (2001) The ecophysiology of tropical savannas, with special reference to phenology, water relations and photosynthesis. *Advances in Ecological Research* **32**, 114-197.

Engelhardt KAM & Ritchie M (2002) The effect of aquatic plant species richness on wetland ecosystem processes. *Ecology* **83**: 2911-2924.

Esser G (1998) NPP Multi-Biome: Global Osnabruck Data, 1937-1981. Data set. Available on-line [<http://www.daac.ornl.gov>] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.

Farrington P, Salama RB (1996) Controlling dryland salinity by planting trees in the best hydrological setting. *Land degradation and development* **7**, 183-204.

Felsot AS, Foss SL, Yu JB (2003) Deposition of pesticides in riparian buffer zones following aerial applications to Christmas tree plantations. *American Chemical Society Symposium Series* **853**, 241-260.

Field BCB, Behrenfeld MJ, Randerson TJ, Falkowski P (1998) Primary Production of the Biosphere: Integrating Terrestrial and Oceanic Components. In '*Science*'. pp. 237-240.

Field BCB, Randerson JT, Malmstrom CM, (1995) Global NPP: combining ecology and remote sensing. *Remote Sensing of the Environment* **51**, 74-88.

Fonseca MS, Zieman JC, Thayer GW, Fisher JS (1983) The role of current velocity in structuring

eelgrass (*Zostera marina* L.) meadows. *Estuarine, Coastal and Shelf Science* **17**, 367-380.

Fortes MD (1991) Seagrass-mangrove ecosystems management: A key to marine coastal conservation in the ASEAN region. *Marine Pollution Bulletin* **23**, 113-116.

Friendlingstein P, Joel, G, Field, CB, Fungs, IY (1999) Toward an allocation scheme for global terrestrial carbon models. *Global Change Biology* **5**, 755-770.

Gaston KJ, Spicer JI (2004) Biodiversity: An Introduction. Second Edition. Blackwell Science Ltd, Oxford.

George R, Clarke CJ, Hatton TJ (2001) Computer modelled groundwater response to recharge management for dryland salinity control in Western Australia. *Advances in Environmental Monitoring and Modelling* **2**, 3-35.

George R., Nulsen RA, Ferdowsian R, GPR (1999) Interactions between trees and groundwaters in recharge and discharge areas - A survey of Western Australian sites. *Agricultural Water Management* **39**, 91-113.

Goodman JL, Moore KA, Dennison WC (1995) Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. *Aquatic Botany* **50**, 37-47.

Harmel RD, Haan CT, Dutnell R (1999) Bank erosion and riparian vegetation influences: Upper Illinois River, Oklahoma. *Transactions of the American Society of Agricultural Engineers* **42**, 1321-1329.

Hatton TJ, Moore SJ, Reece PH (1995) Estimating stand transpiration in a Eucalyptus populnea woodland with the heat pulse method: measurement errors and sampling strategies. *Tree Physiology* **15**, 219-227.

Hatton TJ, Nulsen RA (1999) Towards achieving functional ecosystem mimicry with respect to water cycling in southern Australian agriculture. *Agroforestry systems* **45**, 203-214.

Hatton, TJ., Reggiani P and Hodgson G (2002) The role of trees in the water and salt balances of catchment. In *Trees, Water and Salt*. Eds R Stirzaker, R Vertessy and A Sarre. RIRDC publication 01/086. Canberra, Australia.

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Hogberg P, Huss-Danell K, Joshi J, Jumpponen A, Korner

C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M., Schulze ED, Siamantziouras ASD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S and Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. *Science* **286**: 1123-1127.

Hemminga MA, Harrison PG, van Lent F (1991) The balance of nutrient losses and gains in seagrass meadows. *Marine Ecology Progress Series* **71**, 85-96.

Herbert RA (1999) Nitrogen cycling in coastal marine ecosystems. *FEMS Microbiology Reviews* **23**, 563-590.

Hobbs RJ, Cramer VA, Kristjanson LJ (2003) What happens if we cannot fix it? Triage, palliative care and setting priorities in salinising landscapes. *Australian Journal of Botany* **51**, 647-653.

Hook PB (2003) Sediment retention in rangeland riparian buffers. *Journal of Environmental Quality* **32**, 1130-1137.

Hutley LB, O'Grady AP., Eamus D (2000) Evapotranspiration from Eucalypt open-forest savanna of Northern Australia. *Functional Ecology* **14**, 183-194.

IACSEA (1998) Socio-economic Assessment Guidelines for River, Groundwater and Water Management Committees. Independent Advisory Committee on Socio-economic Analysis.

Ives A.R. & Cardinale B.J. (2004) Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* **429**, 174-177.

Jansson A, Folke C, Langaas S (1998) Quantifying the nitrogen retention capacity of natural wetlands in the large-scale drainage basin of the Baltic Sea. *Landscape Ecology* **13**, 249-262.

Jansson A, Folke C, Rockstrom J, Gordon L (1999) Linking freshwater flows and ecosystem services appropriated by people: the case of the Baltic Sea drainage basin. *Ecosystems* **2**, 351-366.

Johnston C (1991) Sediment and Nutrient Retention by Fresh-Water Wetlands - Effects on Surface-Water Quality. *Critical Reviews in Environmental Control* **21**, 491-565.

Jones JA, Post DA (2004) Seasonal and successional streamflow response to forest cutting and regrowth in the northwest and eastern United States. *Water Resources Research* **40**, Art. No W05203.

Jørgensen NOG, Blackburn TH, Henriksen K, Bay D (1981) The importance of *Posidonia oceanica* and *Cymodocea nodosa* as contributors of free amino acids in water and sediments of

seagrass beds. *Marine Ecology* **2**, 97-112.

Kaiser J (2000) Rift over biodiversity divides ecologists. *Science* **289**: 1282-1283.

Keith, H, Raison, RJ, and Jacobsen, KL (1997) Allocation of carbon in a mature eucalypt forest and some effects of soil phosphorous availability. *Plant and Soil* **196**, 81-99.

Kington EA, Pannell DJ (2003) Dryland salinity in the Upper Kent River catchment of Western Australia: farmer perceptions and practices. *Australian Journal of Experimental Agriculture* **43**, 19-28.

Kirschbaum MUF, Eamus, D, Gifford, RM, Roxburgh, SH, Sands, PJ (2001) Definitions of some ecological terms commonly used in carbon accounting. In 'Net Ecosystem Exchange workshop proceedings'. Canberra pp. 2-5. (Cooperative Research Centre for Greenhouse Accounting)

Kuczera, GA (1985) Prediction of water yield reductions following a bush fire in Ash mixed species Eucalypt forest. Melbourne and Metropolitan Board of Works, Catchment Hydrology Research Report MMBW-W-0014.

Kuo J (1982) Notes on the biology of Australian seagrasses. *Proceedings of the Linnaean Society of NSW* **106**, 225-245.

Lal P (2003) Economic valuation of mangroves and decision-making in the Pacific. *Ocean and Coastal Management* **46**, 823-844.

Larkum AWD, West RJ (1982) Stability, depletion and restoration of seagrass beds. *Proceedings of the Linnaean Society of N.S.W* **106**, 201-212.

Lawton JH (1999) Are there general laws in ecology? *Oikos* **84**, 177-192.

Leadbitter D (1986) The relationships between seagrasses and the processes of accretion and erosion at Towra Point, Botany Bay. *Wetlands (Australia)* **6**, 33-37.

Lee KS, Dunton KH (1997) Effects of *in situ* light reduction on the maintenance, growth and partitioning of carbon resources in *Thalassia testudinum* Banks ex Konig. *Journal of Experimental Marine Biology and Ecology* **210**, 53-73.

Lee K-H, Isenhardt TM, Schultz RC, Mickelson SK (2000) Multispecies riparian buffers trap sediment and nutrients during rainfall simulations. *Journal of Environmental Quality* **29**, 1200-1205.

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD,

- Shurin JB, Law R, Tilman D, Loreau M & Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**, 601-613.
- LeVeque C. & Mounolou J-C. (2003) Biodiversity. John Wiley & Sons Ltd, Sydney.
- Littleboy M, Piscoppo G, Beecham R, Barnett P., Newman L, N. A (2001) Dryland Salinity: Extent and impacts. *Technical report for the National Land and Water Resources Audit*.
- Loneragan NR, Bunn SE, Kellaway DM (1997) Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. *Marine Biology* **130**, 289-300.
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime J, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D & Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**: 804-808.
- Lu JB, Sun G., McNulty SG, Amatya DM (2004) Modeling actual evapotranspiration from forested watersheds across the Southeastern United States. *Journal of the American Water Resources Association* **39**, 887-896.
- Luck GW, Daily GC and Ehrlich PR (2003) Population diversity and ecosystem services. *Trends in Ecology and Evolution* **18**: 331-336.
- Lyons J, Trimble SW, Paine LK (2000) Grass versus trees: Managing riparian areas to benefit streams of central North America. *Journal of the American Water Resources Association* **36**, 919-930.
- Madsen JD, Chambers PA, James WF, Koch EW, Westlake DF (2001) The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* **444**, 71-84.
- Marcar N, Crawford D, Leppert P, Jovanovic T, Floyd R and Farrow R (1995) Tree models as they relate to soil/pasture/tree interactions in agroforestry and forestry. In: *Farming Action Catchment Reaction: the effect of dryland farming on the natural environment*. CSIRO Publishing, Melbourne.
- May RM (1992) Bottoms up for the oceans. *Nature* **357**, 278-279.
- McComb AJ, Cambridge ML, Kirkman H, Kuo J (1981) The Biology of Australian seagrasses. In: Pate JS, McComb AJ, (Eds), *The Biology of Australian Plants*. pp. 258-293, University of Western Australia, Nedlands.

- McJannet DL, Vertessy RL, Clifton CA (2000) Observations of evapotranspiration in a break of slope plantation susceptible to periodic drought stress. *Tree Physiology* **20**, 169-177.
- Medlyn B, Barrett, D, Landsberg, J, Sands, P, Clement, R (2003) Conversion of canopy intercepted radiation to photosynthate: review of modelling approaches for regional scales. *Functional Plant Biology* **30**, 153-169.
- Mickelson SK, Baker JL, Ahmed SI (2003) Vegetative filter strips for reducing atrazine and sediment runoff transport. *Journal of Soil and Water Conservation* **58**, 359-367.
- Mitsch WJ, Gosselink JG (2000a) *Wetlands*; John Wiley and Sons, New York 920 pp
- Mitsch WJ, Gosselink JG (2000b) The value of wetlands: importance of scale and landscape setting. *Ecological Economics* **35**, 25-33.
- Moberg F, Rönnbäck P (2003) Ecosystem services of the tropical seascape: interactions, substitutions and restoration. *Ocean and Coastal Management* **46**, 27-46.
- Montgomery JLM, Targett TE (1992) The nutritional role of seagrass in the diet of the omnivorous pinfish *Lagodon rhomboides* (L.). *Journal of Experimental Marine Biology and Ecology* **158**, 37-57.
- Mumby PJ, Edwards AJ, Arias-González JE, Lindeman KC, Blackwell PG, Gall A, Gorczyńska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CCC Llewellyn G. (2003) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**, 533-536.
- Muscutt AD, Harris GL, Bailey SW, Davies DB (1993) Buffer zones to improve water-quality - a review of their potential use in UK agriculture. *Agriculture Ecosystems and Environment* **45**, 59-77.
- Naeem S (1998) Species redundancy and ecosystem reliability. *Conservation Biology* **12**: 39-45.
- Naeem S (2002) Ecosystem consequences of biodiversity loss: the evolution of a paradigm. *Ecology* **83**: 1537-1552.
- Naiman RJ, Decamps H (1997) The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics* **28**, 621-658.
- Napier GM (1992) Application of laboratory derived data to natural aquatic ecosystems. PhD Thesis, Macquarie University, Australia.
- National Land and Water Resources Audit (2001) Australian Dryland Salinity

Assessment 2000. Canberra, Commonwealth of Australia.

Nilsson C, Svedmark M (2002) Basic principles and ecological consequences of changing water regimes: Riparian plant communities. *Environmental Management* **30**, 468-480.

Odegaard AJ (1987) Streambank erosion along two rivers in Iowa. *Water Resources Research* **23**:1225-1236.

O'Grady AP, Eamus D, Hutley LB (1999) Transpiration increases during the dry season: patterns of tree water use in eucalypt open-forests of northern Australia. *Tree Physiology* **19**, 591-597.

O'Grady AP (2000) Patterns of tree and stand water use in the eucalypt open-forests in the savannas of northern Australia. PhD thesis, Northern Territory University.

Olesen, B (1996) Regulation of light attenuation and eelgrass *Zostera marina* depth distribution in a Danish embayment. *Marine Ecology Progress Series* **134**, 187-194.

Osborne LL, Kovacic DA (1993) Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology* **9**, 243-258.

Patty L, Real B, Gril JJ (1997) The use of grassed buffer strips to remove pesticides, nitrate and soluble phosphorus compounds from runoff water. *Pesticide Science* **49**, 243-251.

Pollard DA (1984) A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. *Aquatic Botany* **18**, 3-42.

Power ME, Tilman D., Estes JA, Menge BA, Bond WJ, Mills S, Daily G, Castilla JC, Lubchenco J & Paine RT (1996) Challenges in the quest for keystones. *BioScience* **46**: 609-620.

Prior LD, Eamus, D, Duff, GA (1997) Seasonal and Diurnal Patterns of Carbon Assimilation, Stomatal Conductance and Leaf Water Potential in *Eucalyptus tetradonta* Saplings in a Wet-Dry Savanna in Northern Australia. *Australian Journal of Botany* **45**, 241-258.

Procaccini G, Alberte RS, Mazzella L (1996) Genetic structure of the seagrass *Posidonia oceanica* in the Western Mediterranean: ecological implications. *Marine Ecology Progress Series* **140**, 153-160.

Pusey BJ, Arthington AH (2003) Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research* **54**, 1-16.

Ravenga C, Murray S, Abramovitz J, Hammond A (1998) *Watersheds of the world*. World Resources Institute, Washington, DC.

- Rein FA (1999) An economic analysis of vegetative buffer strip implementation - Case study: Elkhorn Slough, Monterey Bay, California. *Coastal Management* **27**, 377-390.
- Roderick M, Farquhar, G, Berry, S, Noble, I (2001) On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia* **129**, 21-30.
- Ross MS, Ruiz PL, Telesnicki GJ, Meeder JF (2001) Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida. *Wetlands Ecology and Management* **9**, 27-37.
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Biodiversity - Global biodiversity scenarios for the year 2100. *Science* **287**: 1770-1774.
- Sala OE, Lauenroth WK, McNaughton SJ, Rusch G, Zhang X (1995) Temperate grasslands. In: Global Biodiversity Assessment (Ed. Heywood V.H.), pp. 361-366. Cambridge University Press, Cambridge.
- Saunders DL, Kalff J (2001) Nitrogen retention in wetlands, lakes and rivers *Hydrobiologia* **443**, 205-212.
- Sax DF, Gaines SD (2003) Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution* **18**: 561-566.
- Schimel DS, Braswell, B.H., Holland, E.A., McKeown, R., Ojima, D.S., Painter, T.H., Parton, W.J. and Townsend, A.R. (1994) Climatic, edaphic and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles* **8**, 279-293.
- Schofield NJ (1990) Determining reforestation area and distribution for salinity control. *Hydrological Sciences* **35**, 1-19.
- Schroeder PB, Thorhaug A (1980) Trace metal cycling in tropical-subtropical estuaries dominated by the seagrass *Thalassia testudinum*. *American Journal of Botany* **67**, 1075-1088.
- Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**: 297-305.
- Short FT, Burdick DM, Short CA, Davis RC, Morgan PA (2000) Developing success criteria for restored eelgrass, saltmarsh and mud flat habitats. *Ecological Engineering* **15**, 239-252.

- Short FT, Short CA (1984) The seagrass filter: purification of estuarine and coastal waters. In: Kennedy VS, (Ed), *The Estuary As a Filter*. pp. 395-413, Academic Press, New York.
- Short FT, Wyllie-Echeverria S (1996) Natural and human-induced disturbance of seagrasses. *Environmental Conservation* **23**, 17-27.
- Silberstein RP, Vertessy RA, McJannet D, and Hatton, T (2002). Tree belts on hillslopes. In *Trees, Water and Salt*. Eds R Stirzaker, R Vertessy and A Sarre. RIRDC publication 01/086. Canberra, Australia.
- Snowdon P, Eamus, D, Gibbons, P, Khanna, P, Keith, H, Raison, J Kirschbaum, M (2000) 'Synthesis of allometrics, Review of Root Biomass and Design of Future Woody Biomass Sampling Strategies.' (Australian Greenhouse Office)
- Standing Committee on Science and Innovation (2004). *Science overcoming salinity: coordinating and extending the science to address the nation's salinity problem*. House of Representatives, The Parliament of the Commonwealth of Australia, Canberra.
- Statzner & Moss (2004) Linking ecological function, biodiversity and habitat: a mini-review focusing on older ecological literature. *Basic and Applied Ecology* **5**, 97-106.
- Stirzaker R, Vertessy, R. and Sarre, A. (eds) (2002) *Trees, Water and Salt: An Australian guide to using trees for healthy catchments and productive farms*. RIRDC report 01/086. Canberra, Australia.
- Thayer GW, Murphey PL, LaCroix MW (1994) Responses of plant communities in western Florida Bay to the die-off of seagrasses. *Bulletin of Marine Science* **54**, 718-726.
- Thorburn P (1996) Can shallow water tables be controlled by the revegetation of saline lands? *Australian Journal of Soil and Water Conservation* **9**, 45-50.
- Tilman D (1997) Biodiversity and ecosystem functioning. In: *Nature's Services: Societal Dependence on Natural Ecosystems* (Ed. Daily G.C.), pp. 93-112. Island Press, Washington D.C.
- Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**: 718-720.

- Timms W, Acworth RI, Berhane D (2001) Shallow groundwater dynamics in smectite dominated clay on the Liverpool Plains of New South Wales. *Australian Journal of Soil Research* **39**, 203-218.
- Tockner K, Stanford JA (2002) Riverine flood plains: present state and future trends. *Environmental Conservation* **29**, 308-330.
- Turner K, Paavola, J, Cooper, P, Farber, S, Jessamy, V, Georgiou, S (2003) Valuing nature: lessons learned and future research directions. *Ecological Economics* **46**, 493-510.
- Ucar T, Hall FR (2001) Windbreaks as a pesticide drift mitigation strategy: a review *Pest Management Science* **57**, 663-675.
- Upadhyay VP, Ranjan R, Singh JS (2002) Human-mangrove conflicts: the way out. *Current Science* **83**, 1328-1336.
- Vertessey RA, Benyon RG, O'Sullivan SK, Gribben PR (1995) Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiology* **15**, 559-567.
- Vertessey R.A. HTJ, Reece P, O'Sullivan SK and Benyon RG (1997) Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Physiology* **17**, 747-756.
- Vertessey RA, Watson FGR, and O'Sullivan SK (2001) Factors determining relations between stand age and catchment water balance in mountain ash forests. *Forest Ecology & Management* **143**, 13-26.
- Walker BH (1992) Biological diversity and ecological redundancy. *Conservation Biology* **6**: 18-23.
- Walker GR, Zhang L, Ellis TW, Hatton TJ, CP (2002) Estimating impacts of changed land use on recharge: review of modelling and other approaches appropriate for management of dryland salinity. *Hydrogeology Journal* **10**, 68-90.
- Walsh KB, Gale MJ, Hoy NT (1995) Revegetation of a scalded saline discharge zone in Central Queensland .2. Water use by vegetation and watertable drawdown. *Australian Journal of Experimental Agriculture* **35**, 1131-1139.
- Wang YP, Barrett DJ (2003) Estimating regional terrestrial carbon fluxes for the Australian continent using a multiple-constraint approach. *TELLUS* **55B**, 270-289.

Watson FGR and Vertessey RA (1996) Estimating leaf area index from stem diameter measurements in Mountain Ash forest. CRC for Catchment Hydrology Report 96-7 Monash University, Australia 102pp.

West RJ, Larkum AWD (1982) Seagrass primary production - a review. *Proceedings of the Linnean Society of NSW* **106**, 213-223.

Woodward RT, Wui YS (2001) The economic value of wetland services: a meta-analysis. *Ecological Economics* **37**, 257-270.

Wullschleger SD, Meinzer FC, Vertessey RA (1998) A review of whole-plant water use studies in trees. *Tree Physiology* **18**, 499-512.

Zaimes GN, Schultz RC, Isenhardt TM (2004) Stream bank erosion adjacent to riparian forest buffers, row-crop fields, and continuously-grazed pastures along Bear Creek in central Iowa. *Journal of Soil and Water Conservation* **59**, 19-27.

Zavaleta E (2000) The economic value of controlling an invasive shrub. *Ambio* **29**, 462-467.

Zeppel MJB., Murray BR. and Eamus D (2003) The potential impact of dryland salinity on the threatened flora and fauna of NSW. *Ecological Management and Restoration* **4**, 53-59.

Zieman JC (1975) Tropical sea grass ecosystems and pollution. In: Ferguson Wood EJ, Johannes RE, (Eds), *Tropical Marine Pollution*. pp. 63-74, Elsevier Scientific Publishing Company, Amsterdam.

Figure 6. A conceptual model of interacting ES provided by terrestrial and aquatic ecosystems. A metaecosystem approach highlights the exchange of mass and energy between ecosystems in the provision of ES.

