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The role of wetlands in the changing ecophysiology and distribution of plant species: a comprehensive review

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ABSTRACT

Wetlands are important ecosystems globally. Changes in plant species physiology, species composition, species distribution and phenology have occurred with changes and modifications of wetland ecosystems. This paper reviews the role of wetlands in relation to the ecophysiology of plants and extend to which the current change in wetland ecosystems has affected growth, physiology, distribution and performance of wetland plant species. The paper reports on the past and the future of our current wetland ecosystems.

Keywords: Ecophysiology, ecosystems, eutrophication, nutrients, wetland conservation.

INTRODUCTION

What are wetlands?

Wetlands are transitional areas between land and water and are distinguished by wet soils, plants that are adapted to wet soils and a water table depth that maintains these characteristics (Kamau, 2009). The ability of wetlands to transform and store organic matter and nutrients has resulted in wetland being described as 'the kidneys of the landscape (Brix, 1994). This ability is being exploited in wetlands used for water quality improvement (Brix, 1994). Wetlands are areas that are wet for long enough periods that the plants and animals living in or near them are adapted to and often dependent on wet conditions for at least part of their life cycle (Anonymous, 1996). Wetlands cover nearly 10% of the earth's surface of which 2% are lakes, 30% bogs, 26% fens, 20% swamps and 15% floodplains (Anonymous, 1999). Wetlands are highly dependent on ground water levels, and so changes in climatic conditions that affect water availability highly influence the nature and function of specific wetlands. The annual cumulative period between which these wetlands become effectively flooded and when they are completely drawn down following drought is regarded as the hydroperiod (Gathumbi *et al.*, 2005).

Global climate change has been shown to influence the distribution and functions of wetlands by altering their hydrological regimes (changing water availability and depth, duration, frequency, and season of flooding) outside their normal range (Galbraith and Huber-Lee, 2005). Climatic parameters, landscape

factors, seasonal availability of water and nutrients, as well as soil characteristics determine largely the production potential of a wetland. The vulnerability of wetland resources depends on the direction and magnitude of human activities, and climate changes. Global warming and its possible effects on wetlands is a major concern to the general public today.

Functions of wetlands: Wetlands provide important ecosystem functions. Ecosystem functions are defined as 'the capacity of natural processes and components of natural or semi-natural systems to provide goods and services that satisfy human needs" (De Groot, 1992). Wetlands are important ecosystems from perspectives of regional biological diversity, hydrologic functioning, and productivity (Gathumbi *et al.*, 2005).

Wetlands are regulators of water quantity and water quality (Nzengy'a and Wishitemi, 2001). Natural and constructed wetlands can remove large amounts of nutrients and suspended solids from surface water flowing through them (Beadle *et al.*, 2004; Huang and Pant, 2009). Wetlands can remove and store large amounts of N and later released to the ecosystems mostly in organic forms. Previous studies in Kenya have revealed that *Cyperus papyrus* swamps are efficient in nutrient removal for the purpose of wastewater quality improvement (Nzengy'a and Wishitemi, 2001). Nitrogen retention in the wetlands occurs through a variety of mechanisms including filtration, adsorption, ion exchange, biological assimilation, and denitrification (Lee and Caporn, 1998; Huang and Pant, 2009). Several types of wetlands are known to act as hydrological buffers.

For example, floodplain wetlands store water when rivers over-top their banks, reducing flood risk downstream. Wetlands not only regulate the quantity of water flow but also regulate its quality (Anonymous, 1999).

Wetland plants are known as important wetland regulators since they remove pollutants and excessive mineral nutrients from the water (Romero *et al.*, 1999). Nitrogen can be removed from wetland waters by bacterial denitrification and plant accumulation (Beadle *et al.*, 2004; Huang and Pant, 2009). Nitrate uptake by aquatic plants acting as, 'temporary' sinks, may be important in young wetlands or trivial in mature vegetation stands (Huang and Pant, 2009). Constructed freshwater wetland can provide reliable tertiary treatment of municipal wastewater (Nzengy'a and Wishitemi, 2001). The accomplishment of wetlands in the removal of nutrients, trace metals, organics and pathogens is attributed to diverse wetland processes such as sedimentation, filtration, chemical precipitation, adsorption, microbial interaction and uptake by vegetation (Nzengy'a and Wishitemi, 2001).

Many components of wetland ecosystems provide resources for direct human consumption including: water for drinking, fish and fruit to eat, reeds for thatching houses and handicrafts, timber for construction, peat and fuelwood for fire (McAllister *et al.*, 1997). Harvesting of wetland goods, while respecting the production rate and the regenerative capacity of each species, can provide significant benefits to society (Acreman and Hollis, 1996).

Recreational uses of wetlands include fishing, sport hunting, bird watching, photography, and water sports. Tourism is one of the leading income generating industries globally and the economic value of these wetlands can be considerable. Maintaining wetlands and capitalizing on wetland values can be a valuable alternative to more disruptive uses and degradation of these ecosystems.

Eutrophication and ecophysiology of wetland plants: Eutrophication is a natural phenomenon of ageing in lakes, where organic material gradually accumulates in the lake basin during the geological history of the lake (UNEP, 1993). Eutrophication can also be defined as the enrichment of water body with plant nutrients particularly nitrates and phosphates, resulting in the nuisance of algal blooms and aquatic macrophytes (Awange and Ong'ang'a, 2006).

Increased concentrations of nutrients through runoff from agricultural land and changes in land use which increase run off contribute to eutrophication (Nzengy'a and Wishitemi, 2001). There are usually two consequences of eutrophication on plant communities: (1) an increase in emergent plant biomass and (2) a decrease in plant species diversity at high production levels (McJannet *et al.*, 1995). The numbers of rare plants in wetland communities are also known to decrease as nutrient supply increases (McJannet *et al.*, 1995). Changes in species composition, loss of overall plant diversity, conversion of a unique flora to one dominated by a few common species, and replacement of native species by exotics have been reported in connection with nutrient enrichment in several types of wetlands (Verhoeven and Schmitz, 1991).

Comparative studies have shown that high species diversity is frequently associated with low nutrient status and that species-rich wetlands typically have moderate productivity and standing crop (Verhoeven and Schmitz, 1991). Natural or constructed wetlands are used for removal of pollutants from wastewater or for treatment of storm water runoffs from agricultural lands and other non-point sources (Romero *et al.*, 1999; Huang and Pant, 2009). The ability of vegetation to remove nutrients and pesticides from water is related to plant productivity, which is directly dependent upon carbon fixation. Increased productivity is generally accompanied by greater total nutrient sequestration, and the larger plants resulting from greater productivity provide a large surface area for mechanical and biological interactions with water (Pierce *et al.*, 2007).

The construction of wetlands to reduce the amount of pollutants and nutrients from runoff and waste waters from different sources has become more common in recent years, as a measure to prevent the pollution and eutrophication of the recipient water bodies (Huang and Pant, 2009). Constructed wetlands have been successfully used to retain nutrients from treated wastewaters (Gale *et al.*, 1993; Romero *et al.*, 1999). Macrophytes remove pollutants by (i) directly assimilating them into their tissues, (ii) providing a suitable environment for microbial activity and (iii) slowing down water movement flow rates and thereby allowing sedimentation to take place (Nzengy'a and Wishitemi, 2001). Wetlands may be an integral part of integrated riparian management systems and are highly efficient at denitrification because of their large quantities of organic sediments and decaying plant material (Schultz *et al.*, 1994).

Future increases in the nutrient enrichment of wetlands are expected to have a marked influence on plant physiology and ecosystem functioning (Huang *et al.*, 2009). Reducing pollution, avoiding vegetation removal, and protecting wetland biological diversity and integrity are important activities to maintain and improve the resiliency of wetland ecosystems so that they continue to provide important services under changed climatic conditions (Kusler *et al.*, 1999).

Within-stand cycling of nutrients is an important feature of wetland systems that provides a basis for understanding their nutrient status, productivity, and degree of eutrophication (Gathumbi *et al.*, 2005). Little is known about the combined effects of climate change with those human activities already influencing lakes and rivers. The influence of climate change on water quality issues such as eutrophication is unclear, particularly because many of the climate-influenced processes leading to eutrophication (e.g., precipitation, snow melt, ice cover, runoff, thermal stratification) have interacting and often opposing effects. Thus, effects of climate change on nutrient recycling will most likely be site-specific and could lead to either a greater or reduced susceptibility to eutrophication.

A major challenge in predicting plant responses to elevated CO₂ is understanding the complex relationships between these effects and other factors, especially nutrient availability, which plays a central role in plant growth (Causin *et al.*, 2006). Numerous observations show that growth responses to elevated CO₂ are lessened or even eliminated under low N nutrition (Causin *et al.*, 2006). This effect is the result of the coordination that exists between C and N regulatory systems in the plant. The increase of the content of nitrogen and phosphorus in wetlands plays a major part in problems of eutrophication (Rozema and Leendertse, 1991).

Species with particular adaptations can be categorised according to life-form, life-history or functional type (McJannet *et al.*, 1995; Stohgren., 2001). A good approach to scientific research with wetland plants is to consider the requirements of particular species, their acquisition and use of resources and the plant response to natural environmental stresses such as excessive fertilization. It may be differences in the abilities of the plants to acquire resources and cope with nutrient stress that determines their distribution, rather than changes in the availability of resources or the severity of a particular abiotic factor. Actually it is the combination of both changing abiotic factors and

plant adaptation that determines the plant growth preferences. This approach requires extensive research relating species specific physiology to environmental conditions (ecophysiology). A greater understanding of the response of various wetland plant species to nutrient availability will enable us to predict the future responses of the entire groups of species to wetland nutrient enrichment or eutrophication (Huang and Pant, 2009) and hence plan for future wetland conservation and restoration.

Nutrient dynamics and impact on wetland plant species: Land use practices such as agriculture exert a major influence on plant productivity, soil and plant nutrient content, and within-stand nutrient cycling in wetlands (Gathumbi *et al.*, 2005). Nutrients create long term problems to wetland ecosystems (Oketch, 2006). Supply of mineral nutrients plays a major role in distribution of plants. An excess of minerals may result in toxic reactions and may thus be decisive for the occurrence of plants in natural communities (Janiesch, 1991).

Vegetative wetlands can be effective at immobilizing, storing and transforming chemical inputs from uplands (Schultz *et al.*, 1994). Use of inorganic fertilizers associated with agricultural activities is known to increase nutrients in sediments and surface waters and overland flow (Qualls and Richardson, 1995; Gathumbi *et al.*, 2005). These human activities may change the degree of nutrient transformations within the wetlands (Qualls and Richardson, 1995). To maintain the typical species composition of wetlands and their rare species, all influences resulting in eutrophication need to be addressed (Pauli *et al.*, 2002).

Changes in pasture land use practices also lead to alteration in wetland plant community composition and structure and seasonal net primary productivity, which has a direct impact on within-stand nutrient cycling (Gathumbi *et al.*, 2005). Nitrogen is one of the most pervasive of the chemical non-point source (NPS) pollutants. Field studies have shown that P deficiency induced by N enrichment increases root turnover and decreases nutrient retention by the vegetation (Güsewell *et al.*, 2003). Data from the literature indicate that nutrient retention by wetland plants depends on the type of nutrient limitation (Güsewell *et al.*, 2003). Species composition influences nutrient retention of ecosystems because individual species differ in their tissue nutrient quality (Tilman *et al.*, 1997; Evans and Poorter, 2001). Developing an understanding of how species respond to the effects of human activities on

wetlands is essential to predicting the future impacts of human influence on both species composition and ecosystem function.

Studies have examined environmental effects on species performance (Casanova and Brock, 2000), and competitive dynamics (Keddy *et al.*, 2000), but few studies have combined the effects of environmental conditions such as climate change and nutrient enrichment to predict species composition. Many genetic and environmental factors influence the species composition of a particular wetland, thus linking species composition to particular environmental conditions is difficult.

Increased fertilizer use, particularly N, in modern agriculture has increased concentrations of nutrients in both ground and surface waters (Gathumbi *et al.*, 2005). Nutrient enrichment increases plant available nutrients, potentially shifting competitive advantages to different species and altering species composition (McJannet *et al.*, 1995). A shift in species composition to more productive, aggressive species may alter the nutrient cycling and productivity of the wetland ecosystems.

Many changes are typical of nutrient enrichment, including increased biomass production, dominance of faster growing plant species, accelerated N cycling and reduced N retention (Rochette *et al.*, 2004). Croplands contribute 43% of the annual nitrogen input to surface waters while pasture and rangelands contribute 25% (Schultz *et al.*, 1994). Despite the magnitude of these estimates, there is paucity of knowledge on the effects of excess nutrients on the ecophysiology of growth and photosynthesis of plants in wetlands.

Plants can assimilate and immobilize nutrients such as nitrogen and phosphorus (Bolan and Adriano, 2001) as well as heavy metals and pesticides (Sadik *et al.*, 1987; Schultz *et al.*, 1994; Prasad, 2004). Microbial processes are important in reducing Non-point sources of pollution in the landscape. Nitrogen and other nutrient dynamics during decomposition of litter is complex, as the nutrients often occur in different forms and are subject to various transformations (Hall *et al.*, 2006). Bross *et al.* (1995) observed a temporary increase in N concentration during decomposition, because of N immobilization during early biomass loss. Generally the concentration of nutrients is found to decrease with depth, the highest levels in the litter and a sharp decrease down the mineral horizon (Gupta and Rorison, 1975). The content of phosphorus in

wetlands has greatly increased as a result of discharge of phosphates from rivers. In an experimental study where application of sewage sludge to the Great Sippe Wisset salt marsh in Northern America was done, plant biomass increased significantly in the upper and lower parts of the salt marsh (Rozema and Leendertse, 1991). The tall form of *Spartina alterniflora* in the lower parts of the salt marsh increased strongly with nutrient enrichment (Rozema and Leendertse, 1991). In addition, ecological processes and biogeochemical cycles (especially the N cycle) are currently disturbed by human activities. Consequently, it has become necessary to improve the scientific knowledge concerning the characteristics of mineral N uptake by the major species of the wetland community. It is especially important to understand the dynamics of wetlands processes and develop predictive methods to determine optimal widths and management intensities needed to increase nutrient recycling and reduce negative effects on the wetland's ecosystem functions.

A biotic environment related to plant adaptations:

Concerns about the rising atmospheric CO₂ levels have prompted considerable interest in recent years regarding the sink potential of soil organic carbon (SOC). Elevated CO₂ increases biomass production in plants (Centritto *et al.*, 2002). The increase of atmospheric CO₂ concentration is expected to enhance photosynthesis, thus resulting in increased growth and yield of many plants. Past research has found that elevated CO₂ increases the growth of most plants, due primarily to increased rates of photosynthesis, altered carbon partitioning, and increased water and nutrient use efficiencies (Smith *et al.*, 2008).

Increased atmospheric concentrations of CO₂ and other greenhouse gases will cause an increase in mean global temperature by 1-3.5 °C and is likely to increase evapotranspiration and changes in regional precipitation (Tans, 1993). The pattern and frequency of stomata on any leaf surface are under tight genetic control, but may be modified by environmental parameters such as the availability of CO₂ (Croxdale, 2000). Environmental conditions affect stomatal density and this has implications for plant development. Collection of data on stomatal densities from sites which have experienced environmental pollution can provide a baseline against which to assess anthropogenic impacts on these species elsewhere (Zarinkamar, 2007). This has potential to facilitate appropriate monitoring and analysis of

environmental changes, using stomatal characteristics as an indicator of physiological and genetic response (Zarinkamar, 2007).

A decline in stomatal density would be expected to result from expansion of epidermal cells without the formation of new stomata. Stomatal conductance depends on the density of stomata on the leaf and on their aperture opening, which controls diffusion through individual stomata. Stomatal conductance is decreased by elevated atmospheric CO₂ concentration (Causin *et al.*, 2006). Stomates are sensitive to environmental stress and will usually close during times of stress (Maricle *et al.*, 2007). A decrease in stomatal conductance reduces incoming CO₂ and thus can reduce photosynthesis rates (Maricle *et al.*, 2007). Stomatal closure causes a decrease in internal CO₂ concentration. Subsequently, a concomitant decline in photosynthesis results from the diminished availability of CO₂ for carbon fixation. Reduction of CO₂ concentration increases the amount of harmful reactive oxygen species within the leaf due to ongoing light reaction, which leads to senescence and even death of the plant (Kuan-Hung *et al.*, 2006).

Physiological changes associated with environmental stress in crops and pastures include a reduction in photosynthetic rate. Flood-induced decrease in photosynthetic rate has been associated with a reduction in Rubisco activity, interpreted as an early indicator of flooding stress. Influences of rising global CO₂ concentration and increasing nutrient levels on plant growth and ecosystem function have become major concerns, but how photosynthesis changes with CO₂ and excessive nutrition in wetland plant species is poorly understood.

The atmospheric concentration in N₂O is increasing at a rate of 0.25% annually (Hall *et al.*, 2006). Agricultural sources are estimated to emit approximately 80 mg N₂O-N yr⁻¹ or 60% of the total anthropogenic emissions (Hall *et al.*, 2006). These N₂O emissions are largely attributed to nitrification and denitrification of N that is added to the soil to sustain crop productivity (Kamara *et al.*, 1997). Wetlands can provide beneficial functions and minimize adverse effects such as N₂O emissions to the atmosphere (Lee and Caporn, 1998; Huang and Pant, 2009).

Under natural conditions in seasonal environments, nutrient levels may vary during the growing season and may decline gradually as a result of plant uptake and leaching. Element accumulation by plants

typically proceeds more rapidly during growth than with carbon accumulation, although there is considerable variation in relative accumulation rates (Benner and Bazzaz, 1988). Accumulation and distribution of carbon and other elements can be affected by physiological and morphological constraints imposed by plant development (Benner and Bazzaz, 1988). Plants enrich the top soil through litter fall, thus acting as net to trap nutrients which otherwise would be leached down the profile (Kanmegne *et al.*, 1999).

With increased diversification in industrialization and extensive use of metal-based fertilizers, the concentrations of metal pollutants in wetlands continue to rise through natural run off. Presence of metal pollutants in wetland ecosystems is known to disturb the delicate balance of the ecosystems (Ipinmoroti, 1993; Bais *et al.*, 2006).

Invasive species have devastated many of the world's wetland ecosystems (Kourtev, 2003), due to a combination of anthropogenic alteration and nutrient enrichment of wetlands. Invasive plants have higher rates of carbon assimilation and/or water use efficiency relative to native plant species, which may contribute to their spread (McDowell, 2002). For plants, with a high rate of net carbon assimilation can result in higher biomass accumulation, favouring future growth and reproduction as well as competitive status (Brock and Galen, 2005). Studies indicate that elevated CO₂ will stimulate the growth and competitiveness of invasive plants (Froud-Williams, 1996), perhaps to a greater degree than other plant species because of their ability to rapidly adapt to new environments (McDowell, 2002). Currently, very little effort has been focused on obtaining empirical data to determine the extent of increased nutrition by wetland plant species and how this might impact the management of these species in a changing global environment. Therefore, it is important to understand how wetland plant species will be impacted by excess nutrients in their natural ecosystems. The growing interest in trees and forests under the influence of environmental pollution and changing global climate makes it desirable to select one or a few plant species to study more intensively (Posthumus, 1991).

CONCLUSIONS

Future increases in the nutrient enrichment of wetlands are expected to have a marked influence on plant physiology and ecosystem functioning. The review of the role of wetlands in the ecophysiology

and distribution of wetland plant species is necessary in understanding major challenges facing the current ecosystems and hence predicting the future state of wetland ecosystems. The description of ecophysiological characteristics of wetland plants and other factors that determine their distribution by observation of the past and present situations that are similar to the expected future global environmental changes are needed to understand the fate of these wetland ecosystems.

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