

Future wet grasslands: ecological implications of climate change

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Abstract. Wet grasslands are threatened by future climate change, yet these are vital ecosystems for both conservation and agriculture, providing livelihoods for millions of people. These biologically diverse, transitional wetlands are defined by an abundance of grasses and periodic flooding, and maintained by regular disturbances such as grazing or cutting. This study summarizes relevant climate change scenarios projected by the Intergovernmental Panel on Climate Change and identifies implications for wet grasslands globally and regionally. Climate change is predicted to alter wet grassland hydrology, especially through warming, seasonal precipitation variability, and the severity of extreme events such as droughts and floods. Changes in the diversity, composition, and productivity of vegetation will affect functional and competitive relations between species. Extreme storm or flood events will favor ruderal plant species able to respond rapidly to environmental change. In some regions, wet grasslands may dry out during heatwaves and drought. C₄ grasses and invasive species could benefit from warming scenarios, the latter facilitated by disturbances such as droughts, floods, and possibly wildfires. Agriculture will be affected as forage available for livestock will likely become less reliable, necessitating adaptations to cutting and grazing regimes by farmers and conservation managers, and possibly leading to land abandonment. It is recommended that agri-environment schemes, and other policies and practices, are adapted to mitigate climate change, with greater emphasis on water maintenance, flexible management, monitoring, and restoration of resilient wet grasslands.

Key words: *agricultural production; biodiversity; climate extremes; disturbance; drought; ecosystem services; flooding; mitigation; Special Feature: Wetlands and Global Climate and Land-use Change; wetland.*

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Introduction

Wet grasslands are biologically diverse wetlands dependent upon hydrological regime and vegetation management for their particular characteristics, but the sustainability of both these key controls is threatened by climate change. These wetlands are defined by an abundance of grasses (or sedges), as well as periodic flooding with fresh or brackish water, or a high water table for some of the year, sufficient to influence the vegetation (Joyce and Wade 1998). Climate change, which is manifested particularly through increased temperature, variations in precipitation, and extreme events, has the potential to severely disrupt nature conservation and agricultural management regimes in wet grasslands, thereby impacting upon human livelihoods and society

(Brotherton and Joyce 2015). The aims of this study were to introduce pertinent climate change scenarios and identify key impacts on wet grasslands globally and regionally, by elucidating the likely ecology of future wet grasslands under climate change environments, and indicating climate mitigation and adaptation measures.

Wet grasslands can be considered as transitional wetland ecosystems occupying a hydrological gradient between permanently inundated wetlands, such as reed swamps, and dry grasslands in which water is insufficient to define the vegetation. Many are “seminal”, formed by drainage of other wetland types or forest clearance on floodplains but still largely comprised of characteristic native plant species (Dixon et al. 2014). Typically, they are located in lowland landscapes (e.g., <1,000 m in elevation; Table 1). These wetlands are found on peat, alluvial, or mineral substrates and may be known regionally or locally by a variety of terms (Table 1; see Fig. 1 for examples). However, all wet grasslands are

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Table 1. Subcategories of wet grassland landscapes, examples of terms used to describe types, and sources of disturbance.

| Landscape setting | Examples of types | Typical disturbance |
|-------------------|--|-------------------------|
| Floodplain | Riparian, alluvial, flood pulse, monsoonal, flood meadow | Flooding, cutting, fire |
| Coastal | Seashore, grazing marsh, deltaic marsh | Grazing, inundation |
| Lacustrine | Inundation | Flooding, grazing |
| Mire | Fen meadow | Cutting |
| Depressional | Damboat, wet prairie, wet steppe, wet savanna | Grazing, fire |
| Human | Washland, polder‡, water meadow | Inundation, grazing |

Notes: See Fig. 1 for images of example grasslands.

†Seasonally waterlogged, grassy depressions bordering headwaters in central and southern Africa.

‡Low-lying wet grasslands claimed from the sea or other bodies of water.

maintained by disturbance (Table 1), which prevents establishment by trees or shrubs. Often, disturbance is imposed by flooding and vegetation management as part of an agricultural system that utilizes primary production to support domestic herbivores directly through either grazing (pastures) or hay fodder (meadows; Joyce and Wade 1998). Burning is also practiced on some wet grasslands, such as in tropical regions, often to remove coarse or woody vegetation and maintain soil productivity (Woodward 2003). Natural wet grasslands also exist, usually subject to disturbance by flooding, waterlogging, or herbivory, which constrain colonization by shrubs and trees. Savanna-type wetlands, which particularly occur in the tropics, support scattered trees but retain the dominant cover of grass or grass-like species. Thus, wet grasslands can appear to represent a heterogeneous resource, with different types located in a variety of landscapes, but all have a common eco-hydrological template defined by regular disturbance (Table 1). These wetlands consequently show similarities in their vegetation structure and composition (Fig. 1) and in the management of their valuable attributes. Such similarities provide a unifying basis on which to evaluate the likely impacts of climate change on wet grasslands.

Wet grasslands can ameliorate the effects of climate change through their provision of ecosystem services. These wetlands regulate surface runoff, attenuate flooding, recharge aquifers, and provide fresh water, as important components of the water cycle (Joyce and Wade 1998). Wet grasslands contribute to carbon storage and sequestration (Fidelis et al. 2013), mostly in below-ground biomass, especially in some tropical grasslands and peat-based systems. Coastal wet grasslands provide protection against storms and flooding (Gedan et al. 2011, Ward et al. 2015). The productivity of wet grasslands is harnessed by humans to yield forage for livestock, providing a livelihood for millions of people. Some species provide unique services, such as the golden grass (*Syngonanthus nitens*) of the Jalapão region of Brazil, which is harvested to make jewelry and house decorations for sale by local people (Schmidt et al. 2007). Climate change may have particularly important consequences for wet grassland stakeholders, because climate events such as flooding or drought can delay or alter vital management activities such as hay cutting, livestock

grazing, or burning, leading to loss of income or nature conservation benefits.

Wet grasslands are not often specified in wetland inventories or reports (e.g., Russi et al. 2013) and are overlooked in the climate change literature, including assessments by the Intergovernmental Panel on Climate Change (IPCC). However, these wetlands provide an interesting case for elucidating climate change effects, being widely distributed, geographically varied, but with key hydrological, vegetation, and management features in common. These wetlands may be particularly sensitive to climate change as they are ecotonal, transitional between terrestrial and aquatic systems, and maintained in a dynamic equilibrium by disturbance yet responsive to hydrological fluctuations (Toogood et al. 2008, Berg et al. 2012). Moreover, wet grasslands show limited topographic variation (Ward et al. 2013) so that species may lack refuges from floods or climate warming. In addition, many remaining wet grasslands are fragmented or isolated (Casanova 2012) and the characteristic and rare plant species of diverse communities (e.g., orchids) tend to lack mobility due to low dispersal rates (Joyce 2014). Thus, wet grasslands might provide an early warning of climate change impacts upon ecology, especially as diverse systems can allow small or rapid responses to be discriminated (Joyce 2001).

This review introduces the main climate change scenarios that will affect future wet grasslands and then identifies key impacts related to hydrological change, plant community responses, and human management. The review also proposes mitigation and adaptation approaches to climate change for wet grasslands.

Climate Change Scenarios

Climate change predictions made by IPCC (2014) and others are seldom generated specifically for wetlands. Climate change incorporates the global temperature increase and other longer-term climatic changes related to increases in greenhouse gases in the atmosphere, and also short-term extreme events. Although not developed for wet grasslands, IPCC (2014) predictions for climate change until 2100 can be summarized into four main drivers of hydrological and vegetation change in these wetlands: (1) an increase in temperature, probably



Fig. 1. Examples of wet grassland types. (a) Floodplain grassland, England; (b) fen meadows, Biebrza, Poland; (c) Baltic coastal grassland, Estonia; (d) wet prairie, Indiana, United States; (e) depressional grassland, Victoria, Australia; (f) tropical wet grassland landscape, Marajo, Brazil.

affecting high latitudes more than tropical and subtropical wetlands, reducing snow and ice cover; (2) changes in total precipitation and precipitation seasonality and patterns, including snow cover and melt; (3) a rise in sea level impacting coastal wetlands; and (4) an increase in climate variability and extreme events, notably intense precipitation and extreme temperatures with consequent heatwaves, storms, drought, and floods. Contrasts between wet and dry regions, and wet and dry seasons, are expected to increase. Monsoons are likely to intensify. Wet grasslands could also be affected by more wildfires, especially if they dry out at the surface or if biomass has accumulated, and altered salinity, particularly due to salt-water intrusion into freshwater systems. Moreover, an accumulation of greenhouse gases, especially carbon dioxide (CO₂), will affect soil biogeochemistry, plant production, and species competitive relationships. Interactive effects are also likely to exacerbate climate change, such as droughts concentrating salinity at the soil surface to create particularly stressful conditions for vegetation (Eliáš et al. 2013). Climate change and the rate of change are likely to affect social, economic, and agricultural functioning (IPCC 2007), and cause environmental concerns such as biodiversity and habitat loss (McCarty 2001).

The climate change scenarios predicted by IPCC (2014) include extreme episodes driven by high temperatures and/or intense precipitation, yielding events such as droughts or floods. Smith (2011) describes extreme climate events as those defined by great magnitude over short temporal scales that may cause profound ecosystem responses, often disproportionately greater than those predicted under steady change scenarios. Extreme events are likely to be particularly relevant to wet grasslands as these will disrupt hydrological regimes and vegetation, with consequences for human management. Grasslands on floodplains or the coast may be especially susceptible to flooding and storms, and peat-based grasslands are vulnerable to drought. From an ecological perspective, climate events can be considered a disturbance that impacts plant functioning, biodiversity, and ecosystem processes (Brotherton and Joyce 2015). Globally, extreme weather or climate events are expected to become more frequent and increase in intensity and duration in response to the changing climate (Tebaldi et al. 2006, IPCC 2012). Already, heatwaves have become more frequent in Europe, Asia, and Australia and extreme precipitation events have increased in North America and Europe (IPCC 2013).

Climate Change Impacts on Wet Grassland Ecology

Climate change impacts on wet grasslands will be manifested through hydrological and vegetation changes, and these will have important implications for agricultural management. However, it should be noted that projected effects of climate change on wet grasslands and other

wetland types are generally not well understood (Erwin 2009). Wet grasslands, in common with other wetlands, are located across numerous biomes and there is no single climatic template. Regional predictions of the consequences of climate change are complicated by the distribution of wet grasslands on land masses in different climatic zones and constrained by a lack of data availability (Junk et al. 2013). Nevertheless, the potentially widespread and severe effects of climate change on wet grasslands can be summarized by considering predicted scenarios and identifying types likely to be affected (Table 2). This synthesis indicates that wet grasslands located in tundra or boreal climates are likely to be affected by less ice and snow cover. Temperate humid wet grasslands could be subject to increased precipitation and sea level rise, the latter leading to coastal squeeze. More intense precipitation and floods could impact temperate continental or semiarid wet grasslands, which could also be affected by fires, heatwaves, and droughts, with reduced river flows. Mediterranean wetlands, and those located in desert regions, could be increasingly prone to drought and fires in a climate change future. Tropical humid wet grasslands could experience more intense rainfall and flooding, as well as sea level rise in coastal marshes and meadows. It is expected that greater rainy and dry season variations will influence wet grasslands in tropical semiarid areas, with intensification of the monsoon, heatwaves, and droughts. The case of South America alone reinforces the multiple suite of threats that wet grasslands face. Melting snow and ice in the glaciers of Patagonia and the Andes will alter surface runoff into interior wetlands, sea level rise of between 20 and 60 cm will destroy coastal marshes, and an increase in extreme events, such as storms, floods, and droughts, will affect biodiversity in wet grasslands (after Junk et al. 2013).

The potential impacts of climate change on wet grasslands are complex and severely damaging (Table 2); however, some regions may benefit from enhanced wet grassland creation and productivity. For example, the Hadley Centre's climate and vegetation model predicts conversion of Amazon rain forest to cerrado (savanna-type) vegetation from 2050 to 2100 (Jenkins et al. 2005). Also, warmer and wetter conditions will enhance soil water availability and primary productivity in wet prairies in some eastern parts of the northern plains of the United States and southern Canada (Polley et al. 2013). Greater water availability in some regions where precipitation is forecast to increase (e.g., northern Europe, Table 2) may also offer opportunities to restore or create new wet grasslands, possibly from intensively managed grasslands or croplands.

Hydrological changes

Climate change will have its most pronounced effects on wet grasslands through alterations in hydrological regimes, especially the nature and variability of flooding

Table 2. Regional climate scenarios (after Ramsar 2002; IPCC 2013, 2014), stressors, and examples of wet grassland types likely to be impacted.

| Scenario | Stressors | Examples of wet grasslands impacted |
|--|--|--|
| Europe | | |
| Increased precipitation in northern Europe | Increased fresh water in brackish or saline waters | Seashore grasslands in Baltic coastal wetlands |
| Decreased precipitation in southern Europe | Drought | Mediterranean grasslands |
| Decreased snow cover and more rapid snow melt | Reduced water availability and altered flood pulse | Central European floodplain grasslands downstream of mountains |
| More frequent heatwaves | Heat stress and drought | Continental flood meadows, for example, Rhine floodplain, Germany |
| Wildfires | Fire damage | Steppe wet grasslands |
| Sea level rise | Salt water intrusion, sedimentation, storms, and erosion | Grazing marshes along the North Sea; Baltic and Mediterranean grasslands |
| Asia | | |
| Earlier loss of ice cover and reduced semipermanent permafrost | Invasion of southern species northward and spread of shrubs | “Tundra” wet grasslands of the Himalayas and in Siberia; semitundra wet grasslands, for example, Sanjiang Plain, northeast China |
| More frequent and intense rainfall events in south Asia | Flooding | Seasonal floodplain grasslands, for example, Mekong and Yangtze; seasonal marshes in Heilongjiang Province, northeast China |
| More frequent heatwaves | Heat stress and drought | Central Asian steppe grasslands of the Dauria ecoregion; seasonal monsoonal marshes on floodplains of the Ganges, Indus, and Brahmaputra |
| Sea level rise | Erosion and salt water intrusion | Deltaic marshes, for example, Mekong and Yangtze; Yellow Sea saline meadows, China |
| Intensification of the monsoon | Extreme floods and storm damage | Coastal grasslands behind barrier islands, for example, east coast of Sri Lanka; wet–dry floodplain grasslands of the Ganges, Indus, and Brahmaputra |
| Decreased snow cover and therefore melt in the Himalayas | Decreased water availability and more seasonal river flow and groundwater recharge | Groundwater-fed grasslands of the Himalayan terai |
| North America | | |
| Reduced snow and ice in mountains and in northern regions, earlier snow melt and reduced permafrost in the north | Altered surface and groundwater flow; and less ice and flooding in winter | Wet prairie, prairie fen, and riparian grasslands in northwest America |
| More frequent, intense floods | Extreme flooding and vegetation change to flood-tolerant species | Wet grasslands in the prairie pothole region |
| More frequent heatwaves and protracted drought (megadrought) | Heat stress, drought, and summer drying | Continental depression grasslands and prairie potholes, for example, reduced breeding wildfowl habitat |
| Sea level rise | Erosion and saline intrusion | Atlantic and Gulf coasts of America |
| Wildfires | Fire damage, smouldering peat fires, and peat loss | Wet rangelands, for example, expansion of invasive species |
| Increased severe rain events | Increased suspended sediments and diffuse pollutants in rivers | Riparian grasslands |
| Reduced river flow in continental rivers due to more evaporation, less rain, and more abstraction by humans | Penetration of coastal salt water wedge further inland | Freshwater coastal grassland and floating grasslands, for example, Mississippi River lower delta and northern Gulf Coast |
| Neotropics | | |
| Reduced snow and ice in mountains | Altered surface and groundwater flow, and less ice and flooding | Wet paramo of Central and South America; Andean grasslands; Beni savannas of the Amazon basin, Bolivia |
| More frequent and intense precipitation events in the tropics | Flash flooding and erosion along floodplains | Flood pulse grasslands; tropical wet–dry wetlands, for example, Palo Verde in western Costa Rica |
| More frequent floods | Extreme flooding and vegetation change | River floodplain ecosystems, for example, Pantanal, Brazil |
| More frequent drought | Atypical seasonal drying and loss of biodiversity | Central Chilean grasslands; savanna wet grasslands, Gran Sabana, Venezuela |

(continued)

Table 2. (continued)

| Scenario | Stressors | Examples of wet grasslands impacted |
|--|---|---|
| Wildfires | Fire damage and shift toward fire-tolerant species | Wet savanna grasslands, North Rupununi, Guyana; Amazonian grasslands |
| Greater rainy and dry season variations | Altered fire-flood patterns and loss of biodiversity | Llanos esteros grasslands, Venezuela; seasonally flooded Campos, Brazilian Parana |
| Food production, water availability for humans, and livelihoods at risk | Forage quality and quantity | Rangelands; natural (hay) grasslands; Llanos grasslands, Venezuela |
| Africa | | |
| More frequent intense precipitation events in the tropics and enhanced monsoons in west Africa | Flooding and erosion | Flood pulse grasslands and savanna, for example, Niger and Zambezi floodplains; Tana River Delta, Kenya; Nile Delta floodplain grasslands |
| Droughts | Drought stress and drying | Dambos in southern Africa; Okavango Delta, Botswana |
| Wildfires | Fire damage | Mara River basin savanna grasslands |
| Greater rainy and dry season variations | Biodiversity loss and invasion by trees in the dry season | Seasonally flooded grasslands of the Zambezi, Zambia |
| Enhanced evaporation loss from rivers and lakes | Reduced runoff and discharge | Okavango Delta; Lake Victoria papyrus grasslands |
| Food production and livelihoods at risk | Biomass and forage quality and quantity | Hand-gathered cattle forage; Mara River basin savanna grasslands |
| Oceania | | |
| Reduced snow and ice, and fewer frosts | Altered seasonal river flows | Headwater valley grasslands, New Zealand |
| More hot days and warm periods | Heatwaves and drought | Seasonal wet grasslands become intermittent |
| Less rainfall in the cool season, especially in southern Australia | Reduced water supply | Swampy meadows, for example, south-east Australia |
| Sea level rise and increased height of extreme sea level events | Saline intrusion and habitat squeeze near the coast | Coastal freshwater floodplains in Australia and New Zealand; dunal meadows; Murray River grasslands |
| Increased intensity of El Niño and extreme rainfall events | Flooding | Murray River mudgrass grasslands; wet-dry grasslands of the Northwest Territory |
| Increased rainfall in northern Australia and southern Papua New Guinea | Land-use change through water storage, dam building, and drainage | Wet grasslands converted to palm oil cultivation or crops |
| Harsher fire-weather climate and contracting winter wet season | Longer fire season and greater fire frequency | Productive grasslands damaged |

and the severity of extreme events. Key relationships are those involving (1) reduced precipitation and increased evapotranspiration under warming scenarios, leading to drying of wetlands; (2) altered precipitation patterns affecting seasonal water availability, snow melt, and the timing and extent of flooding; (3) sea level rise, storminess, and saline intrusion in coastal grasslands; and (4) intense rainfall events that generate extreme flooding. The following sections on climate warming, altered precipitation, sea level rise, and extreme events discuss the possible effects of these climate change impacts on wet grasslands and their ecology.

Climate warming

A combination of higher temperatures and decreasing rainfall predicted under many climate change scenarios is likely to exacerbate deficits in water budgets for many temperate wet grasslands through increased evaporation and evapotranspiration (Dawson et al. 2003, Acreman

et al. 2009, Thompson et al. 2009). For example, important herbaceous wetlands in East China could be threatened as rainfall decreases but evapotranspiration increases (Ramsar 2002). A model of floodplain dynamics under different climate scenarios predicts that the number of shallow flood events in the UK would decrease by up to 90% because of reductions in available water (Thompson et al. 2009). Therefore, some wet grassland species in England are expected to migrate northwards as a result of increased temperatures reducing water tables (Dawson et al. 2003), potentially resulting in the loss of dominant functional species, which may affect ecosystem processes. In western Victoria in Australia, rainfall is predicted to decrease and temperatures increase, leading to overall drier grassy wetlands that inundate less frequently, and for shorter periods. Historical average inundation was six or seven years of flooding in every decade (Casanova and Powling 2014), but in the last two decades these wetlands have only been inundated approximately four times per

decade. One consequence of fewer filling events has been to encourage a change in land use from grazing to cropping, which had significant effects on the biodiversity and ecological integrity of these wet grasslands (Casanova 2012). Reduced water supply to wet grasslands could also initiate a negative feedback loop in which these wetlands would be unable to recover, favoring a more terrestrial community (Čížková et al. 2013) and leading to changes in nutrient cycling, decomposition, soil microbes, and primary production (Öquist and Svensson 1996). In some regions, such as southeast Europe, higher temperatures and increased aridity will lead to wet grasslands becoming subhalophytic where evaporation of water causes a high concentration of salts in the soil (Eliška et al. 2013) and some Mediterranean wet grasslands could even disappear. Under drying climate scenarios, conditions will become suboptimal for wading birds, because their distribution is strongly related to surface wetness (Eglington et al. 2008).

Increased summer temperatures, longer dry seasons, and more extreme temperatures are predicted to increase the incidence of wildfires in many regions (Table 2). The extent to which fires will impact wet grasslands is debatable because many will already be damaged by drought, and burning can maintain diversity in some wetlands (Middleton 2002). However, predictions for greater seasonal climate variability suggest that wetter winters may allow intermittent wetlands to persist into the summer rather than drying back in spring, so that droughts may then make them vulnerable to wildfires. The extensive wet campos meadows of the Brazilian Parana are characterized by a diversity of herbaceous species and a highly seasonal tropical climate that leads to massive flooding and fires (Dixon et al. 2014). Greater seasonal contrasts may alter this disturbance regime and induce vegetation change, especially if more fires and less flooding encourage savanna habitat. Thus, prolonged dry seasons, especially following wet years when biomass has accumulated, could lead to a greater risk of severe fires in some tropical wet grasslands (Fidelis et al. 2013).

Altered precipitation including snow

Wet grasslands in transitional climates or with a low hydrological buffer capacity, such as those impounded by embankments or with small catchments, are likely to be especially sensitive to changed precipitation patterns. For example, prairie pothole wetlands in North America could be highly impacted by seasonal rainfall shifts during climate change due to their location between the wet east and arid west of the continent (Junk et al. 2013, Mallakpour and Villarini 2015). Moreover, wet grasslands can respond more markedly to precipitation increases than drier grasslands; Guo et al. (2012) found that humid meadow steppe productivity in China increased linearly with greater mean annual precipitation, and more so than drier steppe grasslands. Even river-fed wet grasslands that are not directly dependent upon rainfall,

such as riparian meadows and floodplain grasslands, will be susceptible to altered precipitation patterns if surface water is a dominant supply (Öquist and Svensson 1996, Brinson and Malvárez 2002).

Seasonal climate changes likely to affect some wet grasslands include the extent and duration of snow or ice cover (Table 2). For example, spring snow cover in the Northern Hemisphere is likely to decrease by up to 25% by the end of the 21st century (IPCC 2014), so that many boreal and submontane systems will have reduced or no snow in winter. Snow and (sea) ice is a controlling factor for these wet grasslands (Kont et al. 2007), influencing soil biogeochemistry, plant ecology, and grazing management. Higher snow lines in both Australia and New Zealand are likely to impact on the seasonal variation in river flow. Even if precipitation does not decrease, precipitation as rain is likely to contribute to river flow immediately, rather than seasonally as it does when it falls as snow and melts in the spring. Reduced snow cover or earlier melt will affect the flood pulse in downstream wet grasslands, diminishing its influence or forcing it earlier, with attendant negative consequences for the plants, animals, and people that depend upon predictable flooding. The Beni wet savannas of the Amazon basin in Bolivia typically have a relief of 2–6 m and 50–60% of the land floods each year between December and May as a result of high rainfall and snowmelt in the Andes (Dixon et al. 2014). Disruption to this hydrological regime will have substantial consequences for biological diversity, as the Beni wetlands are a refuge and wintering ground for many migrant waterfowl.

Sea level rise

It is estimated that 20% of coastal wetlands, which includes brackish wet grasslands, could be lost in Europe due to sea level rise (Russi et al. 2013) if they are constrained on their landward side, or starved of sediment. Wet grasslands along seas with low tidal ranges, such as the Baltic and Mediterranean, are most threatened by future sea level rise because these tend to have low relief and their constituent species are adapted to relatively stable water regimes with irregular flooding (Ward et al. 2014, 2015). Moreover, the Baltic countries of Europe will experience more ice-free seas, which may reduce protection from coastal erosion, while strong storms and surges will potentially deposit sediment further inland on depositional coasts (Ward et al. 2014). If this is the case, wetlands could prograde and lower shore wet grasslands close to the sea could benefit, especially if sea level rise is compensated by isostatic uplift (Ward et al. 2015). However, sea level rise could lead to sea shore grasslands being replaced by swamp or land recession around shallow bays, where extensive and important wet grassland landscapes currently exist (Kont et al. 2007). The saline meadows inland of the Yellow Sea, China, which are flooded at high tide (Dixon et al. 2014), could also be threatened if salinity patterns are altered or the grasslands are unable to migrate inland. In Mediterranean

countries, saline intrusion can fundamentally alter the vegetation and related biodiversity of wet grasslands fed by fresh groundwater, especially near the coast but also much further inland (Rey Benayas et al. 1998). Coastal freshwater floodplains in Australasia (particularly in southern Australia, Kakadu in northern Australia, and New Zealand) and Asia (such as the Mekong delta) are likely to experience major changes as sea level rise will inundate near-coast wetlands and estuarine systems. The grassy Kakadu wetlands in northern Australia will be squeezed between the sea and the Arnhemland escarpment (Eliot et al. 1999). In southern Australia, sea level rise, coupled with lower rainfall and less runoff in rivers and onto floodplains, will constrain freshwater wet grasslands between encroaching estuarine conditions and existing agricultural or urban land use. In general, coastal regions are highly utilized for urban development, aquaculture, and farming. It is unlikely that areas used in this way will be converted or managed to mitigate wetland loss.

Extreme climate events

Although wet grassland species possess various attributes to survive flooding (Blom and Voesenek 1996), field studies have indicated that extreme precipitation and flood events can have profound impacts on community composition. Less flood-tolerant plant species can show reduced distribution for many years following extreme flooding, in contrast to more flood-tolerant riparian species (Vervuren et al. 2003). Although vegetation abundance on floodplains does not necessarily decrease after extreme flooding (Sparks et al. 1990), diversity and species turnover can be immediately affected (Ilg et al. 2008). For wet grasslands, it seems that the magnitude and duration of extreme flood events will both be critical, potentially prompting more rapid responses than those reported from some terrestrial communities (Toogood and Joyce 2009). Berg et al. (2012) observed that winter storms and subsequent flooding affected Baltic coastal wet grassland communities much more than cutting management, including changing species dominance. Unseasonal inundation, such as summer flooding in temperate wet grasslands, is particularly problematic because it can induce plant community, soil nutrient, and biodiversity impacts, including damage to the terrestrial invertebrate fauna (Burgess et al. 1990, Benstead et al. 1999, Antheunisse and Verhoeven 2008). Moreover, prolonged flooding can kill or expel invertebrates in the soil or litter that are not adapted to extended submersion, with potentially harmful consequences for the wading birds that feed upon them (Ausden et al. 2001).

From an ecological perspective, extreme storm or flood events represent intense disturbance. Joyce (1998) compared two floodplain grassland plant communities in the UK with contrasting responses to disturbance. A flood-meadow community with a stable disturbance regime was characterized by competitive, stress-tolerant species

with belowground storage. In contrast, an inundation community intensely disturbed by flooding supported limited species richness and ruderal strategists with short life cycles and high potential growth rate (e.g., via rhizomes or stolons). The latter environment offers an insight into possible future wet grassland scenarios under climate extremes, characterized by greater variability and dynamism, and potentially more reliance on seeds and propagules (Casanova 2015). Such grasslands, consisting of fast-growing, short-lived species, have responded rapidly to experimental climate change treatments (Zavaleta et al. 2003) and are likely to be sensitive to climate events. Further evidence from Baltic coastal landscapes suggests that wet grasslands from dynamic hydrological environments respond rapidly to environmental change while diverse communities with more stable hydroperiods show resistance to perturbation (Berg et al. 2012).

The effects of heatwaves and drought on wet grasslands are not known, and will vary due to differences in soil permeability affecting moisture retention. However, as these are typically only seasonally inundated or saturated wetlands, some wet grasslands may become intermittent or even dry out completely, such as in southern Europe and southern Australia. Moreover, lower groundwater levels may increase the availability of nitrogen and phosphorus in the soil, leading to eutrophication and acidification (Van der Hoek and Braakhekke 1998). In theory, drought events could act as a disturbance and increase diversity by reducing competition in wet grasslands, but this is likely to be beneficial only in abandoned meadows and pastures, and probably offset by the damaging impacts of drought stress. Drought effects are likely to be more severe if grazing or other vegetation management continues, as this exacerbates loss of species and cover in grasslands (Archibold 1995). There is evidence from other vegetation types, such as woodland, that changes following drought and other extreme climate events may be irreversible (Allen and Breshears 1998, Holmgren et al. 2001).

Plant community responses

For wet grasslands, climate change may be expected to affect community composition by modifying dominant plant traits (i.e., adaptations to particular environmental conditions), competition, distribution, and diversity (Easterling et al. 2000, McCarty 2001, Reyer et al. 2013). Climate change could also influence communities through increased CO₂ uptake, which critically influences biomass development and grassland productivity. The following sections examine possible consequences of climate change on vegetation by focusing upon both community composition and production.

Community composition

Plant responses to climate change are complex and will modify competitive relations between species, which

may be crucial in wet grasslands where a diversity of perennial species coexist. For example, drier soils will reduce waterlogging and anoxia stress, favoring competitive species such as widespread grasses at the expense of more specialized, often rare wetland species. Elevated atmospheric CO₂ will directly stimulate photosynthesis and plant growth (the “fertilization effect”). Enhanced CO₂ could reduce the negative effects of drying or even drought (Soussana and Lüscher 2007) in a warmer climate by increasing plant water-use efficiency (Polley et al. 2013), although this crucially depends upon soil water availability in wet grasslands. Sajna et al. (2013) found that a wetland sedge (*Carex rostrata*) increased biomass under conditions of enhanced CO₂ and elevated soil water content in a central European wet meadow, perhaps because the species is well adapted to waterlogged soil and hypoxia. Elevated CO₂ could reduce diversity in wet grasslands if increased CO₂ delays senescence of the dominant plant canopy at the end of the growing season, constraining the window of light availability for late-flowering and small-statured species (Zavaleta et al. 2003).

Climate change could favor particular plant adaptations, traits, or functional groups over others, such as the ability to spread laterally and rapidly using stolons following gap creation by storms (Berg et al. 2012). Examples of informative functional groups in wet grasslands include legumes, herbs or forbs (i.e., all nonwoody flowering species not including grasses), competitors and ruderals, and annuals and perennials (Toogood et al. 2008, Toogood and Joyce 2009). Legumes, for example, can facilitate the flowering of other grassland species under both extreme drought and precipitation (Jentsch et al. 2009). Forbs might be particularly sensitive to climate changes (Zavaleta et al. 2003) and often comprise most of the plant diversity in wet grasslands. Studies on keystone components of wet grassland communities, such as dominant grasses, robust sedges, or herbs, or rare species of nature conservation importance, would provide valuable information on community functioning and management in the face of climate change.

The distribution of wet grassland plant species will likely undergo contraction at the margins of their climate range due to limited dispersal opportunities and/or the pace of climate change. In Great Britain and Ireland, for example, Berry et al. (2002) suggested that species at the southern limit of their distribution will be reduced by climate warming, such as flat sedge (*Blasmus rufus*), which could be progressively lost from Wales, northern England, and Scotland. However, species at their northern range margin could expand their distribution northwards, including greater burnet (*Sanguisorba officinalis*), a dominant forb in the rare English flood-meadow plant community. Some wet grassland species are expected to migrate northwards as a result of increased temperatures reducing water tables (Dawson et al. 2003), perhaps into other wetlands. Greater water deficits in temperate

regions could lead to reduced climate suitability for various peat-based wet grassland plant species in particular, because these tend to have narrow hydrological niches (Newbold and Mountford 1997).

C₄ grasses could benefit under warming scenarios because these grow at higher temperatures (optimum 30–35°C), absorb CO₂ more efficiently, and have greater water-use efficiency than C₃ grasses (t’ Mannetje 2007). The distribution of C₄ species is related to winter temperatures because these are impaired by the cold (Archibold 1995). Thus, warmer winters may be especially important for their expansion into and within temperate wet grasslands. C₄ grasses also have a greater production capacity than C₃ grasses. However, the forage value is less because of a lower proportion of digestible tissues, leading to negative implications for agricultural management and livelihoods should C₄ species expand in wet grasslands. Increases in climate extremes may suppress C₃ species and promote C₄ species, including weeds, due to faster migration rates, greater seed production, and rapid maturity (White et al. 2001). C₄ grass species that could conceivably spread within wet grasslands in a climate change future include many within the Panicoideae subfamily, which prefer humid, wet environments. For example, *Chrysopogon gryllus* and *Dichanthium ischaemum* are already widespread in humid central and southern Europe, and could increase in abundance (t’ Mannetje 2007) and move northwards. Bermuda grass (*Cynodon dactylon*), which like many C₄ grasses is a common constituent of many tropical wet grasslands, could also be favored by climate change. This species is already a widespread invader of temperate grasslands and coexists with C₃ species as a non-native in Pampean grasslands in Argentina (Omacini et al. 1995). Other traits that may be favored in the future include those related to fire tolerance, such as storing energy in roots to aid recovery, if the incidence of wildfires increases as predicted for some wet grassland systems. Fires in winter or early spring encourage C₄ grasses at the expense of C₃ grasses in some South American grasslands (Overbeck et al. 2007).

Droughts, storms, floods, and fires tend to open the vegetation canopy and create gaps, suitable for colonization by non-native plant species and those with invasive traits. Wet grasslands are not especially prone to invasion, but there are a number of examples where invasion has followed deliberate introduction or disturbance, often through farming activities such as intensive cattle grazing. The flood-tolerant koronivia grass (*Brachiaria humidicola*) was introduced from Africa into the Pantanal of South America where ranchers have helped distribute it across the region because they believe it can improve pasture quality (Junk et al. 2013). Similarly, the Pampean grasslands of Argentina contain numerous exotic plant species, especially grasses, playing a defining role in their vegetation dynamics (Facelli et al. 1989, Omacini et al. 1995). Rychnovská et al. (1994) report that

an abandoned meadow in central Europe was infested by the weed *Epilobium ciliatum* after mowing opened the canopy to colonization. In North America, problems with invasive species in restored wet grasslands are common, especially sedge meadows and wet prairies where rehabilitation is severely constrained by the dominance of aggressive species such as reed canary grass (*Phalaris arundinacea*), which preempts the establishment of native vegetation (Adams and Galatowitsch 2006). Thus, the increasing frequency and magnitude of extreme events that typify climate change scenarios are likely to provide greater opportunities for invasive species to colonize and dominate wet grasslands in the future.

Production

Primary productivity is dependent upon an interacting suite of climatic factors, including precipitation, temperature, and carbon and nutrient availability, so the precise outcome of climate change for wet grassland regions is difficult to determine. Biomass accumulation is driven by seasonality so climate changes will affect carbon stocks and storage, such as in the dry season in tropical wet grasslands. In markedly seasonal wet grassland ecosystems, climate change could alter biomass provision as plants allocate resources below ground during the dry season and reallocate resources above ground to produce new leaves, shoots, and reproductive organs when the rainy season begins (Fidelis et al. 2013). Warmer climates will generally extend the growing season and enhance productivity, as higher temperatures accelerate plant growth, especially of grasses (Kudernatsch et al. 2008). For example, agricultural productivity could be increased in northern Asia (Ramsar 2002) and in northern Europe due to rises in temperature and CO₂ (t' Mannetje 2007). Warming could also accelerate senescence of the early-season grass canopy, increasing subsequent resource availability (Zavaleta et al. 2003). Increased annual precipitation can also enhance grassland productivity (Guo et al. 2012) although wet grasslands in humid regions may not respond if these are already at maximal production (Yang et al. 2008). Moreover, enhanced productivity under increased precipitation in certain regions (Table 2; Ramsar 2002) will alter vegetation composition and structure, potentially reducing nesting and feeding opportunities for birds if the sward becomes too dense or tall, especially early in the season. Excessive precipitation or floods could shorten flowering duration of grassland species (Jentsch et al. 2009) and reduce production by damaging vegetation or inducing community or physiological changes, such as in height, cover, biomass, and species composition.

Human implications

Climate change effects on wet grasslands threaten human livelihoods in many regions (Table 2) because these wetlands are a vital source of income for millions of

people who use their agricultural and other ecosystem services. The following section highlights interactions between climate change and humans in wet grasslands, particularly insecurities over agricultural grassland productivity and management.

Climate change will fundamentally affect the availability of biomass for forage in wet grasslands. For example, altered river hydrology will affect the quality of grazing of the Sudd grasslands in the Sahel, Africa, and the number of cattle that can be supported, as well as other ecosystem services such as fish production (Junk et al. 2013). Productive grasslands in northern China have less annual available herbage and carrying capacity for livestock under the warmer and drier climate of recent decades (Qian et al. 2012). The annual hay yield decreased by up to 50% under reduced experimental precipitation in floodplain meadows along the Rhine River, Germany, due to less productivity in the second harvest (Ludewig et al. 2015). Also, elevated atmospheric CO₂ concentration may alter the feeding value of forage, for example, by affecting the crude protein content and C:N ratio (Soussana and Lüscher 2007). Even a relatively simple projection of warmer and wetter springs would produce increased biomass early in the growing season while drier falls would reduce late season biomass (Ma et al. 2010), necessitating adaptations by farmers and conservation managers in respect to (earlier) cutting dates and (earlier, lighter) grazing regimes. Ironically, this early-season scenario is reminiscent of the traditional water meadow system, which has largely fallen out of favor, in which farmers utilized river water to irrigate their grassland in spring using a network of drainage channels to provide an "early bite" for livestock (Sheail 1971).

A probable outcome of climate change is that agricultural production in many regions, such as southern Europe, may become less secure because of water shortages (t' Mannetje 2007) and extreme events. In Europe, low-intensity agricultural management has been practiced in wet grasslands for hundreds or thousands of years as a vital part of the farm economy, coincidentally producing highly valued and protected cultural landscapes such as the English flood meadows, subalpine wet pastures and central European wet meadows (Joyce and Wade 1998). Reduced or unreliable production due to climate change represents a challenge to the vestiges of these agri-environmental systems and their cultural heritage, as these are already considered to be of marginal economic utility (Joyce 2014). The consequence could be the withdrawal of grazing and cutting management from wet grasslands. This withdrawal would soon alter the ecology and then lead to the loss of sites that depend upon regular extensive agricultural management to maintain their characteristic biodiversity and ecosystem services, including many remaining in Europe and North America. Studies of wet grassland abandonment reveal that plant community changes have been measured within three years, including species elimination as competitors expand and woody

plants encroach (Joyce 2014). Little is known about the effects of abandonment on other important components of biodiversity, although invertebrates may eventually decline in unmanaged wet grasslands (Joyce 2014).

Climate change will interact with other human pressures, such as land use and water extraction, such that stakeholder responses will be vital for wetlands, potentially exacerbating or moderating impacts. For example, intensifying droughts could lead to negative feedback for floodplain grasslands if dry conditions provoke greater water extraction (e.g., for irrigation and municipal purposes) and so reduce water availability for wetlands. Intensive agricultural management has already led to severe losses of wet grasslands and their biodiversity (Joyce 2014), and climate change represents an emerging threat to the relatively few diverse sites that have escaped agricultural intensification, for example, in Europe, Australia, and North America. Agricultural intensification could also compound climate change effects as the process often incorporates flood defences and/or land drainage, as well as the use of inorganic fertilizers, herbicides, and pesticides. Ultimately, such reclaimed areas may be overgrazed or cultivated for crops, reducing their ability to buffer the impacts of climate change. Agricultural grasslands are more sensitive to climatic variability than natural landscapes because drainage and grazing will typically reduce water infiltration and increase surface runoff and pollutant loading (Erwin 2009, Zacharias and Zamparas 2010). Examples of interactions between climate change and actions of stakeholders that could have detrimental implications for wet grasslands can be found in Australia and South America. In northern Australia, increased rainfall and government policy may lead to more dam building, water storage, and drainage schemes, which could facilitate the conversion of wet grasslands into palm oil plantations, or other forms of cultivation (Finlayson et al. 2013). In South America, biofuel demand has increased

the pressure on wet grasslands of the Brazilian cerrado and Argentinian chaco (Junk et al. 2013).

Climate Mitigation and Adaptation

Mitigation here refers to reducing the effects of climate change, while adaptation describes modifications to policies and practices in response to expected climate change. The most successful initiatives for wet grasslands are likely to focus upon hydrology, landscape management, and restoration or creation, and integrate planning, monitoring, and practices (Table 3). Interdisciplinary schemes that incorporate the environmental services that wet grasslands provide, and initiatives that promote hydrological and ecological resilience to buffer climate change effects, are emphasized in the following section.

Integration of climate change mitigation and adaptation objectives within environmental, and also agricultural, policies would be particularly beneficial for wet grasslands. Agri-environment schemes are key instruments because they have been implemented in many countries and generally offer financial incentives to encourage the types of low-intensity, low-input agriculture that produces the most diverse and important wet grasslands for nature conservation. Moreover, these schemes can adopt a landscape, catchment, or whole-farm approach and integrate conservation objectives (such as raising water levels or delayed cutting dates to protect nesting birds) with providing a viable income (Glaves 1998). Such schemes could be adapted to reflect the mitigation priorities of a climate change future (Table 3), for example, focusing upon hydrological management and wet grassland restoration or creation to provide ecosystem services such as carbon sequestration and groundwater recharge. Farmers could also be offered incentives to use hardy, often traditional, breeds of livestock adapted to climate extremes, or even consider

Table 3. Mitigation and adaptation initiatives (partly after Ramsar 2002) for wet grasslands to combat climate change.

| Initiative category | Mitigation | Adaptation |
|-------------------------|---|--|
| Hydrology | Store water at peak periods to counteract high evaporation rates Irrigate drought-afflicted sites Lower the ground surface to facilitate inundation | Address pressures on freshwater supply Expand water management plans |
| Landscape | Desalinate sea water to provide fresh water Provide corridors and networks of sites to promote resilience Assist species movement using seed and hay transfer Acquire inland buffer zones to mitigate sea level rise | Set back flood and coastal defences and infrastructure Restore and create wet grasslands away from vulnerable coasts |
| Planning and monitoring | Monitor and control invasive species Retain seed banks Protect climate-vulnerable species | Focus on climate-resilient sites and ecosystems Modify agri-environment schemes to support climate mitigation Utilize climate-resilient forage species and livestock breeds Manipulate disturbance regimes, including cutting dates and grazing |

novel grazers for wet grasslands such as water buffalo (Wiegand and Krawczynski 2010). The unique properties of wet grasslands as transitional ecosystems with characteristic vegetation dependent upon human intervention make them ideal candidates to trial such “agri-climate” schemes. An example could be the use of riparian grasslands to buffer impacts of suspended sediments and pollution reaching rivers due to increased incidence of severe rain events.

Generally, there will be a need for a greater focus on hydrological functioning, monitoring, and management of wet grasslands in a climate change future (Table 3). Water management plans and water budgeting should therefore assume more importance and widespread use. The design and maintenance of water control infrastructure, such as drainage channels, bunds, levees, and sluices, will become even more critical, as it can be used to drain water from grasslands experiencing extreme or unseasonal floods or to store water and irrigate dry wetlands. However, active water-level monitoring will be required in order to allow rapid adjustments to be made, especially due to extreme climate events. It will be important to maintain inundation in many wet grasslands, as flooding can import seeds or other propagules and also create gaps in the sward to facilitate establishment. For example, a rapid restoration of abandoned alluvial meadows in the Czech Republic was likely due to flood-borne seeds penetrating the dense vegetation from sources nearby (Prach et al. 1996). If flooding is absent, raising water levels and reinstating inundation can be effective for rehabilitating wet grasslands (Toogood and Joyce 2009). Diverting or pumping water from rivers, reservoirs, or groundwater is likely to be required for some sites, provided there is sufficient water and it is of suitable quality. Rehabilitating drought-affected wet grasslands could include water storage during the rainy season, for example, by reservoir construction or using natural water bodies, so that this can be used to irrigate the wetland during dry periods (Table 3). In severe cases where wet grasslands may be subject to extended drying and persistent low water levels, lowering the grassland surface may be an option, as has been attempted in western Europe using turf and topsoil stripping (Van der Hoek and Braakhekke 1998, Klimkowska et al. 2007).

Nature conservation will need to adapt to climate change by prioritising the protection and management of resilient wetlands and adopting more flexible approaches to management. Resilient wet grasslands are likely to be those with a diversity of plant functional traits that enhance capacity to resist or tolerate drought or prolonged inundation (Brotherton and Joyce 2015). Conservation management should embrace a more flexible rather than overly prescriptive approach given the increasing climate variability forecast. Cutting dates and livestock grazing will need to vary in relation to disturbance events (Table 3), notably flooding, and stress such as drought, in order to maintain a dynamic equilibrium for optimal diversity and production. Management will

need to be adaptive, and will require flexibility over stocking densities and perhaps greater use of rotational grazing. Cutting dates for conserving wet meadows will need to accommodate changed reproductive phenology under future climates, for example, brought forward where warming advances maturation so that biomass does not accumulate and a diversity of species can be sustained.

Restoration and creation of wet grasslands to combat climate change should attempt to generate a resilient network of sites capable of facilitating species survival at the landscape or regional scale (Table 3). Although isolated sites can act as refugia or protect against invasion by harmful species, small sites are likely to be more vulnerable to the detrimental effects of extreme climate events. Therefore, it is probable that the scale of restoration projects will need to increase to consider entire catchments or substantial landscapes, with an emphasis on restoring natural functions (e.g., water storage) and facilitating movement of species (Table 3). For example, wet grasslands could be restored along floodplains so that the river system can function as a corridor (Casanova 2015). Restoration cannot often rely upon the seed bank, however, because many wet grassland seeds are rather transient (Jensen 1998, Falińska 2000). Also, many typical wet grassland plants, such as sedges, have low colonization efficiency due to limited dispersal ability or viability following drying (Kettenring and Galatowitsch 2011). Unless a local species pool is readily available, with a suitable natural vector and receptor environment, human intervention may be needed for restoration. Isolated sites and constrained plant species or guilds (e.g., meadow perennials, rare species) may require particular efforts to restore them. Seed transfer, with topsoil removal and careful rewetting, has been recommended to restore severely degraded fen meadows (Klimkowska et al. 2007) while cut hay has been moved between sites to restore floodplain grasslands (Manchester et al. 1998). Such techniques could also be used to assist the migration of species threatened by changing climate. Plant traits can be used in restoration or creation schemes to design more robust wet grassland systems, capable of adapting to future climate conditions.

Conclusions

Wet grasslands are at risk from predicted climate changes, yet these wetlands provide vital ecosystem services, biodiversity, and agricultural and cultural value. These ecosystems have a role to play in mediating some consequences of climate change, especially wetlands that are functionally diverse. For climate change planning, there is a lack of information and focus on wet grasslands in wetland inventories and mapping, especially for Africa and the Neotropics, partly due to difficulties to accurately identify and define these systems. It is evident, however, that some of the most important wet grassland systems in

the world are threatened by climate change, including those in the prairie region of North America, Baltic and North Sea coastal wetlands in Europe, the South American flooding pampas, some of the largest flood pulse grasslands in Africa, and extensive deltaic marshes in Asia and Australia. Consequently, the livelihoods of millions of people will be affected as climate changes and wet grassland function is threatened.

The ecology of wet grasslands will be fundamentally modified by climate change, especially by altering hydrology and exposure to extreme climate events. Scenarios for future wet grasslands under climate change projections suggest that these wetlands would become characterized by more variable hydrology, with more intense disturbance events such as storms and floods. Wetland productivity would also become more variable, with increased susceptibility to invasion by woody, non-native, and C_4 species, and possibly reduced biodiversity. Consequently, the conservation status and agricultural value of wet grasslands would be compromised.

Adaptive management strategies for wet grasslands will be needed to combat climate change. Conservation and restoration should focus on resilient sites with diverse functional traits and natural ecosystem processes. Management practices will need to integrate climate effects, for example, by adopting responsive water management, variable cutting dates, and flexible grazing plans; otherwise, there is a risk that economically marginal wet grasslands will be abandoned (Joyce 2014). Conservation and management planning should ideally be on a regional or landscape scale based on expected specific climate changes, especially water availability, and adequate monitoring. Thus, flexible and resilient practices will be required to conserve the biodiversity and agricultural production of wet grasslands in a climate change future.

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