Fire on the water
A review of the effect of burning on wetlands

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1 Introduction

1.1 Background and purpose to the document

Burning of herbaceous (non-woody) wetlands in order to enhance their wildlife value is carried out widely in the US, and in the 1980s and early 1990s there were several investigations of the biogeochemical consequences of these fires (e.g. Faulkner and de la Cruz, 1982; Wilbur and Christensen, 1983; and Schmalzer and Hinkle, 1992). Since then, however, there has been little specific research on the effects of burning on wetland functioning. Smith et al. (2001) highlight that compared with terrestrial systems, there have been few studies of fire on wetland functioning. This is despite the fact that wetland burning has potentially wide-ranging environmental consequences, from the most local scale to broader scales of catchments, and ultimately to the global scale, where vegetation burning effects the emissions of compounds that modify atmospheric composition and ultimately modifies weather and climate (Langmann et al., 2009). Furthermore, the long-term effects of fire on soil, water and nutrients generally in southern Africa is not well understood (Mills and Fey, 2004).

With growing concern over deteriorating water quality, both globally and in South Africa, and emissions contributing to global climate change, there is a need to better understand the effect of wetland fires on biogeochemical cycling. Besides the review of Kotze and Breen (1994), there appears to have been little attempt to synthesise current understanding of the effects of burning on wetlands. An important need was therefore identified to undertake such a synthesis. This was further prompted by the need of Mondi, a large forestry company in South Africa, for an informed basis on which to assess the environmental health of their wetlands. Mondi's herbaceous wetlands are subject to a wide range of fire regimes (some have been subjected to long term annual burning at the beginning of the dry season, while others have been subject to the suppression of fire).

A fire regime is defined as the typical combination of frequency, season, intensity and type of fires that characterize an area (Gill, 1975; van Wilgen, 2009). A fire regime results from a series of individual fire events, and the response of ecosystems to fire depends not only on the effects of a single fire, but also on the legacies inherited from previous fires (Gill, 1975; van Wilgen, 2009). However, ecosystem managers often focus on, and respond to, fires as events, e.g. resulting in management decisions being mainly around suppressing and containing unplanned fires, or predicting conditions which are suitable for a prescribed burn (Gill et al., 2002; van Wilgen, 2009). van Wilgen (2009) emphasizes the importance of moving beyond the management of fires as isolated events, and towards the concept of managing fire regimes.

The purpose of this document is to review the effect of wetland burning on the structure, composition and functioning of wetlands[1]. In the past, the main focus has been on the effects of burning on fauna, and therefore this review deals specifically with the effects of fire on vegetation, hydrology and biogeochmical cycling[2]. Geographically, the focus is particularly on mesic grasslands, which is where most of the forest plantations in South Africa are concentrated. The scope of the review recognizes that wetlands are generally connected strongly with other components of the broader catchment, and therefore cannot be seen in isolation of the burning of their upstream catchments. An accompanying document (Kotze, 2010) provides guidelines for the burning of wetlands within timber forestry estates, drawing on the findings of this review.

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[1] Although fairly comprehensive, it does not provide an exhaustive review of the literature relating to wetlands and burning

[2] For a review of the effect of burning on wetland dependent fauna see Kotze and Breen (1994), for which it is recognized that there is a need for updating.

1.2 Fire as a force shaping South Africa's mesic grassland and wetland vegetation

Fire is a significant evolutionary force, and has helped to shape global biome distribution and maintain the structure and function of fire-prone ecosystems (including wetlands) for hundreds of millions of years, and fire is one of the first tools that humans used to re-shape our world (Bond and Keeley, 2005).

In the mesic grasslands of South Africa, where fuel loads are generally high and the lightening strike rates amongst the highest in South Africa, the vegetation, including wetlands, evolved under a regime of frequent fires. Thus, one finds that the wetlands in these areas are overwhelmingly dominated by herbaceous, fire-adapted plants, mainly sedges and grasses. Humans have been responsible for further increasing the frequency of fires, and evidence suggests that hominids were using fire intentionally since at least 1.5 million years ago in southern Africa (Brain and Sillen, 1988; Schülze, 1990; Bond, 1997).

Although climate sets the limits to plant growth, fire and herbivores determine the pattern of the vegetation (Bond, 1997). In fact, fire can be seen as a large generalist herbivore, sometimes competing, sometimes replacing and sometimes facilitating vertebrate herbivory (Bond, 1997; Bond and Keeley, 2005). Although usually treated as a disturbance, fire differs from other disturbances, such as cyclones or floods, in that it feeds on complex organic molecules (as do herbivores) and converts them to organic and mineral products. Fire differs from herbivory in that it regularly consumes dead and living material and, with no protein needed for its growth, has broad "dietary preferences", and plants that are inedible for herbivores commonly fuel fires (Bond and Keeley, 2005).

Fire is only possible where there is sufficient fuel to burn, and is most frequent in the more humid (mesic) parts of South Africa, predominantly 'sourveld', where fuel is continuous and where herbivore impact is generally minor. Fire is much rarer in the arid west and interior of South Africa and in the arid to semi-arid savannas, predominantly 'sweetveld', where offtake by herbivores generally leaves little fuel to burn. Only in exceptionally high rainfall years when grass growth exceeds grazing capacity is fire possible in these ecosystems (Bond, 1997).

1.3 Some positive and negative effects of burning wetlands

Burning of herbaceous wetlands has several potential positive effects, including: (1) maintaining native fauna and flora; (2) assisting in alien plant control; (3) increasing plant productivity by removing litter; (4) improving the habitat value for wetland dependent species (e.g., flufftail species) (it is widely used as a tool for wildlife management) and (5) improving grazing value.

However, burning may also have several potential negative effects: (1) the young of wetland-dependent species, e.g. wattled crane (*Grus carunculata*), are vulnerable to the direct effects of heat and asphyxiation; (2) fire may contribute to increased levels of erosion, especially where burning is every year and attracts high concentrations of grazing animals; (3) burning at the beginning of the dry season in wetlands subject to severe frosts results in an absence of loose surface and standing plant litter for the entire winter, thereby increasing the evaporative loss of water (particularly from permanently wet areas) and reducing the cover for wetland-dependent fauna; and (4) soil organic matter (SOM) levels may be depleted when the burning frequency is high, particularly if burning results in prolonged exposure of the soil, as described in (3).

1.4 Determinants of wetland fires

Several key factors affect the type, nature and severity of fire, including the following:

- State of the potentially combustible material (fuel load, proportion of green vs. dead material)
- Weather conditions at the time of the fire (temperature, humidity, wind-speed)
- Time of year of the burn
- The hydrological conditions in the wetland at the time of the burn

Plants vary greatly in their susceptibility to fire. The moisture content of plants is one of the chief determinants of flammability – dead plant material generally has the lowest moisture content. Leaves that are well defended against herbivores through high fibre content and high specific weight will generally burn more easily because of their lower moisture content and because the litter that they produce decomposes more slowly (Bond, 1997). This applies to many herbaceous wetland areas, where mature growth typically has a high fibre content. The cell wall component of *Typha domingensis*, for example, has been shown to comprise over 70% of the dry weight of the plant (Howard-Williams and Thomson, 1985). The shape, size and arrangement of plant parts also influence flammability. Small-sized plant parts (e.g. narrow leaves) have a large surface area to volume ratio, which increases flammability. Oils, fats, waxes and turpenes further increase flammability. Tussock grasses generally provide excellent fuels, because of their high surface area to volume ratio and low moisture content when cured by frost or winter drought (Bond, 1997).

Two main types of wetland fire occur in wetlands: surface fires and sub-surface (ground) fires. In surface fires, which are the most common and least severe, only the above-ground plant parts are burnt[3]. Sub-surface fires consume below-ground plant parts as well as SOM, and typically take place in wetlands with organic (peat) soils. They may occur naturally during particularly dry years and be facilitated by the human-induced drying out of a wetland. Page et al. (2002), for example, highlight that peat fires are most prevalent in Indonesian peat forests during El Niño periods (which delay the Monsoon season and result in very dry conditions) and, although under natural circumstances peat fires are very rare, the incidence of such fires is greatly increased by artificial drainage and logging.

The incidence, intensity and pattern of fire may be influenced by the particular habitats present in a wetland. For example, in the Everglades wetlands, Florida, fires were less patchy and more intense, in higher elevation plant communities (e.g., high pine savannas) than in lower elevation communities (e.g., long-hydroperiod prairies) probably because of drier conditions and more pyrogenic fuels (Slocum et al., 2003). Within a herbaceous wetland, initially the greater the level of wetness, generally the greater the level of biomass production, and therefore the higher the fuel load. However, with high levels of flooding, particularly if areas of open water are present (even if very small), fire is suppressed. It is not surprising, therefore, that in an assessment of the relationship between flooding and fire in the Okavango Swamps wetland, Heinl et al. (2007) found that there was a high correlation between flood frequency and fire frequency. Areas of the wetland that are inundated about every second year show the highest fire frequency, with a mean fire return interval of about 5 years. Both drier and wetter areas of the wetland showed mean fire return intervals of about 7–8 years (Heinl et al., 2007).

Given the influence of hydrology over both surface and sub-surface fires, it would be anticipated that the fire regime of a wetland may be influenced indirectly by human impacts on hydrology. For example

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[3] A third type of fire, typically taking place in shifting agriculture systems, is where sub-surface plant material (mainly rhizomes) is burnt on the soil surface. Here, soil is tilled, the rhizomes are removed from the soil, allowed to dry out and then burnt on the soil surface.

Smith et al. (2003) describe how the frequency and severity of fires increased when large sections of the Florida Everglades marsh were completely or partially isolated by a network of canals and dykes. Nutrient enrichment from both soil oxidation and agricultural runoff further increased vegetation productivity, thereby generating more fuel. An index of peat fire risk was calculated for the Florida Everglades marsh by Smith et al. (2003) based on a number of biophysical variables (e.g. soil type, and vegetation type) and weightings were assigned to each variable relative to their importance for creating conditions favourable for peat fire.

2 Impacts of burning on wetland structure and functioning

The impacts of burning on wetland structure and functioning are considered in terms of the following main components[4]:

- Soil biogeochemical cycling
- SOM matter levels
- Catchment hydrology
- Wetland vegetation structure and composition

In all of these components, fire has primary effects which take place during the fire itself (e.g. combustion of plant material) and secondary effects (e.g. a change in the soil pH as a result of the ash). Although dealt with in separate sections, the hydrological and biogeochemical effects of burning are particularly closely inter-related (Figure 2.1). Further close connections exist between these components and the vegetation and fauna of the wetland (e.g. the fire-induced increased availability of nutrients may be to the disadvantage of plant species that are especially adapted to low nutrient conditions).

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[4] The effects of emissions associated with burning on global climate is dealt with only briefly as part of the component on biogeochemical cycling. It is recognized that there is a need to better develop this component in its own right given the immense threat to the environment that is posed by global climate change.

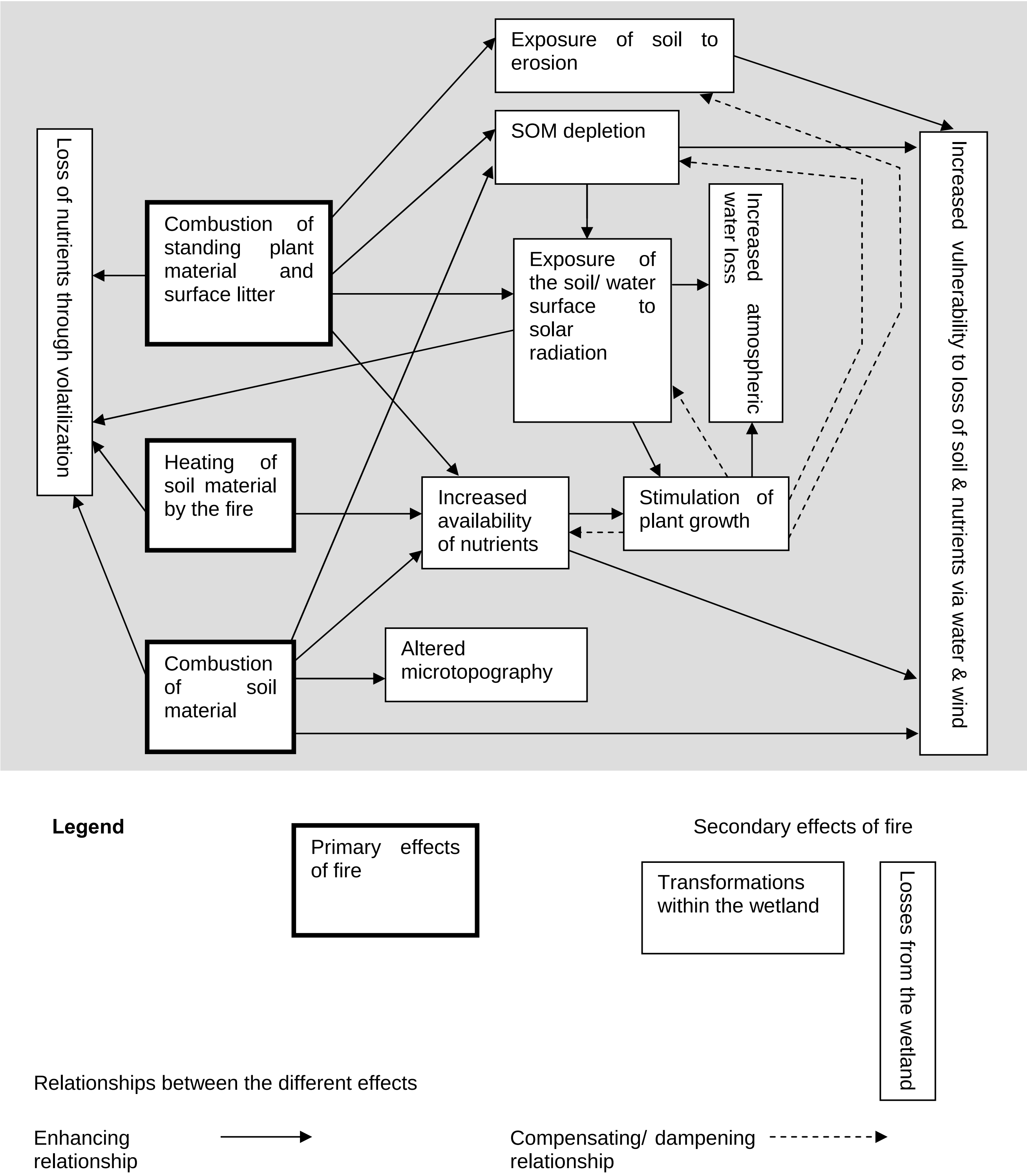

Figure 2.1: A conceptual diagramme of the inter-related biogeochemical and hydrological effects of wetland burning. (The effect that burning has in promoting soil crusting and reducing infiltration is not common in mesic grasslands [characteristically occurring in drier areas with dispersive soils] and is therefore not represented in the figure).

2.1 Effects of burning on soil biogeochemical cycling

2.1.1 Effects of burning on nutrient availability in the soil

The following general effects of burning on nutrient availability were revealed by Faulkner and de la Cruz (1982), Wilbur and Christensen (1983) and Schmalzer and Hinkle (1992).

- Soil pH increases immediately post-burn, but returns to pre-burn levels within a month or so.

- Ca, Mg, K and phosphates all increase in availability in the first month, and these increases persist for several months, sometimes for over a year.

- There is little discernable effect of fire on nitrogen levels in the soil. The concentrations of the different N-species showed marked changes during the course of the year, with both the burnt and unburnt treatments generally showing similar patterns. These patterns were more as a result of changing seasons and water tables than as a result of the fire itself.

The general effect that ash has in rapidly increasing soil pH and plant-available nutrient levels in a variety of ecosystems has been widely demonstrated, e.g. Strømgaard (1984b), Ohno (1992), Giardina et al., (2000) and Park et al (2004). The nutrient content of ash depends on several factors, including the intensity of the fire and the nature of the vegetation, e.g. Qian et al. (2009) found that it declined with increasing fire temperature and was higher in *Cladium jamaicense* ash than in *Typha domingensis* ash.

Also influencing the outcome of fire on the availability of ash-borne nutrients, is the fate of the ash from the fire (i.e. does most of the ash remain in the burnt wetland or is most of it removed from the wetland?). Retention of ash-borne nutrients in marsh sediments after a fire may be largely a function of meteorological factors such as precipitation and wind, but is also influenced by topography of the marsh (Faulkner and de la Cruz, 1982). White and Grossman (1972) showed that a decline in (NH4) OAc-extractable cations in annually burnt plots in the highveld grasslands was directly related to the rainfall in the month following the burn, and they concluded that the decline in nutrient status was due to the removal of ash by surface runoff. The removal of ash (and the nutrients therein) by surface runoff has been reported by several workers in other biomes, e.g. for Mediterranean shrublands by Gimeno-Garcia et al. (2000). It is important to add, that if wetlands are depositional sites in a landscape that is burnt overall then fire across this landscape (as opposed to in the wetland only) may result in the net accumulation of nutrients in the wetland, as upslope ash is washed out of the surrounding non-wetland areas and deposited in the wetland.

In addition to the inputs from ash, the increased pH that results from the ash has been widely shown to further increase the availability of P in acidic soils (Sanchez, 1976). Furthermore, the heating of soils may also convert some nutrients already present in the soil from an unavailable form into an available form (Box 1). For example, the dramatic increase in extractable P observed by Faulkner and de la Cruz (1982) following a burn could not solely be attributed to ash from the burnt standing crop, which had inherently very low P levels prior to burning. Thus, Faulkner and de la Cruz (1982) suggest that P release from sediments is likely to have occurred through the heating of the soil by the fire. Giardina et al. (2000) report that soil heating may, in fact, have a larger influence on soil P (and N) availability than the direct inputs of the ash to a savanna system.

Box 1: The availability of nutrients present in the nutrient pool
For each nutrient required for plant growth, a "pool" is present in the soil, with the size of this pool varying greatly from one soil to the next. Some soils are inherently rich in particular nutrients (i.e. the pool is large), while others are inherently poor (i.e. the pool is small). It is important to also recognize that from a plant-growth perspective, any given nutrient (e.g. N) is present in two main sub-pools, the first pool is readily available to plants and the second is unavailable to plants. Several factors (e.g. pH and temperature) may affect how nutrients are moved between these two sub-pools, and these factors will vary according to the particular nutrient. Nutrients may be unavailable because they are bound tightly with other minerals as precipitates (e.g. under low pH, P is precipitated as Al and Fe phosphates) or because they are present within organic material. By changing the conditions of the soil, nutrients may be moved between the two sub-pools. For example, if the pH is increased in a very acidic soil (i.e. a soil with a low pH) some of the precipitated P will be made available. Or, to give another example, if the oxygen content of the soil is increased then this will increase the rate of decomposition of organic material, which in turn will increase the amount of nutrients such as N, P and K in the available pool.

Fires in wetlands and other ecosystems may play an important role in moving nutrients between the unavailable and the available pools. The burning of organic matter acts like decomposition to transfer nutrients from the unavailable pool to the available pool, except that this is far more rapid than decomposition, and therefore the nutrients become more immediately available to plants.

Although the conversion of nutrients into a more plant-available form has positive implications for plant growth, it also renders the nutrients more vulnerable to loss through leaching (particularly for N and K, but much less for P). This has particular relevance to wetlands with open drainage which are subject to high levels of lateral water movement. (However, it is important to note that no studies could be located documenting increased loss of nutrients through leaching as a result of a surface fire).

Fire is responsible for large losses of N to the atmosphere from the combusted material as a result of volatilization (Kleinman et al., 1996) (see Section 2.1.2). Despite these losses, significant amounts of plant-available N may still remain in the ash (Strømgaard, 1984b; Giardina et al., 2000). However, in the studies of Faulkner and de la Cruz (1982), Wilbur and Christensen (1983) and Schmalzer and Hinkle (1992) these amounts of nitrogen appear to have been insufficient to be detected in the soil analyses undertaken.

The general biogeochemical effects of fire described in the above studies were observed in surface fires. Similar, but more intense effects have been described for sub-surface fires, given that the greater the fire intensity, generally the greater the effect on soil nutrients (de Ronde, 1990). For example, burning of organic soils may be the catalyst for rapid alterations in the bioavailability and solubility of P. Prior to soil fires, soil P pools were 88% organic P and 12% inorganic P, shifting to 49% organic P and 51% inorganic P measured after a soil fire (Leeds et al., 2009) which may result in corresponding shifts in vegetation composition (as described in Section 2.4). In the Okavango delta, sub-surface fires in desiccated papyrus peat rapidly release retained nutrients, and facilitate the conversion of a declining permanent wetland area to a seasonally inundated floodplain or mixed terrestrial/aquatic habitat (Ellery et al. 1989).

A comparison of the effect of a surface and a sub-surface fire on the availability of nutrients was investigated by Smith et al. (2001), showing that surface fire had less effect on nutrient concentrations (see Table 2.1) and plant growth than sub-surface fires. In fact, seedlings grown in surface burned soils generally displayed lower growth than those from non-burned soils. One possible explanation given by Smith et al. (2001) is that surface-burned soils cannot initially support the growth and development of symbiotic mycorrhizae, which had been destroyed or severely depleted during burning. As such, seedlings growing in surface-burned soils might see no significant increase in P availability and at the same time experience reduced mycorrhizae development. In a series of smouldering experiments with organic soils, Rein (2008) showed that the temperature-time distribution inside and at the edges of the burned layers far exceeded that employed in sterilization methods used to kill microorganisms.

Table 2.1: Mean bulk densities and nutrient concentrations in the 0–10 cm layer (from Smith et al. 2001)

Burn treatment	**Bulk density (g/cm^3)**	**Total nitrogen (µg/cm^3)**	**Total carbon (µg/cm^3)**	**Total phosphorus (µg/cm^3)**	**Inorganic phosphorus (Pi) (µg/cm^3)**
Sub-surface burn	0.40	6 145	81 383	132	13.11
Surface burn	0.31	7 062	95 311	133	6.44
Non burn	0.30	8 785	106 831	125	5.90

In sub-surface fires, it seems that increased Pi more than compensates for N reduction and any loss of mycorrhizae. Differences in microbial activity among the soil types were also evident. Non burnt seedling roots and container walls showed a high degree of iron-oxide plaquing, suggesting enhanced microbial activity in these compared to surface and sub-surface burns. This may be the result of differences in 1) microbial populations, 2) iron concentrations, and/or 3) rates of oxygen diffusion from plant roots (i.e., thin vs. thick roots) within the different soil types (Smith and Newman, 2001).

Conversion of soil Po (organic phosphorus) to Pi (inorganic phosphorus) by sub-surface burning (see Table 1) seems the most obvious explanation for the observed growth responses. However, the enhanced growth and P concentration in sub-surface burn seedlings also may be due to greater bulk densities of these soils (Smith et al. 2001; see Table 2.1). Where non-volatile elements (e.g., P and Ca) have been physically concentrated by soil collapse during sub-surface fire, plant roots have access to more soil per unit volume and, thus, shorter growing distances to exploit each micro-site containing these elements. The sub-surface fire documented by Smith et al. (2001) collapsed approximately 10 cm of soil into 2 cm. In contrast, elements that can be volatilized during the fire are generally less concentrated per unit volume despite increased bulk density (Smith and Newman, 2001).

In the analysis of a long term burning trial of upland grassland, Mills and Fey (2004) showed that soil from 0–1 cm in burnt plots had lower total N (0.07% vs. 0.23%), (NH4)OAc-extractable Ca (7 vs. 17 mmolc kg_ 1), Mg (2 vs. 7 mmolc kg_ 1), K (0.8 vs. 1.5 mmolc kg_ 1) and a greater exchangeable Na percentage (17% vs. 8%) (Mills and Fey, 2004). They suggest that nutrients are lost from burnt plots over time, probably by the removal of ash in surface runoff, and that Ca, Mg, and K were lost more readily than Na probably because plants take up these nutrients in greater concentration than Na. As discussed in Section 2.1.1, the extent to which this applies to wetlands will depend on the extent to which ash is washed from a wetland. If a wetland is a depositional site, it may, in fact, accumulate minerals concentrated in the ash. The hydrological consequences of the increased exchangeable Na for soil infiltration are explored in Section 2.3.

Given that high levels of loss of N to the atmosphere take place when plant material is combusted, wetland burning could potentially be used to contribute to increasing the effectiveness of a wetland in removing N from a catchment's waters. However, Ostendorp (1995) showed that in the case of a *Phragmites australis* reed bed, this contribution was small. Prior to senescence, 50 to 60% of the N in the culms is translocated down into the rhizomes, leaving the culms very low in N (4 mg g^{-1} dry matter). Harvesting of living material in the growing season from a fully grown reed stand would result in much higher nutrient export. Sieghardt and Maier (1985, cited in Ostendorp, 1995) estimated that 6.2 to 31.8 g m^{-2} from live material, with the comparable value for the study of Ostendorp (1995) being 3.6 g m^{-2}. Harvesting of living material would also obviously be much more effective in removing non-volatilized nutrients, notably P.

2.1.2 Atmospheric emissions from burning

Vegetation fires emit a complex mixture of gases, and the diversity of composition of combustion products results from a wide range of fuel types, fuel chemistry and fire behaviour for fires in the natural environment (Ward, 1990). Burning of vegetation represents an important source of atmospheric CO_2, CO, CH_4, H_2, CH_3Cl, NO, HCN, CH_3CN, COS, and particulate carbon. These chemical species play important roles in the atmospheric photochemical cycle and in the Earth's radiation balance (Crutzen and Carmichael, 1993) and fire is a globally significant source of greenhouse gas emissions (Archibald, 2009).

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Season of burn has an important influence on the quantity and type of emissions from grassland fires (Korontzi , 2005). The fuel tends to be less cured and wetter in early dry season burns than late dry season burns, resulting in less complete combustion and more smoldering emissions per unit area compared with the late burns, which in turn result in much higher CO, CH4 emissions (Korontzi, 2005). The particular chemical species associated with flaming combustion are generally very distinct from those associated with smoldering combustion (Table 2.2) (Lobert and Warnatz, 1993).

Table 2.2: Emissions from biomass fires during the two different burning stages, the flaming stage and the smoldering stage (from Lobert and Warnatz, 1993)

Flaming stage compounds	Ambiguous compounds	Smoldering stage compounds
Carbon Dioxide (CO_2) Nitric Oxide (NO) Sulfur Dioxide (SO_2) Nitrous Oxide (SO_2) Nitrogen (N_2) Particles (high elemental carbon content)	These are compounds which cannot be clearly attributed to either flaming or smoldering combustion Ethine (Dioxide (C_2H_2) Cyanogen (NCCN)	Carbon Monoxide (CO) Methane (CH_4) Most hydrocarbons (NMHC, PAH) Ammonia (NH_3) Hydrogen Cyanide (HCN) Acetonitrile (CH_3CN) Amines, Heterocylces, Amino acids Methyle Chloride (CH_3Cl) Most Sulfur compounds (H_2S, COS, DMS, DMDS)

Although a late dry season burn, which is more complete than an early burn, results in higher CO_2 emissions, this may be offset by the lower emissions (Table 2.2) of chemical species (e.g. methane) which are much more potent greenhouse gases than CO_2 (Crutzen and Carmichael, 1993) (Table 2.3).

Table 2.3: Emission factors (EFs) (in gkg^{-1}) for three selected chemical species for grassland fires during the dry season (adapted from Crutzen and Carmichael, 1993)

Chemical species	Early season EF	Late season EF	Ratio
Carbon Dioxide (CO_2)	1636 ± 45	1755 ± 65	0.93
Carbon Monoxide (CO)	100.7 ± 23.1	39.3 ± 33.3	2.56
Methane (CH_4)	3.14 ± 0.88	0.799 ± 1.270	3.93

The situation described for grasslands above is likely to apply to herbaceous wetlands, particularly to those which are subject to an extended dry season. In addition, sub-surface fires, as characteristically occur in wetlands, are characterized by smoldering combustion, leading to high emissions of CO, volatile organic compounds and polyaromatic hydrocarbons, which have potentially serious consequences for human health (Rein et al. 2008; Blake et al., 2009). Given the considerable amount of organic matter stored in peat, emissions from combustion of this soil may be very high. Levine (1999, cited by Langmann et al 2009), showed that during the 1997 fires in Indonesia peat contributed only about 20% to the total area burned but nearly 90% to the total emissions. Similarly, although the aerial extent of peat fires currently burning in the drained and desiccated peatlands surrounding Moscow are much less than the forest fires, it is estimated that they are contributing 80-90% of the air pollution in Moscow, resulting in major health risks to residents (Wetlands International, 2010).

2.2 Effects of burning on the accumulation of soil organic matter (SOM)

2.2.1 Surface fires

Leaf litter input makes a significant contribution to SOM in the top few centimetres of soil, and therefore its removal by fire potentially reduces the SOM content in the top soil layer. Soil organic matter tends to decline in landscapes that are burnt regularly (Jones et al., 1990; Seastedt et al., 1990; Bird et al., 2000; Mills and Fey, 2004). Mills and Fey (2004) found that total C, total N, labile C and soil respiration in incubated samples showed a consistent trend of being lower in burnt plots than unburnt plots. The decrease in total C in the top 0–1 cm layer as a result of burning in the southern Kruger National Park is particularly noteworthy, with means of 0.8% and 2.3% for burnt and unburnt plots, respectively. This surface layer of soil, which Mills and Fey (2004) refer to as the pedoderm, affects ecosystem function in a disproportionate manner compared with deeper layers, as it controls water and air entry into the soil.

Mills and Fey (2004) attribute the decline in total C and N as a result of frequent burning to several processes operating simultaneously.

- Inputs of organic matter to the soil are reduced by burning because of the combustion of aboveground biomass and leaf litter.

- The removal of vegetation tends to increase the number of wetting and drying cycles in the soil surface, due to greater soil temperature and less interception of rainfall in the exposed post-fire environment (Moyo et al., 1998), which increases the rate of mineralisation of organic matter.

- Soil temperatures tend to increase after burning because of greater exposure to sunlight, and this is likely to increase microbial activity. Knapp et al. (1998), for example, recorded a 20–55% increase in CO_2 flux after burning in tallgrass prairie, with unburnt prairie averaging 10 Amol CO_2 $m^{-2}s^{-1}$ and burnt prairie 15 Amol CO_2 $m^{-2}s^{-1}$. Soil temperatures were greater in burnt prairie than unburnt prairie and differences in CO_2 flux were attributed to this temperature difference.

- Soil microbes tend to respond favourably to the deposition of alkaline ash in the post-fire environment (Greenwood, 1968; Knapp et al., 1998). An increase in pH also tends to increase labile C concentration, which will tend to favour microbial growth (Curtin et al., 1998).

In a long term burning and mowing trial running over a 50 year period in a mesic grassland, Fynn et al. (2003) found that timing of the burn strongly influenced the effect of fire on organic C in the surface 2 cm. Annual and biennial spring burning did not result in a decrease in organic C, yet autumn and winter burning on an annual and biennial basis, and even autumn burning on a triennial basis, did cause a decrease. This highlights the importance of timing of burn. It is suggested that in summer rainfall areas, when burning is practiced in spring, the opportunity exists during the preceding winter for litter to be incorporated into the soil, whereas in autumn burning no such opportunity would be provided. The effect of burning on deeper soil layers through its influence on leaf litter is negligible because most of the organic matter here originates from root turnover. Even the treatment having the greatest impact on the uppermost 2 cm of soil (i.e. autumn burning) did not affect the SOM content in the 2-4 cm layer

(Fynn et al., 2003). Research on mesic grasslands has shown that by removing standing dead material and increasing primary production, burning can, in fact, act to increase root production, and the increased organic matter from roots offsets the reduced inputs from litterfall (Seastedt and Ramundo, 1990). The results of Fynn et al. (2003) and Seastedt and Ramundo (1990) are likely to be applicable to hygrophilous grassland wetland, which are generally subject to short periods of saturation. These results are probably also relevant to some extent to the wetter zones of a wetland, and Mook and van der Troon (1982) and Thompson and Shay (1985) both showed that below-ground production of *Phragmites australis* reed, growing under conditions of prolonged saturation, was, in fact, stimulated by fire.

2.2.2 Sub-surface fires

Sub-surface fires, by nature, involve the combustion of SOM, and therefore may have dramatic impacts on SOM levels. Sub-surface fires are a natural feature of some wetlands, generally taking place during particularly dry years (Cypret, 1961; Kotze et al., 1994). The desiccation of wetland areas with organic soils as a result of natural geomorphological change in a wetland may also result in sub-surface fires. For example, in the Okavango delta, natural channel abandonment (caused by accumulated sediment) results in desiccation of the peat that has formed beneath papyrus swamp in the channel, thereby exposing the peat to sub-surface fires (Ellery et al., 1989).

Sub-surface fires may also be precipitated by anthropogenic modifications to the wetland. In particular, fire may have a strong interactive effect with anthropogenic factors which desiccate wetlands, resulting in burns which would otherwise have negligible effects on the carbon balance of a wetland, initiating extensive ground fires and the dramatic depletion of accumulated carbon stores.

Sub-surface fires are not common in larger valley bottom systems, although they have been recorded from some of these systems, e.g. Wakkerstroom, which has a hydrological regime little altered by human intervention (Kotze et al., 1994). In Wakkerstroom, as in the Okefenoke swamps, sub-surface fires result in the creation of open water areas (Cypret, 1961; Kotze et al., 1994). The areas that are opened by sub-surface fires create opportunities for new vegetation to become established, as discussed in Section 2.3.

As discussed in Section 1.4, drainage and logging have greatly increased the incidence of peat fires in Indonesian peat forests, which has profound implications for CO_2 emissions. Hooijer et al. (2006 as cited by Jaenicke et al. 2008) estimated the annual CO_2 emissions from peatland fires in Indonesia over the ten year period from 1997 to 2006 to be 1.4–4.3 Gt, which is equivalent to 19–60% of mean annual global carbon emissions from fossil fuels. Drainage of peat has also been a major factor, together with particularly hot and dry conditions, contributing to the current peat fires in areas surrounding Moscow (Wetlands International, 2010).

2.3 Effects of burning on catchment hydrology

2.3.1 The effects of burning on soil infiltration

To determine whether frequent burning increases the tendency of soils to crust and alters soil chemistry, Mills and Fey (2004) examined topsoils from 19 (non-wetland) sites in Mpumalanga, KwaZulu-Natal and the Eastern Cape where annual burning and fire exclusion experiments had been conducted for at least 28 years. A comparison of soils from burnt and unburnt plots revealed that burnt plots had lower laboratory infiltration (means of 59 vs. 75 mm h^{-1} for burnt and unburnt plots, respectively), electrical conductivity (EC) of 1:5 extracts, water-soluble K, water-soluble NH4, total C, total N and labile C. Burnt plots had higher pH in KCl, water dispersible clay and modulus of rupture. Rate of soil respiration (0–2 cm) from burnt plots was lower than from unburnt plots (means of 21 vs. 36 ng C g^{-1} s^{-1}). Rainfall simulation demonstrated that burnt plots crusted more rapidly than unburnt plots (19 vs. 35 mm h^{-1}), while results from sampling at 1-cm intervals revealed that the greatest differences between burnt and unburnt plots were in the 0–1 cm layer.

The results indicate that for the majority of soils sampled from long-term burn experiments in South Africa, frequent burning changes soil chemistry in a manner that increases the tendency of the soil to crust. Mills and Fey (2004) cite several other studies (Daubenmire, 1968; Schacht et al., 1996; Bijker et al., 2001) which also show that frequent burning can reduce the rate of infiltration of rainwater into soil. The following factors are suggested by Mills and Fey (2004) as contributing to the diminished infiltration after fire.

- Soil organic matter, which usually increases soil aggregation and consequently the rate of infiltration (Cook et al., 1992), tends to decline in landscapes that are burnt frequently (Bird et al., 2000).

- Ash particles may block pores at the soil surface (Mallik et al., 1984).

- The removal of vegetation increases the exposure of soil to raindrop impact, which will increase breakdown of aggregates, dispersion of clay and thus soil crusting (Hillel, 1998).

- Dispersion of clay and hence crusting of soils, as a result of Ca, Mg, and K being lost more readily than Na, thereby increasing the exchangeable sodium percentage (ESP), which increases the tendency of the soil to crust (Mills and Fey, 2004). Sodium is not an essential nutrient for plant growth and consequently the foliar concentration of Na tends to be considerably lower than nutrients such as Ca, Mg and K (Whitehead, 2000). It is suggested therefore that the increase in ESP is due largely to preferential removal of Ca, Mg and K from the soil profile by plants and the loss of these nutrients when ash is washed off-site by surface runoff.[5] It should be noted, however, that this phenomena described by Mills and Fey (2004) applies to areas with inherently dispersive soils, which are fairly rare in the mesic grassland areas.

As indicated in Section 2.2 and emphasized by Mills and Fey (2004), the top few centimetres of soil are likely to have a disproportionate effect on ecosystem functioning by influencing the rate of infiltration and mineralization of SOM.

The effect that fire could potentially have on diminished infiltration would be particularly applicable to a wetland's upstream catchment, and are likely to result in an increase in surface runoff during storm events and a decrease in the sustained supply of sub-surface water to the wetland. The magnitude of this change in hydrological inputs and the consequences of this for the wetland would depend on the specific circumstances in the wetland, but could potentially lead to gully erosion in the wetland and

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[5] This finding raises the possibility of soil structure being degraded (due to an increase in ESP) by removal of plants through means other than fire (e.g. herbivory or cropping). Mills and Fey (2004) concur with Mullins et al. (1987) that crusting soils are not always hard-setting soils. Such a crust can be a temporary phenomenon during a rain event, but may be scarcely visible when the soil surface is dry. Because soil pores are blocked during a rain event by dispersed clay and material from broken aggregates, the tendency of a soil to crust is to a large extent related to the dispersibility of the clay fraction and the stability of soil aggregates (Mills and Fey, 2004).

possibly also wetland desiccation (Macfarlane et al. 2008). Unfortunately, empirical studies examining the effect of burning in the catchment of wetlands appear to be lacking. Reduced infiltration would also have applicability to temporarily saturated areas within the wetland, which are generally only saturated to the soil surface for brief periods during the wet season. Wetter areas in a wetland, particularly those which remain permanently saturated throughout the year would not be directly affected because their infiltration potentials are inherently very low.

2.3.2 Effects of burning on the atmospheric loss of water

A key factor limiting the extent to which wetlands store water is that water is lost from the wetland through evapo-transpiration. Although in temporary wetlands, where the water table generally lies well below the soil surface, the upper layers of soil limit evaporative loss during the dry season, wetlands that remain flooded or saturated to the soil surface are exposed to the greatest potential evaporative loss of water during the dry season. However, where natural winter dieback of the leaves takes place, as characteristically occurs in areas experiencing frequent winter frosts, then this loss is greatly reduced during the winter period. This is particularly important where the winter season coincides with the dry season, which pertains to the summer rainfall areas of South Africa, and all of the mesic grasslands in the country. The dense layer of reflective non-transpiring material limits heating up of the soil as well as limiting the movement of air across the water or soil surface. Donkin (1994) showed that evapo-transpirative loss of water during winter from a wetland with abundant standing dead material was significantly lower than the evaporative loss from open water. Thus, the higher the level of frosting back, the greater the reduction in potential loss of water through transpiration. This situation applies to much of the mesic grasslands of South Africa given the widespread occurrence of frost in the biome.

In the case of permanently saturated/flooded areas, fire may have a profound effect on the presence of the protective layer of non-transpiring plant material that would otherwise limit atmospheric loss of water. If the fire place at the beginning of the dry season then the wetland is left exposed throughout the dry season, and if the water table is at or above the soil surface this could greatly increase water loss.

The removal of standing dead material allows greater heating of the soil and improved light conditions for photosynthesizing tissue enhances early spring growth. This, in turn, promotes transpirative loss of water from the wetland. Sharrow and Wright (1977), for example, found that primary production in the early growing season was considerably higher where litter had been removed by fire. This effect is, however, generally short-lived and unlikely to last more than a few weeks.

2.4 Effects of burning on vegetation structure and composition

2.4.1 Differential adaptation of wetland plant species to fire

Fire affects plants directly through the combustion of plant material (including dead and living material) as well as indirectly through the various effects that it has on biogeochmical cycling and hydrology (described in Section 2.2 and 2.3). Fire also affects plant seeds, either stimulating germination or destroying seeds. Fire generally acts to open up the canopy, increase nutrient cycling, remove litter, and often does not greatly affect seed survival. Therefore fire often initiates or stimulates new growth (Mendelssohn et al., 1988).

Although sedges and grasses are generally well adapted to burning, a few species such as *Cyperus papyrus* are less well adapted than the others. *Cyperus papyrus* produces rhizomes that are situated above ground level and are susceptible to destruction by fires. As such, this species, which is able to dominate in situations where meristems are permanently submerged, and therefore protected from fire, is unable to tolerate seasonal desiccation and burning. In contrast, other species such as *Phragmites mauritianus* and *Pennisetum glaucocladum* thrive because they produce underground creeping stems (stolons) that survive the dry season because meristems are protected from seasonal burning, and re-sprout following burning (Ellery et al., 2003).

An example of a wetland grass that is well adapted to fire is *Spartina argentinensis*, which has a rapid growth response after fire even under drought conditions (Feldman et al., 2004; Feldman and Lewis, 2007). Feldman and Lewis (2007) found that re-sprout percentages were very high, probably because: (1) fire damage was not important due to fire velocity as well as stem meristem protection by leaf sheaths, and (2) abundant reserves both in rhizomes and in the leaf lamina bases. *Spartina argentinensis* rapidly produced a dense population of new aerial tillers which in a few months, had no density difference with non-burnt plants. Burnt plants of *S. argentinensis* increased their recruitment rate, results that are consistent with those found by other authors working with C_4 grasses (e.g. Svejcar and Browning 1988). Therefore, there was a qualitative difference in *S. argentinensis* plants after the fire, module population rejuvenated and the photosynthetic area was larger, so there was a higher availability of photosynthates which enables a larger differentiation of asexual and sexual reproductive structures (Feldman et al., 2004; Feldman and Lewis, 2007).

Fire is widely used for promoting the growth of favoured indigenous plants and controlling invasive alien species. For example, In a comparison of burnt and unburnt areas of Nylsvley, Otter (1992) found that in the burnt area the abundance of *Themeda triandra* and *Oryza longistaminata* (both indigenous species valuable for grazing wildlife) was greater and the abundance of *Asclepias fruticosa* (an invasive alien species) was considerably lower.

A US example is described by Clark and Wilson (2001) in the Willamette Valley, Oregon, where before the mid-1800s, the indigenous people burnt the wetlands annually during the dry season (late summer and early autumn) to facilitate hunting and food gathering (Clark and Wilson, 2001). These fires reduced the abundance of shrubs and trees, favoured the growth of native grasses such as *Deschampsia cespitosa*, and promoted a rich variety of native forbs. Today less than 1% of the original native wetland prairies remain, and they are considered among the rarest of Oregon's ecosystems, which are in critical need of protection and restoration (Clark and Wilson 2001). Succession to shrubland and forest now threatens most of the few remnants of undeveloped prairie wetland. In addition, weedy non-native herbaceous species introduced with settlement have spread rapidly with habitat disturbance, often dominating and suppressing native vegetation (Pendergrass et al., 1998; Clark and Wilson, 2001). In an investigation of plant species responses to experimental burning, hand-removal of woody species, and mowing with removal of cut material, it was shown that native herbaceous species are fire-adapted, with prescribed burning promoting or maintaining their abundance, and that many non-native herbaceous species are not adapted to fire, with prescribed burning inhibiting or at least not promoting the population size of these species. Hand-removal of woody species was also effective at reducing woody cover and promoted the abundance of some native species, but it sometimes increased the cover of non-native herbaceous species. Mowing with removal of cut material was ineffective in reducing woody cover and tended to promote non-native herbaceous species (Clark and Wilson, 2001).

An analogous situation to that described above is found in the wetlands of the Dukuduku/ Kwambonambi area, Zululand coastal plane, South Africa, which is characterized by flat to gently undulating topograpgy, shallow water tables in the lower lying areas and extensive wetlands. Henkel et al. (1936) record that most of this area was subject to regular fires, which they noted was of great ecological importance in hindering the expansion of forest. Thus, much of the wetland component of this landscape is naturally dominated by herbaceous vegetation well adapted to regular fires. These wetlands support a rich diversity of wetlands, including the only known wild population of the crtically endangered *Kniphofia leucocephala*, as well as other Red Data plant species, notably *Asclepias gordon-grayae* (Scott-Shaw, 1999). Henkel et al. (1936) record that some of the wetlands Dukuduku/ Kwambonambi area were naturally dominated by forest, but generally confined to locations protected from fire. However, in the last four decades in particular, the area, has been subject to very high levels of transformation to tree plantations, sugar cane and human settlements, leading to the reduced incidence of fire, which in turn has resulted in extensive encroachment of the herbaceous wetlands by woody plants, notably *Macaranga capensis*. Lowering of the water table by the extensive tree plantations in the area would appear to have compounded the effect of reduced fire, as will be discussed later in this section.

Fire has been shown to be generally useful for controlling invasive alien plants in wetlands, as illustrated by the example given by Otter (1992) earlier in this section. When infestations are dense, fire generally needs to be used together with other control methods in an integrated approach. For example, in isolation, herbicide, mechanical clearing and fire were not effective in controlling dense *Mimosa pigra* thickets on an Australian floodplain, but several combinations of techniques cleared mimosa thickets and promoted establishment of competing vegetation that inhibited *M. pigra* regeneration from seed (Paynter and Flanagan, 2004). Furthermore, van Wilgen (2009: 339) referring specifically to the situation in the Fynbos Biome[6], where the main invasive plants are *Acacia*, *Pinus* and *Hackea* species, all generally very well adapted to fire, notes that “Invasive alien plant seedlings germinate after fires, and usually increase the density and extent of infestation. It is necessary to control these flushes of seedlings to prevent them becoming dominant over the next few years. Extensive unplanned fires will precipitate the need for additional effort in the form of ‘follow-up’ operations.” Therefore, as was the case in the example described by Paynter and Flanagan (2004), in the fynbos biome, fire must be integrated with other methods of control.

In certain cases it may be desirable to reduce the strong dominance of dominant indigenous species (e.g. *Phragmites australis*), usually in order to enhance habitat diversity. In such cases, the timing and nature of the burn may be specially selected in order to reduce this dominance. An example of this is the summer burning of *P. australis*, which was shown to decrease its dominance and increase species diversity in marshes (Thompson and Shay, 1989), as discussed later in this section. Another example is that of purposeful sub-surface fires designed to reduce the abundance of *Typha*. Mallik and Wein (1986) showed that burning when the water table had been lowered was more effective in decreasing the dominance of *Typha* than burning under higher water table conditions.

The destruction of existing vegetation (and seed banks) by a ground fire, creates a physical and biological ‘‘opening’’ in the landscape, and this, together with changes in biogeochmical cycling and hydrology (described in Section 2.2 and 2.3) may result in dramatic vegetation changes. In contrast to the above example, Newman et al. (1998) describes how ground fires may also sometimes favour undesired species, in this case a sub-surface fire in the Florida Everglades favoured *Typha domingensis* over the existing dominant, *Cladium jamaicense*. The ground fire resulted in a lowering of soil elevations as the organic matter was combusted. Given its positive response to flooding, *T. domingensis* is presumably well-suited for growth in the newly formed depressions. However, changes in soil nutrients as a result of the burning process may also play an important role in its establishment and growth in these areas (Newman et al. 1998) given that *C. jamaicense* is adapted to low P environments

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[6] Invasion by alien plants (especially woody species) poses arguably the greatest threat to the conservation of fynbos ecosystems (van Wilgen, 2009), some of the highest alien plant infestations occur in riparian areas, and extensive riparian areas are wetlands.

(Miao & Sklar 1998; Leeds et al., 2009). Further evidence of ground fires increasing the bioavailability of soil phosphorus, thus providing a competitive advantage for *Typha domingensis* is provided by Smith and Newman (2001) who used the seedlings of *T. domingensis* to assay the nutrient availability of burnt organic soil in the Florida Everglades soils. After two months of growth, plant height, number of leaves, culm diameter, number of rhizomes, length of rhizomes, live leaf biomass, and above- and belowground biomass were all affected positively by the burnt soil.

Surface fires may also have a strong influence over the species composition of wetlands. For example, Ladderman (1989, as cited by Mitsch and Gosselink, 2000) showed that fires eliminate the shrubs and brush of other species and favouring germination and seedling establishment of pond cypress trees. Ford and Grace (1998) examined the influence of fire on the competitive balance between different species in a *Sagittaria* marsh, where *Spartina patens* cover was reduced while cover of *Sagittaria lancifolia* and *Vigna. luteola* increased as a result of burnig (Figure 2.1). Mendelssohn et al. (1988, as cited by Ford and Grace, 1998) also found fire to suppress *S. patens* cover, allowing a species that would otherwise be an inferior competitor to increase.

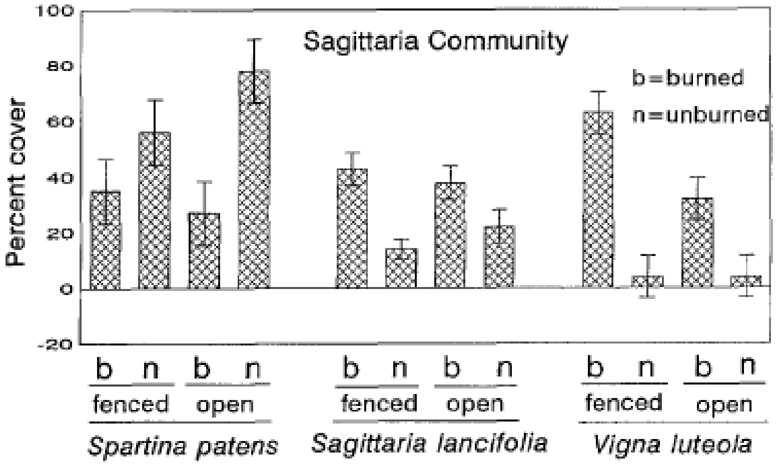

Figure 2.1: Effects of burning and fencing on plant cover of *Spartina patens*, *Sagittaria lancifolia* and *Vigna. Luteola* in *Sagittaria* marsh (b=burned, n=unburned). Error bars represent ± 1 standard error. Fenced areas exclude the two main herbivores in the marsh, wild boar, which are indigenous, and nutria, which are introduced (from Ford and Grace, 1998).

2.4.2 The effect of fire frequency and timing

While most herbaceous wetland plant species are well adapted to the direct effects of fire, they vary in their relative responses to differences in fire frequency. Like *P. australis*, *Spartina* spp. are generally be well adapted to frequent burning. For example, above-ground biomass production, inflorescence density and plant height at anthesis were found to be significantly greater in *Spartina pectinata* wetland that was burnt annually than in the same wetland that was burnt biennially (Johnson and Knapp, 1993).

Species characterized by complete die-off of the above-ground parts at the end of each growing season (e.g. *Phragmites australis*) do not loose any living tissue as a result of a surface fire in the dormant season. In contrast, the above-ground portions of certain species generally live for more than a year, in which case a surface fire would inevitably destroy some living tissue, even if the fire occurred within the dormant season. For example, the leaves of *Juncus roemerianus* normally live two to three years (Hackney and de la Cruz, 1981). In a burning experiment conducted in a marsh dominated by *J.*

roemerianus, repeated removal of the vegetation, resulted in a decline in the vigour and growth of *Juncus roemerianus*. The decreasing contribution of *J. roemerianus* to the total community biomass in turn resulted in increased available space, which was taken advantage of by other species through their increased growth (Hackney and de la Cruz, 1981). Thus, Hackney and de la Cruz (1981: 81) suggest that repeated fires, as frequently as possible, will probably convert a mixed *J. roemerianus* marsh to a marsh where *J. roemerianus* is not very important. However, it is important to note that where *J. roemerianus* was dominant, Hackney and de la Cruz (1981) found it very difficult to burn *J. roemerianus* marsh one year after a fire because there was insufficient combustible material. Mono-dominant stands of *J. roemerianus* will resist frequent fires, thereby resisting changes in plant species composition and structure associated with frequent fires (Hackney and de la Cruz, 1981).

As a general rule, it can be concluded that the greater the abundance of vegetation dominated by persistent above-ground portions, the less readily it will burn, whereas the greater the abundance of above-ground portions characterized by annual complete dieback, the converse is true. It would therefore be expected that where species with contrasting levels of dieback co-occur, frequent burning during the dormant season will potentially favour those species with complete dieback during the dormant season over those species with more persistent above-ground portions, whereas infrequent fires would potentially have the reverse effect.

Timing of burns also has a potentially very important influence over individual species and overall vegetation composition, primarily through its effect on the dominant species. For example, spring burning enhanced the performance of *P. australis*, as indicated by higher aerial and below-ground biomass and flowering shoot density, in contrast to summer burning, which lowered performance (Mook and vander Troon, 1982; Thompson and Shay, 1985). Autumn burning appears to have an intermediate effect, resulting in higher biomass but reduced flowering shoot density (Thompson and Shay, 1985). Thus, where *P. australis* occurs as the dominant species in a mixed community, e.g. with *Molinia caerulea* and *Cladium mariscus*, burning to disadvantage *P. australis* would potentially increase diversity by reducing the overriding competitive dominance of *P. australis*, and conversely where it is optimal for *P. australis* then diversity is potentially reduced (Haslam, 1971).

No southern African studies could be found investigating the effect of different frequencies and timing of burning on the less abundant plant species within a wetland. However, the results obtained from mesic grasslands are likely to be relevant. Although Uys et al. (2004) found, in an investigation of three burning experiments, that forb species richness was surprisingly resilient to burning timing and frequency, Fynn et al (2004) showed that in a long-term (> 50 yr) grassland burning and mowing experiment in KwaZulu-Natal, the forb richness was significantly lower in winter-burnt treatments than the spring-burnt treatments. Fynn et al (2004) suggest that this may be as a result of the greater desiccation to which the winter burnt treatment is subjected.

Taxa which are adapted to fire exhibit two main strategies for recovering after a fire, ‘reseeding’, in which the plant is generally killed by fire and regeneration occurs from seed, or ‘resprouters’, in which the pereniating buds of a plant generally survive fire, and regeneration takes place by sprouting of new shoots from protected structural features (e.g. trunks, rhizomes or rootstocks (Bond and van Wilgen, 1996). As a general rule, reseeders are potentially better suited than the resprouting taxa to recruit into any large gaps that may develop between the adult plants following fires. However, if the fire return-interval is shorter than the time it takes the plants to reach reproductive maturity then reseeders will potentially be eliminated. Although resprouters are generally able to tolerate more frequent fires than reseeding taxa, they too could potentially be eliminated if fire is at such a high frequency that there is inadequate time for recovery between fire events (Bond and van Wilgen, 1996).

There are two features that make the individual plants of resprouters potentially better adapted to defoliation (whether from fire, grazing or cutting) than reseeders. Firstly, the pereniating buds are lower relative to the soil surface, making them more protected, especially from fire. Secondly, starch and sugar reserves are larger, potentially allowing adult plants to recover more rapidly from defoliation. In the case of Restionaceae, although the average culm length of seeders is similar to resprouters, seeders have pereniating buds positioned on average 20 mm higher in the soil than resprouters (which makes the plants more vulnerable to fire and to very low cutting), and the mean rhizome diameter of seeders is less than resprouters (2.9mm compared with 3.8mm). In reseeders, rhizomes tend to grow in an ascending fashion, and may extend well above the soil surface with the result that the plant develops a tufted or even stilt-like habit. In addition, expressed in terms of percentages of dry matter of rhizomes, the resprouters as a group show significantly higher mean levels of starch (6.4%) and sugars (3.5%) than do seeders (0.06 and 1.4% respectively; Pate et al. 1999).

The two most dominant families in South African wetlands, Cyperaceae and Poaceae, are generally resprouters. In the fynbos biome, another commonly occurring family in wetlands is Restionaceae, in which resprouting is the most dominant regeneration mechanism, although some hydric species (e.g. *Chondropeatalum mucronatum*) are seeders. Van Wilgen and Kruger (1981, as cited by Linder 1991) report all Restionaceae (both resprouters and seeders) as surviving a fire near Paarl, and resprouting. However, Le Maitre (1986) showed that fire survival of reseeders depends on the burning season. If the fire occurs after the new cohort of culms has been initiated, the plants are killed, while fire which occurs shortly before culm initiation is less lethal.

2.4.3 Interaction of fire with other key vegetation determinants

In assessing the effect of fire on plant species composition, it is important that burning of wetlands be seen in relation to key physical constraints to wetland structure and composition, e.g. soil anoxia (waterlogging) and climatic temperatures; as well as in relation to other disturbances (e.g. grazing) which may potentially interact with fire. The level to which fire acts as a primary determinant of structure and function is likely to vary in relation to these other physical determinants (Figure 2.2). For example, it would appear that fire acts as the strongest determinant of vegetation structure and composition in wetlands where climatic temperatures are mild and the level of soil anoxia is low (i.e. under temporary wetness (Figure 1). In the absence of fire, herbaceous vegetation in these wetland areas most readily becomes dominated by woody plants[7]. Particularly where soil anoxia is high and also climatic temperatures are cold, these determinants together appear to have an overriding, constraining effect on woody plants (Figure 2.2).

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[7] However, if the soils are shallow overlying a harpan or impermeable bedrock then in South Africa's strongly seasonal climate, such areas are often subject to extremes of extended wetness and prolonged dryness, for which graminoid plants are generally better adapted than woody plants, and woody plants may colonize with difficulty irrespective of the fire regime

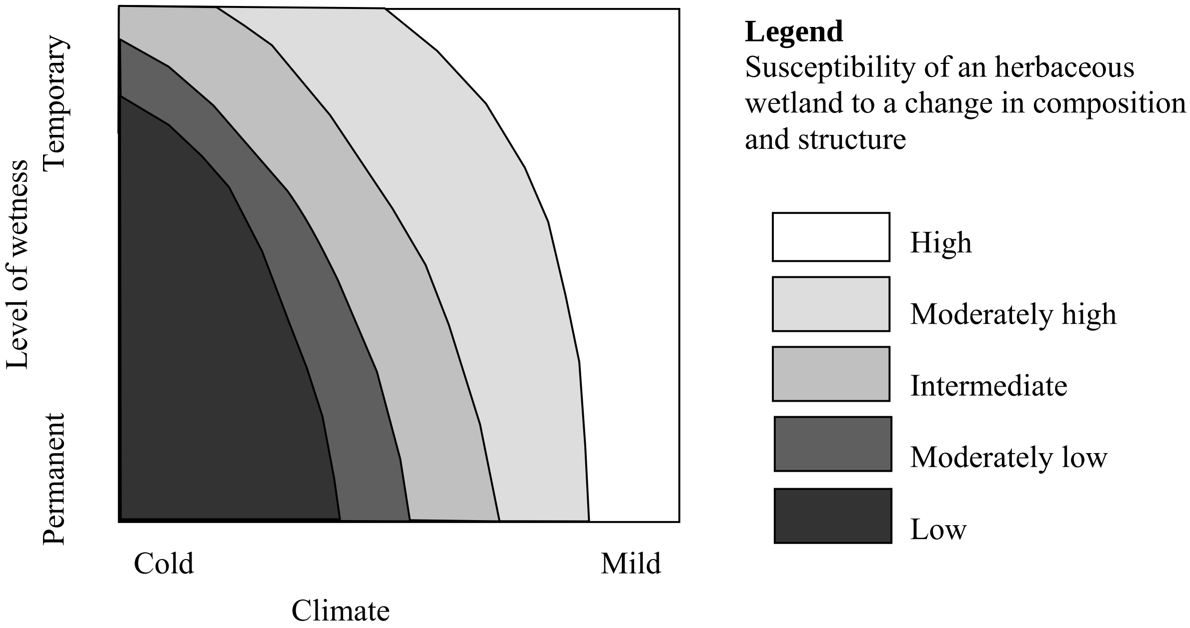

Figure 2.2: Susceptibility of an herbaceous wetland to a change in composition and structure in the absence of fire based on the level of wetness of the wetland area and the local climate.

In South Africa, there are very few areas where a cold climate alone excludes trees, and only the highest grasslands in the Drakensberg may be genuinely “above the tree-line” (Bond et al., 2003). There are a few woody plants in South Africa that are well adapted to the highest levels of wetness encountered in wetlands, notably *Ficus trichopoda*, and these are confined primarily to mild climatic conditions, with *F. trichopoda* confined to the north coast of KwaZulu-Natal. But even under these conditions, woody plants are likely to invade wetlands less readily than in mesic, well drained areas. In an investigation of the effect of fire on the coastal grasslands of Maputaland, including an airphoto comparison from 1937 to 2000, Dalton (2007) showed that the hygrophilous grasslands were considerably less susceptible to encroachment by woody plants than the well drained grassland areas, but were not totally without encroachment. Dalton (2007) suggests that close proximity of the water table and the degree of inundation reduces the susceptibility of the hygrophilous grasslands to encroachment by woody plants, but encroachment could possibly occur during long drier periods. For the maintenance of well drained coastal grasslands, Dalton (2007) recommends that fire should be implemented at least every three years but left for no longer than four years to avoid woody encroachment. Dalton (2007) further indicates that in order to maintain hygrophilous grasslands, burning will also be required, but less frequent than for well drained coastal grassland owing to the lower susceptibility to encroachment of hygrophilous grassland.

In another hygrophilous grassland, located further inland in the sour grassveld of KwaZulu-Natal, with plinthic, seasonally-wet soils, a fire exclusion experiment resulted in invasion by woody plants (Titshall et al. 2000). Although wetlands are less readily invaded by woody plants than mesic well-drained areas, the exclusion of fire may nonetheless allow for herbaceous wetland areas to be completely replaced by woody plants. In a fire exclusion experiment in Catchment 9, Cathedral Peak, KwaZulu-Natal Drakensberg, prior to the exclusion of fire, the wetland area in this catchment consisted of several plant communities, including *Scirpus costatus*, *Oenothera rosea*, *Eleocharis dregeana* herbaceous communities and the *Leucosidea sericea* woody community (Killick, 1961). After 20 years of fire exclusion, the same area was described by Granger (1976) as comprising the single *L. sericea* woody community. Therefore, in this case, the exclusion of fire led to a dramatic decline in the diversity of vegetation types supported by the wetland.

Compounding factors may act together with suppression of fire to enhance the invasion by woody plants. These factors include disturbance of the herbaceous vegetation, lowering of the water table and shading by planted trees. Narrow tongues of wetland within extensive areas of tree plantations are subject to the latter two compounding impacts, and where these wetland areas were previously planted, they are subject to all three of the additional compounding impacts. Over the last 50 years or so there has been extensive loss of herbaceous wetland to swamp forest and riparian forest in the area between St Lucia town and Matubatuba, which contains extensive areas of plantation forestry (Ellery W, 2004. *Pers. comm.* University of KwaZulu-Natal). In the coastal belt, fire plays a critical role in maintaining the herbaceous wetlands. Where fire is excluded, the herbaceous plants, which are well adapted to fire, will tend to eventually be taken over by swamp forest tree species. This will result in a loss of herbaceous habitat and the many different species these areas support, including critically endangered hydric species such as *Kniphofia leucocephala*.

In southern USA, regular, low-intensity burns with return intervals of two to four years create canopies of widely spaced longleaf pine (*Pinus palustris*), which allow sufficient light to support a highly diverse herb-dominated ground flora (Martin and Kirkman, 2009). Periods of extended fire suppression cause a shift in community structure from an herbaceous ground flora to one dominated by shrubs and hardwood sprouts, and with sufficient fire-free periods, hardwood species (e.g. *Quercus* spp.) reach a fire-resistant stage (Glitzenstein et al. 1995; Martin and Kirkman, 2009). Once established, these hardwoods further exclude burns, and as the hardwood canopy develops the increased shade and increased litter layer associated with hardwood dominance nearly eliminates the rich ground flora (Walker and Peet, 1983; Kirkman et al., 2004). This further shifts the available fuels from flammable ground flora to fire-impeding hardwood leaf litter, with the result that the hardwood forest patches move across an ecological threshold and into an alternative state, where fire alone does not restore previous ecosystem dynamics (Brockway & Outcalt 2000; Peterson 2002; Martin and Kirkman, 2009). An analogous situation is likely to apply to South African wetlands that become dominated by woody plants with the suppression of fire, as described in the previous paragraph.

Even if the exclusion of fire in herbaceous wetlands does not lead to an increase in woody plants, species composition of the wetland may be greatly affected by the accumulation of litter, which may act to suppress certain native species, particularly the less abundant and shorter-growing species. These species may, in fact, be lost from a wetland in the absence of burning to remove the litter. Middleton (2002) observed that without fire, herbaceous peat wetlands in North America and Europe generally begin to loose biodiversity because of shading by litter. After a fire in a herbaceous peat wetland not damaged by heavy grazing pressure, a flush of native herbaceous species appears for about two seasons (Middleton, 2002). However, if the wetlands are overgrazed then burning may sometimes result in an increase in non-native species, thereby decreasing biodiversity (Middleton, 2002).

Major vegetation changes that are precipitated by fire often take place through the interaction of fire with other disturbances. One of the most common interactions is between fire and the occurrence of particularly dry years, which, as described in Section 1.4, may lead to ground fires in areas with organic soils. Fire may also interact with other disturbances, as illustrated by the important role that fire is suggested to play, together with its interaction with hurricanes, in maintaining stands of *Arundinaria* bamboo, referred to as canebrakes, within bottomland hardwood forest (BHF) (Gagnon 2009). Canebrakes are mono-dominant stands of *Arundinaria* bamboo, a genus endemic to the United States. *Arundinaria gigantea* (Walt.) Muhl. (giant cane or river cane) occurs on higher ground within southeastern alluvial floodplains (Judziewicz et al. 1999, as cited by Gagnon, 2009). Early European explorers describe vast, dense stands of giant cane frequently growing on levees and ridges in southeastern alluvial floodplains, but currently this vegetation type is much less extensive (Platt and Brantley 1997; Stewart 2007). It appears that the reduced incidence of fire following European settlement compared with that of the indigenous populations has contributed to the decline of canebrakes (Gagnon 2009).

Gagnon (2009) suggests interactions between fire and other disturbances play an important role in maintaining canebreaks, which is similar to the findings by Liu et al. (2008) of interactions between hurricanes and fires on the Alabama Gulf Coast. In BLH, fires are most likely to occur when windstorms or other large canopy disturbances are followed by prolonged droughts. Gagnon (2009) suggests that natural fires could have occurred in the following scenario: 1) A powerful windstorm or other disturbance opens a large canopy gap. 2) Over a few years, the gap fills with dense, regenerating vegetation. 3) Eventually, drought renders this new vegetation flammable and increases landscape connectivity for potential fire. 4) With the onset of spring thunderstorms, lightning strikes cause fires in these large, highly flammable canopy gaps. 5) Canebrakes and adjoining upland pine savannas facilitate fire spread into other parts of BLH. 6) Giant cane and other pyrogenic grasses thrive after burning, producing a flammable fuel bed that can burn again during the next drought. As canebrakes expand over time, they increase the area beyond the initial canopy disturbance that is susceptible to burning in subsequent droughts, and thereby set up a positive feedback. In this way once a large canopy disturbance initiates the sequence, canebrakes and other pyrogenic assemblages within BLH could essentially be self-sustaining (Gagnon, 2009).

Another important disturbance potentially interacting with fire is grazing. Several studies (e.g. Lynch 1941, Kays 1956, Smith and Kadlec, 1985) have shown that, as is the case with non-wetland grasslands, burning stimulates increased herbivory, which is generally owing to the better forage quality of re-growth compared with the old growth. However, although Ford and Grace (1998) in a fire and herbivory exclusion experiment (see Figure 2.1) did not examine herbivory directly, they found no indication of burning leading to a decrease in cover that could be attributable to the increased herbivory of such an effect in this study (Figure 2.1).

The outcome of a fire on vegetation may also be strongly affected by the hydrological conditions at time of the fire. If fire occurs under flooded conditions and much of the litter is submerged, a fire will often not carry through the wetland, particularly where the cover of emergent plants is discontinuous. However, if a fire were to occur in this same vegetation under unflooded conditions, a greater abundance of litter would be available, and the fire would be more likely to carry through the wetland.

In this review, the biotic response is described in terms of vegetation, as this is generally the most important component of the biota affecting wetland structure and function. Thus, the other components of functioning may be affected indirectly through the influence that fire has on vegetation. This is illustrated by the example of a decline in the abundance of *J. roemerianus*, which, as described earlier in this section, may take place as a result of an altered fire regime (Hackney and de la Cruz, 1981). *Juncus roemerianus* is characterized by the high production of rhizomes and roots which act to consolidate the marsh surface (de la Cruz and Hackney, 1977), and Hackney and de la Cruz (1981) note that in some Louisiana marshes where *J. roemerianus* has been replaced by other species, the marsh surface has become less consolidated, leading to the formation of “potholes”, which support breeding mosquitoes.

The section on vegetation will be concluded by drawing the distinction between vegetation which is fire-adapted and that which is fire-dependent. For example, an extensive mono-dominant stand of *Phragmites australis* located in a permanently flooded area under cool climatic conditions is likely to be well adapted to fire. Nevertheless, if fire were to be excluded, the *Phragmites australis* is likely to remain strongly competitive, and the vegetation is unlikely to readily change its structure and composition, unless the change in fire regime was accompanied by a major disturbance, e.g. desiccation of the area. Thus, it would not be considered to be fire-dependent. This contrasts with another example, that of hygrophilous grassland located where the level of wetness was lower than the *P. australis* stand and the climate milder. Such vegetation would be both fire-adapted and fire-dependent, given the fact that if fire were to be excluded the vegetation would become colonized by woody plants, resulting in a dramatic change in vegetation structure and composition.

3. Summary of key findings and knowledge gaps

Factors affecting the incidence and nature of fires in wetlands

The mesic grasslands of South Africa have both high fuel loads and high lightening strike rates, and thus the vegetation, including wetlands, evolved under a regime of frequent fires. It is not surprising therefore that the wetlands in these areas are overwhelmingly dominated by herbaceous, fire-adapted plants, mainly sedges and grasses. Humans have further increased the frequency of fires, and evidence of the intentional use of fire by hominids in southern Africa dates to at least 1.5 million years ago (Brain and Sillen, 1988; Schülze, 1990; Bond, 1997).

General theory relating to vegetation fires in terrestrial ecosystems (see Bond 1997; Bond and Keely 2001; Gill 1975; Gill et al., 2002) also apply to wetlands. As in terrestrial systems, several key factors affect the type, nature and severity of fire, including:

- State of the potentially combustible material (e.g. fuel load, proportion of green vs. dead material). In many herbaceous wetland areas, mature growth typically has a high fibre content, resulting in it burning easily when cured.
- Weather conditions at the time of the fire (temperature, humidity, wind-speed)
- Time of year of the burn

In addition, the hydrological conditions in the wetland at the time of the burn have important consequences for wetlands. Firstly, flooded conditions, particularly open water areas, may potentially inerupt the spread of fire, as is shown for the Okavango (Heinl et al., 2007). The level of soil wetness also affects the susceptibility to combustion of soils, which may potentially occur in wetlands with organic soils, both as a natural process (see Cypret, 1961; Ellery et al., 1989; Kotze et al., 1994) and induced by human interference, e.g. the desiccation of organic soils as a result of draw-down of the water table. This highlights the importance of drawing the distinction between surface fires, which consume only the above-ground plant parts, and sub-surface fires, which consume below-ground plant parts as well as SOM.

Soil nutrient availability

The effect of surface fires on nutrient availability in the soil is mainly short term. Generally, Ph increases and Ca, Mg, K and phosphates increase briefly in availability following the fire and then return to pre-burn levels (Faulkner and de la Cruz 1982; Wilbur and Christensen 1983; Schmalzer and Hinkle 1992). Although there is extensive volatilization of N during the combustion of plant material (Kleinman et al., 1996), soil N levels are not greatly affected by surface fires in comparison to the fluctuations in soil N caused by changing seasons and soil moisture levels (Faulkner and de la Cruz 1982; Wilbur and Christensen 1983; Schmalzer and Hinkle 1992).

An important contributing factor to the pH changes and increased availability of nutrients following a surface fire is the ash from the fire, and the fate of the ash, which is likely to be affected by precipitation and wind soon after the fire and well as by the landform setting of the wetland (Faulkner and de la Cruz, 1982). Three main possibilities exist: (1.) most of the ash is washed or blown out of the wetland, (2.) the ash remains in the wetland, or (3.) the wetland serves as a depositional site for ash generated in the wetland as well as for ash that washes into the wetland from burnt areas in its upstream catchment. The third possibility is most likely in inward draining wetlands.

Direct heating of the soil may also increase the availability of some soil nutrients in wetland soils, notably P (Faulkner and de la Cruz 1982; Giardina et al. 2000)

Sub-surface fires have more dramatic and longer lasting impacts on the availability of soil nutrients than surface fires. An important mechanism through which this occurs is by physical concentration of non-volatile elements (e.g., P and Ca) as a result of collapsing of the soil which is burnt (Smith et al. 2001).

Although the increased availability of nutrients as a result of surface fires promotes plant growth, it is presumed to also render the nutrients more vulnerable to loss through leaching (albeit for a short period) which is most relevant to wetlands with open drainage. In the case of sub-surface fires, most of the plants are killed, which would delay the uptake of nutrients by plants until new plants have become established. In addition, burnt soil may be rendered much more vulnerable to erosion. These factors, combined with the more extreme effect of sub-surface fires in concentrating nutrients, are likely to result in nutrient losses via leaching being much higher in sub-surface fires than in surface fires. However, no studies could be located investigating the effect of either surface or sub-surface fires on the leaching of nutrients from wetlands.

The high volatilization of N during wetland surface fires could potentially be used to contribute to increasing the effectiveness of a wetland in removing N from a catchment's waters. However, Ostendorp (1995) showed that in the case of a *Phragmites australis* reed bed, 50 to 60% of the N in the culms is translocated down into the rhizomes prior to senescence, greatly reducing the amount of N removed compared with harvesting of living material in the growing season, which would also remove non-volatile nutrients such as P.

Atmospheric emissions

Although there has been considerable research on atmospheric emissions from wetlands, notably that of CH_4, there appears to be a dearth of research on the specific effect of burning in these emissions. The importance of addressing this research gap is emphasized. In the meantime, however, research on combustion emissions from mesic grasslands is likely to provide insights of relevance to herbaceous wetlands, particularly to those which are subject to an extended dry season. Burning of vegetation represents an important source of atmospheric CO_2, CO, CH_4, H_2, CH_3Cl, NO, HCN, CH_3CN, COS, and particulate carbon, which affect the atmospheric photochemical cycle and the Earth's radiation balance (Crutzen and Carmichael, 1993) and fire is a globally significant source of greenhouse gas emissions (Archibald, 2009). Season of burn has an important influence on the quantity and type of emissions from grassland fires (Korontzi , 2005). The fuel tends to be less cured and wetter in early dry season burns than late dry season burns, resulting in less complete combustion and more smouldering emissions per unit area compared with the late burns, which in turn result in lower emissions of CO_2, but this is offset by higher emissions of CH_4, which is a much more potent greenhouse gas than CO_2 (Crutzen and Carmichael, 1993).

Sub-surface fires in particular are characterized by smouldering combustion, leading to high emissions of CO, volatile organic compounds and polyaromatic hydrocarbons, which have potentially serious consequences for human health (Rein et al. 2008; Blake et al., 2009). Given the considerable stores of organic matter in peat, combustion emissions may be very high. During the 1997 fires in Indonesia, peat contributed only about 20% to the total area burned but nearly 90% to the total emissions (Levine 1999, cited by Langmann et al 2009) and although the aerial extent of peat fires currently burning in the drained peatlands surrounding Moscow are much less than the forest fires, they are contributing 80-90% of the air pollution (Wetlands International, 2010).

Soil organic matter (SOM) levels

The negative effect of sub-surface fires on SOM levels is obvious, given that these fires are fueled by the organic matter in the soil. However, the effects of surface fires are much more subtle. Given the fact that in most landscapes, wetlands are the areas with the highest SOM levels, it is surprising that there has been such little research on the effect of wetland burning on SOM specifically. Research on mesic grasslands (Seastedt and Ramundo, 1990; Fynn, 2003) has shown that the the greatest impact is from fires immediately after the growing season, which allows for minimal incorporation of litter when compared with a fire at the end of the growing season, which provides for greater opportunity for litter incorporation. This impact is confined to only the top 1 to 2 cm of soil, because at greater depths the reduced leaf litter is generally offset by fire-stimulated primary production leading to increased root production (Seastedt and Ramundo, 1990; Fynn, 2003).

The results of Fynn et al. (2003) and Seastedt and Ramundo (1990) are likely to be applicable to hygrophilous grassland wetland, which are generally subject to short periods of saturation. For wetland areas subject to more prolonged saturation periods, and Mook and van der Troon (1982) and Thompson and Shay (1985) both showed that below-ground production of *Phragmites australis* reed, growing under conditions of prolonged saturation, was, also in fact, stimulated by fire.

Catchment hydrology

As discussed, frequent burning, particularly that immediately after the growing season, reduces organic matter content of the upper 1 to 2 cm of soil, and in dispersive soils burning may also contribute to soil crusting (Mills and Fey, 2004). These effects, in turn, result in reduced water infiltration, which if taking place in a wetland's upstream catchment, is likely to result in an increase in surface runoff during storm events and a decrease in the sustained supply of sub-surface water to the wetland. Although research on the consequences of this for wetlands seems to be lacking, it would be predicted to depend on the specific circumstances in the wetland, and could potentially cause gully erosion (Macfarlane et al. 2008). Reduced infiltration would also have applicability to temporarily saturated areas within the wetland, which are generally only saturated to the soil surface for brief periods during the wet season. Permanently saturated areas would not be directly affected because their infiltration potentials are inherently very low because of the water table being above or very close to the soil surface throughout the year.

Where natural winter dieback of the leaves of wetland plants takes place, as characteristically occurs in areas experiencing severe winter frosts, then evaporative losses from permanently saturated wetlands are potentially greatly reduced by the dense layer of reflective non-transpiring leaf material. Donkin (1994) showed that evapo-transpirative loss of water during winter from a wetland with abundant standing dead material was significantly lower than the evaporative loss from open water. However, a fire at the beginning of the dry season would leave the wetland very exposed to evaporation throughout the winter season. Under warmer, frost-free conditions, pronounced die-back of vegetation is lacking, and therefore extended periods of exposure as a result of early winter burning are unlikely.

The removal of standing dead material allows greater heating of the soil and improved light conditions for photosynthesizing tissue, thereby enhancing early spring growth. This, in turn, promotes transpirative loss of water from the wetland, but this effect usually lasts for only a few weeks (Sharrow and Wright 1977).

Vegetation structure and composition

Fire affects plants through the combustion of dead and living material as well as through its effects on biogeochmical cycling and hydrology (as already discussed). Fire usually stimulates new growth by opening up the canopy, increasing nutrient cycling, removing litter, and it often does not greatly affect seed survival, but may stimulate germination (Mendelssohn et al., 1988).

Sedges and grasses are generally well adapted to burning, e.g. *Spartina argentinensis*, has a rapid growth response after fire even under drought conditions (Feldman et al., 2004; Feldman and Lewis, 2007). However, a few species such as *Cyperus papyrus*, are less well adapted, e.g. because their rhizomes are not as well protected (Ellery et al., 2003).

Fire is widely used for promoting the growth of favoured native plants and controlling invasive alien species. In Nylsvley, South Africa, the abundance of *Themeda triandra* and *Oryza longistaminata* (both native species valuable for grazing wildlife) was greater and the abundance of *Asclepias fruticosa* (an invasive alien species) was considerably lower in the burnt compared with unburnt areas (Otter 1992). In an investigation of plant species responses to experimental burning of the native wetland prairies of Oregon, a highly threatened wetland type, it was shown that native herbaceous species are fire-adapted, with prescribed burning promoting or maintaining their abundance, and that many non-native herbaceous species are not adapted to fire, with prescribed burning inhibiting or at least not promoting these species (Clark and Wilson, 2001).

Where infestations of invasive alien plants are dense, fire alone is generally inadequate to control alien plants in wetlands and account needs to be taken of the fact that fire stimulates germination of invasive species such as *Acacia latifolia* (van Wilgen, 2009).

The effect of fire frequency and timing on vegetation composition is influenced by the growth patterns of the species present, particularly the dominant species. Species characterized by complete die-off of the above-ground parts at the end of each growing season (e.g. *Phragmites australis*) do not lose any living tissue as a result of a surface fire in the dormant season, and are generally favoured by frequent fires. This contrasts with species such as *Juncus roemerianus* with leaves that live two to three years (Hackney and de la Cruz, 1981). Such species are disadvantaged by frequent fires, which increase the available space for other species (Hackney and de la Cruz, 1981). Ford and Grace (1998) examined the influence of fire on the competitive balance between different species in a *Sagittaria* marsh, where *Spartina patens* cover was reduced while cover of *Sagittaria lancifolia* and *Vigna. luteola* increased as a result of burning. Mendelssohn et al. (1988, as cited by Ford and Grace, 1998) also found fire to suppress *S. patens* cover, allowing a species that would otherwise be an inferior competitor to increase.

The effect of timing of burns has been well researched for *P. australis*. Spring burning enhances performance, as indicated by higher aerial and below-ground biomass and flowering shoot density, in contrast to summer burning, which lowers performance (Mook and vander Troon, 1982; Thompson and Shay, 1985). Autumn burning appears to have an intermediate effect, resulting in higher biomass but reduced flowering shoot density (Thompson and Shay, 1985). Where *P. australis* occurs in a mixed community, e.g. with *Molinia caerulea* and *Cladium mariscus*, burning to disadvantage *P. australis* would potentially increase diversity by reducing the overriding competitive dominance of *P. australis* (Haslam, 1971).

Taxa which are adapted to fire exhibit two main strategies for recovering after a fire, 'reseeding', in which the plant is generally killed by fire and regeneration occurs from seed, or 'resprouters', in which the pereniating buds of a plant generally survive fire, and regeneration takes place by sprouting of new shoots from protected structural features (e.g. trunks, rhizomes or rootstocks (Bond and van Wilgen, 1996). As a general rule, reseeders are potentially better suited than the resprouting taxa to recruit into any large gaps that may develop between the adult plants following fires. However, if the fire return-interval is shorter than the time it takes the plants to reach reproductive maturity then reseeders will potentially be eliminated. The two most dominant families in South African wetlands, Cyperaceae and Poaceae, are generally resprouters. In the fynbos biome, another commonly occurring family in wetlands is Restionaceae, in which resprouting is also the most dominant regeneration mechanism, although some hydric species (e.g. *Chondropeatalum mucronatum*) are seeders (Linder 1991).

The effects of burning need to be seen in relation to other determinants of wetland structure and composition, e.g. soil anoxia (waterlogging), climatic temperatures and other disturbances (e.g. grazing) which may potentially interact with fire (Fig. 2.2). The level to which fire acts as a primary determinant is likely to vary in relation to these other physical factors. It would appear that fire acts as the strongest determinant of herbaceous wetland vegetation structure and composition in wetlands where climatic temperatures are mild and the level of soil anoxia is low. In the absence of fire, these areas most readily become dominated by woody plants. Where soil anoxia is high and particularly where climatic temperatures are cold, these two determinants alone appear to have an overriding, constraining effect on woody plants. There are very few woody plants in South Africa that are well adapted to the highest levels of wetness encountered in wetlands, a notable exception being *Ficus trichopoda*, and these species are confined primarily to mild climatic conditions, with *F. trichopoda* confined to the north coast of KwaZulu-Natal. In South Africa, although there are very few areas where a cold climate alone excludes trees, but the highest grasslands in the Drakensberg may be genuinely "above the tree-line" (Bond et al., 2003).

Even under mild climatic conditions, woody plants are likely to invade wetlands less readily than in mesic, well drained areas. For example on the coastal grasslands of Maputaland, between 1937 to 2000, Dalton (2007) showed that the hygrophilous grasslands were considerably less susceptible to encroachment by woody plants than the well drained grassland areas, but were not totally without encroachment.

In another hygrophilous grassland, located further inland in the sour grassveld of KwaZulu-Natal, with plinthic, seasonally-wet soils, a fire exclusion experiment resulted in invasion by woody plants (Titshall et al. 2000). In a fire exclusion experiment in Catchment 9, Cathedral Peak, KwaZulu-Natal Drakensberg, prior to the exclusion of fire, the wetland area in this catchment consisted of *Scirpus costatus*, *Oenothera rosea*, *Eleocharis dregeana* herbaceous communities and the *Leucosidea sericea* woody community (Killick, 1961) but after 20 years of fire exclusion, the same area comprised the single *L. sericea* woody community (Granger 1976). Therefore, in this case, the exclusion of fire led to a dramatic decline in the diversity of vegetation types supported by the wetland.

Compounding factors may act together with suppression of fire to enhance the invasion by woody plants. This appears to be the case in the coastal areas of KwaZulu-Natal between St Lucia town and Matubatuba. Over the last 50 years or so there has been extensive loss of herbaceous wetland to forest in this area (Ellery W, 2004. *Pers. comm.* University of KwaZulu-Natal). It would appear that the following compounding factors have contributed to this change, disturbance and shading of the herbaceous vegetation by adjacent tree plantations, lowering of the water table and reduced incidence of fire.

In a savanna wetland in southern USA, burns every two to four years result in widely spaced *Pinus palustris* trees and a highly diverse herbaceous ground flora (Martin and Kirkman, 2009). Suppression of fire results in a shift to a ground flora dominated by shrubs and hardwood sprouts, ultimately reaching a hardwood (e.g. *Quercus* spp.) stage, which is fire resistant (Glitzenstein et al. 1995; Martin and Kirkman, 2009).

Even if fire suppression in herbaceous wetlands does not favour woody plants, species composition of the wetland may be greatly affected by the accumulation of litter, which may act to suppress shorter-growing native species. Middleton (2002) observed that without fire, herbaceous peat wetlands in North America and Europe generally begin to loose biodiversity because of shading by litter. A flush of native herbaceous species appears for about two seasons after a fire, but if the peatland is overgrazed then burning may sometimes result in an increase in non-native species, thereby decreasing biodiversity (Middleton, 2002).

Major vegetation changes that are precipitated by fire often take place through the interaction of fire with other disturbances. One of the most common interactions is between fire and the occurrence of particularly dry years which allow for the occurrence of a ground fire. The destruction of existing vegetation (and seed banks) by a ground fire, creates a physical and biological ‘‘opening’’ in the landscape, and this, together with changes in biogeochmical cycling and hydrology (described in earlier in the review) may result in dramatic vegetation changes. Newman et al. (1998) describes how ground fires in the Florida Everglades favoured *Typha domingensis* over the existing dominant, *Cladium jamaicense*, which is adapted to low P environments. Natural abandonment of stream channels may also result in desiccation of wetland areas with organic soils, exposing these areas to sub-surface fires, as described in the Okavango delta (Ellery et al., 1989).

The interaction of fire with hurricane-induced disturbances to bottomland hardwood forest (BHF) in promoting stands of *Arundinaria* bamboo, referred to as canebrakes, is described by Gagnon (2009). Another important disturbance potentially interacting with fire is grazing, and burning generally stimulates grazing by improving forage quality (Lynch 1941, Kays 1956, Smith and Kadlec, 1985).

The destruction of existing vegetation (and seed banks) by a ground fire, creates a physical and biological ‘‘opening’’ in the landscape, and this, together with changes in biogeochmical cycling and hydrology (described in Section 2.2 and 2.3) may result in dramatic vegetation changes. In contrast to the above example, Newman et al. (1998) describes how ground fires may also sometimes favour undesired species, in this case a sub-surface fire in the Florida Everglades favoured *Typha domingensis* over the existing dominant, *Cladium jamaicense*. The ground fire resulted in a lowering of soil elevations as the organic matter was combusted. Given its positive response to flooding, *T. domingensis* is presumably well-suited for growth in the newly formed depressions. However, changes in soil nutrients as a result of the burning process may also play an important role in its establishment and growth in these areas (Newman et al. 1998) given that *C. jamaicense* is adapted to low P environments (Miao & Sklar 1998; Leeds et al., 2009).

4. Conclusions

The review confirms the observation of Smith et al. (2001) that, compared with terrestrial systems, there have been few studies of fire on wetland functioning. Although the greatest amount of literature exists on the effects of wetland fire on vegetation composition and structure, this is focussed particularly on northern temperate areas, and mainly on a few vegetation types, notably *Phragmites*- and *Spartina* dominated types. There is extremely little research on the effect of fire on some key wetland process, e.g. the accumulation of soil organic carbon and the leaching of nutrients from wetland soils. Where important issues are encountered in the review where research for wetlands specifically was lacking then some general predictions were offered based on "first principles" and empirical results from comparable ecosystems, notably grasslands. It is proposed that the research gaps identified will help in identifying important research needs and that the general predictions provide potential hypotheses for testing.

The findings of this review highlight that across all of the processes examined, fire has a potentially great effect. However, the specific effects of a particular fire regime depend strongly upon both the specific characteristics of the wetland (including the wetland's climatic and hydro-geomorphological context) as well as upon other drivers which may interact with fire, e.g. grazing. Thus, similar fire regimes may have dramatically different outcomes depending upon the particular nature and context of the wetlands to which they are applied. Therefore, although generalizations can be drawn from the scientific literature, it is dangerous to generalize too broadly.

With global climate change and continued land transformation, increasing human pressure on wetlands will be inevitable, and human influence over the drivers which affect wetland functioning is likely to continue to increase. An example is the effect that warmer summers are predicted to have on increased wildfire frequency as well as on the frequency of ground fires specifically, as organic soils become increasingly desiccated and therefore vulnerable to fire (Rein et al., 2008), as seen in the extensive peat fires currently occurring in areas surrounding Moscow (Wetlands International, 2010).

Thus, it will become increasingly important to set explicit fire management objectives for wetlands in order to minimize impacts on the benefits which wetlands supply to society. Wetlands may be managed for a variety of objectives, e.g. maintaining the native vegetation, optimizing the assimilation of nutrients, and an important question that will need to be addressed is "what fire regime is likely to achieve the specific objectives set for a wetland's management?" For example, if the primary objective is to maintain the native vegetation, and the wetland was in a climatic context which naturally supported regular fires and the vegetation was fire-dependent then to exclude fire from the wetland is likely to result in failure to achieve the objective.

The current understandings captured in this review of the effect of fire on wetland functioning will hopefully allow such predictions to be made on a better informed basis. Models such as the index of peat fire risk for the Florida Everglades marsh of Smith et al. (2003) and the accompanying document of Kotze (2010) which provide checklists and guidelines for burning wetlands in forestry areas, further assist with such predictions. However, as highlighted in the review, there are still many knowledge gaps in terms of how fire affects wetland functioning, and management must therefore be undertaken in an adaptive manner. Central to this approach is monitoring the outcomes of particular management interventions, and in so doing progressively improve understanding, which will require a long term perspective for the management of fire regimes rather than managing fire as isolated events, as emphasized by van Wilgen (2009).

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