

Earth system feedbacks highlighting Savanna ecosystems

1. Abstract:

Goal: my goal is to gain insight into the vegetation dynamics of the savanna ecosystem. These biomes are often described as inherently unstable and marked by dynamic interactions between plant communities and abiotic factors, wherein relatively small shifts may promote transitions from one alternative state to another. Understanding these dynamics between plant communities and external forcing is relevant as it may enhance insight into patterns of present and future land cover changes (Ex: shrub encroachment in some savannas, loss of tree cover in forests and woodlands, type conversions etc), as well as provide insight into the practicality, feasibility and desirability of human interventions, given common land management goals.

Methods: to gain insight into the processes governing vegetation dynamics, I chose the Mediterranean climate, i.e. savannas, as the main biome and to a lesser extent also tropical forests, in order to limit the scope of my literature review. Firstly, I focus on mainstream theories that describe tree-grass interactions which are the “main players” of the savanna biome, summarize the conceptual models that try to explain tree-grass dynamics over time, and identify the ecological thresholds that determine the stability or transition between alternative stable states. Secondly, I describe important ways by which abiotic factors determine tree-grass transitions and distribution as well as mechanisms by which vegetation feeds back to altering abiotic conditions such as climate, rainfall, fire etc, culminating in the presentation of two distinct and somewhat complementary models that identify new positive as well as well-known negative feedback mechanisms involving vegetation, climate, atmospheric composition and biogeochemical cycles; the 1st one being structured around atmospheric CO₂ content and the 2nd one being structured around fire as the central element. Last, I summarize what the main determinants of fire have been during geologic time and wrap it up by briefly describing how the upper and lower limits for atmospheric oxygen have been set, oxygen and climate being the two main determinants of fire regimes historically. The reason I opted for this rather broad approach is due to the assumption that to better understand relatively short-term outcomes relevant for present and future society, it is helpful to aim for the understanding of “bigger picture/timescale” types of processes and trends, as they may offer additional insight about where we are coming from and to where we are headed.

Results: Trees and grasses exhibit different functional traits and efficiencies relevant for acquiring limited resources as well as different adaptive responses to disturbances such as fire, drought and herbivory. Not only do their differential adaptations and responses to disturbances ultimately determine the future relative dominance between trees and grasses, but their relative spatial presence also exerts influences back upon the abiotic determinants, which may lead to certain positive feedback loops outweighing negative ones, until the system transitions to an alternative stable state.

Fire and CO₂ concentrations play central roles in determining large scale land cover configurations and dynamics. CO₂ levels and changes exert influences through manifold mechanisms such as climate and precipitation patterns, by altering the photosynthetic efficiencies of C3 and C4 plants relative to each other, as well as by inducing physiological regulations such as stomatal density and conductance acclimations and adaptations, which influences NPP, vegetation distribution, and rock weathering rates, thus feeding back onto the atmospheric mixing rates of this gas. Plant species have evolved a diverse range of fire related traits ranging from fire suppressing to fire promoting, and both adaptations as well as inter-species dynamics have to be understood within a given historical fire regime. Fire is also a central element when it comes to negative and positive feedback mechanisms between vegetation, atmosphere and climate, and the magnitude of its influence is largest in systems where seasonality is greatest and such of intermediate precipitation levels. Last, fire moderates terrestrial productivity on large time scales by setting an upper limit to atmospheric oxygen rise, which, on its turn, is largely a result of global productivity, yet without such responsive regulation by fire, oxygen rise would have increasingly deleterious effects over most land biota.

Discussion: the dynamic interaction and combination between major abiotic factors such as CO₂ levels, climate, precipitation, seasonality, and oxygen level has produced the diverse types of life forms, only elusively revealed to us through geologic records and reconstructions. Our reality is such that given present day oxygen levels, climate and seasonality (etc), our current state may be characterized by a “fire deficit” or “biomass excess” within a large fraction of terrestrial ecosystems, while at the same time we are largely witnessing land degradation, tree and biodiversity loss. Therefore, it appears that we cannot justify to not engage in restoration, afforestation and reforestation types of endeavors, nor can we afford to undertake such disregarding climatic constraints and ecological lessons learned from recent failures.

2. Introduction:

According to the Weizman Institute, drylands account for at least 10% of the global afforestation potential (Elbein, Saul, 2019). Allowing for natural regeneration of forests or promoting reforestation and even afforestation is seen by many within as well as outside the scientific community as a compelling goal not only due to the inherent carbon sequestration potential, but, possibly even more importantly due to the additional ecosystem services created such as water purification, micro-climate amelioration (mitigating temperature extremes), erosion control, the value of timber and non-woody forest products, and cultural and ecological value to name just a few. The more ambitious reforestation advocates have even gone as far as to suggest large scale afforestation projects involving part of the Sahara or the Australian Outback, assisted by desalination technology and based on the calculation/expectation that once a large enough area is under a sustained forest cover, the micro-climate may change in such a way as to substantially increase local precipitation, ultimately assisted by an alteration of regional wind patterns (teleconnection) leading to a self-sustained increase in the moisture input originated from the ocean (Ornstein et al., 2009). Such projects, despite their high cost,

have a special appeal, as they would not only add value to areas regarded as largely unproductive, but could seemingly also imply in a powerful mechanism to draw down excessive atmospheric CO₂ and ameliorate climate change (Ornstein et al., 2009). The Nature Conservancy estimates that about 40% of the carbon savings needed to stay within the limit of a 2⁰C increase of global temperatures could be achieved via the restoration of degraded soils, safeguarding wetlands, by avoiding tropical deforestation and by planting new forests (Elbein, Saul, 2019). In many cases, ambitious land restoration and reforestation projects have been actually carried out largely successfully, the most extensive ones in China, which alone accounts for about 25% of global reforestation undertaken since the turn of the century (Ornstein et al., 2009). Unfortunately, other recent cases suggest that planting the wrong trees in the wrong areas may even go as far as causing more harm compared to a “no-intervention” scenario. An example of the latter one took place in Canada in April 2016, probably through the most devastating wildfire in this country’s modern history (Elbein, Saul, 2019). In the 1980s, bogs regarded as economically unproductive had been drained and mostly Spruce trees for timber had been planted on these sites. These trees did extremely well and achieved remarkable growth rates and height, however progressively also leading to a drying out of the underground and changing the local microclimate and hydrology. This caused the original peat moss to be replaced by another moss type more adapted to dry conditions, and once the system surpassed a threshold dry enough to render the ecosystem flammable, the drydown triggered the famous Fort Murray Fire, initially spreading through the dry understory moss and achieving its deadly proportions once it turned into an uncontrollable crown fire. Other examples, such as the largely failed efforts to counter the expansion of the Sahara at its southern border, may be less dramatic in its effects, since in the latter case failure has mostly been attributed to drought as opposed to fire (Elbein, Saul, 2019). Further cases, like the indiscriminate pine plantations (monocultures) in California, highlight the fact that failure may also be largely a function of a poor choice of plants species – seemingly attributed to poor adaptation to local/changing conditions and enhanced by insufficient biodiversity/heterogeneity.

In summary, the above cases suggest that restoration, reforestation and afforestation projects cannot be ignored as necessary and primary management tools or nature-based solutions with the goal of increasing our resilience to the negative outcomes of climate change. At the same time, examples like the ones mentioned above show that such projects need to be carried out in tune with climatic and ecological constraints, which largely take form as wildfires and drought but are also influenced by the intricate interaction among plant communities. The savanna biome embodies a context where all these mechanisms or “forces” are simultaneously at play, as not only are plant communities largely determined by climate and disturbance, but in turn exert their own influence over climate itself, as we will discuss further.

This literature review was guided by questions such as: 1) what are the drivers and mechanisms that underlie present day land cover changes; 2) what processes are at play in determining tree-grass interactions as well as state transitions; 3) what are some current “big picture models” that describe the dynamics between terrestrial vegetation, climate, disturbance (fire regimes), the atmosphere (relative mixing rates of gases), and biogeochemistry; 4) what management practices for fire prone ecosystems such as savanna exhibit a favorable tradeoff between increasing ecosystem services such

as carbon sequestration, erosion mitigation, climate amelioration, biodiversity etc, while also limiting the likelihood of large scale catastrophic types of wildfires, with substantial risk upon human life and property as well as with the potential of altering ecosystem structure in a detrimental manner.

3. Results:

3.1. Tree-grass interactions:

Savannas are representative of a scientific conundrum as, especially the more mesic ones, exhibit consistently lower biomass than the climatic and hydrological conditions would otherwise allow/suggest (House et al., 2003). These are ecosystems characterized by strong alternations between wet and dry seasons, as well as a typically balanced distribution of two contrasting life forms in form of woody (tree) and herbaceous (grass) functional types, which will here be represented by the term “trees” and “grasses”, although other types of herbaceous and woody shrubs may be of equal importance.

Tropical savannas cover about an eighth of global land surface, comprising half the area of both Africa and Australia, 45% of South America and 10% of India and Southeast Asia. In North America, temperate savannas occupy over 50 million hectares of land. Savannas also contains large and rapidly growing human populations and the majority of its rangelands and livestock, globally. (Scholes & Archer, 1997b)

Paleo-ecological evidence suggests that the origin of the savanna biome has been a relatively abrupt one when considered within geologic time. It appeared during the late Miocene in equatorial regions “simultaneously” in different continents from where it spread towards higher latitudes. Explanations attributed to the spread and establishment of this new biome has been the decrease of atmospheric CO₂ levels – which favor the C₄ photosynthetic pathway over C₃ – as well as an increase of precipitation seasonality, setting up the right conditions for fires, and associated to the onset of the monsoonal climate of the Miocene. (Bond, 2008)

The spatial pattern and relative abundance of grasses and woody plants in savannas are dictated by complex and dynamic interactions among climate, topography, soils, geomorphology, herbivory, and fire (Ingvar, 1992) (Solbrig & Medina & Silva, 1996). These interactions may be synergistic or antagonistic and may reflect stochastic variation or positive feedbacks. In addition, some savanna vegetation has undoubtedly been derived and maintained by prehistoric, historic, or recent human activities. In many areas, “natural” and anthropogenic factors interact, making it difficult to identify, isolate, or quantify the key determinants of savanna structure. (Scholes & Archer, 1997a)

On the landscape scale, tree and grass densities almost always correlate negatively, meaning their interaction is overall marked by competition. Yet, on an individual tree patch scale, trees may both facilitate as well as hinder grass growth, highly mediated by abiotic factors such as precipitation, soil characteristics, climate, and disturbance (Scholes & Archer, 1997a).

Precipitation has frequently been regarded as the primary determinant of tree cover. (Bond, 2008) found that although there appears to be a weak yet significant correlation between total annual rainfall and percent tree cover, this relationship is largely scattered and marked by a very high variance, suggesting significant co-determination by other factors. One such factor is the interaction between precipitation seasonality and differences in root systems. While grasses are more efficient in acquiring moisture during the growing season, trees are able to access moisture throughout an overall longer period – far into the dry season. Overall, it appears that the relative distribution of rainfall exerts a higher influence over the relative dominance of trees and grasses than *total* precipitation within a year does (Fensham et al., 2009) (Bond, 2008).

The positive correlation between fire frequency and grass dominance appears to overall be the rule across ecosystems, as discussed by different authors/studies (Higgins et al., 2000) (Bond & Midgley, 2012). Grasses respond much faster than trees to pulses in moisture (after rainfall) or nutrients (for example after fire), which enables them to rapidly ramp up growth as soon as conditions become favorable. Above ground biomass produced by grasses also dries out quickly at the onset of the dry season and exhibits low decomposition rates due to high C:N ratios, stemming from very high N use efficiencies. The combination of fast growth, low decomposition rates of dead/dry above ground biomass, and the drying out early in the dry season is especially conducive to frequent surface fires, in some ecosystems as frequent as at annual intervals (Bond, 2008). Since grasses are also more efficient resprouters (than most trees and shrubs) after disturbance, fire events in particular enhance the spread of grasses in detriment of woody vegetation, and more extensive grass cover tends to be considerably more conducive to fire compared to a savanna dominated by trees, often generating a positive feedback loop between fire frequency and grass dominance, maintained by precipitation seasonality.

Just like higher rainfall is correlated with higher tree cover, aridity largely correlates with grass cover (up to a certain threshold), however this relationship is not always true, as for example some treeless grasslands receive more rainfall than savannas where small trees and brush are the dominant vegetation type (Bond, 2008). Trees are generally well adapted in accessing scarce water resources, which is largely unavailable for grasses during most of the dry season, whereas grasses capitalize/respond much more readily once water becomes available. Therefore, overall a more predictable and less seasonal rainfall pattern (small variance) would favor trees, while a more erratic one would favor extended dormancy combined with rapid resprouting, characteristic of grasses (Scholes & Archer, 1997a).

Nutrients tend to be in higher supply under tree cover (Scholes & Archer, 1997a). However, it is not clear whether low nutrient areas/soil are a result or cause for the predominance of grasses, whose thriving tend to be less limited by low nutrient soils than what is typically the case for trees, given that the presence of grasses, due to its favoring of higher frequency fire regimes, may to some degree also cause a higher nutrient depletion (Wood & Bowman, 2012). Another important phenomenon influencing nutrient distribution is the so-called island of fertility. Trees and bushes, especially those adapted to aridity, tend to extend their lateral root systems far beyond the reaches of their canopy

(Scholes & Archer, 1997a). Over time, due to biological rock weathering and litterfall, trees appear to act as nutrient – and water – pumps, with the net effect of concentrating more nutrients and especially organic matter underneath their canopies in detriment of the “in between canopy spaces”, typically occupied by grasses. This phenomenon is thought to be further enhanced by “secondary mechanisms” such as the interception of airborne particles (nutrients) by trees as well as due the occasional presence of shade seeking herbivores or nesting birds, which are expected to spend a larger amount of time underneath canopies especially in more arid sites, which would additionally contribute to nutrient accumulation (Scholes & Archer, 1997a).

Soil types - mostly texture and depth - has been identified as another important factor mediating tree-grass interactions. Generally, less fine textured soils – where percolation is enhanced – and at locations where the soil profile is deeper should enhance tree development and dominance, whereas their finer structured counterparts or soils with some sort of impermeable types of layers/pans should favor the dominance of grasses (Scholes & Archer, 1997a). This outcome is largely attributed to the root niche separation concept, also known as resource partitioning, which we will discuss ahead. At the same time, finer textured soils imply in increased water and nutrient storage and availability, thus along a soil texture gradient, there seems to be a tradeoff between percolation ease and nutrient/organic matter accumulation, both of which are primary factors for tree growth enhancement. *The fact that tree sizes and densities on savanna landscapes are often highest in intermittent drainages characterized by fine-textured soils seems contradictory to the trend for greater sizes and densities on coarse-textured uplands. However, in cases of intermittent drainage, the additional moisture and nutrients received as run-off from upland portions of the landscape apparently override soil texture constraints.* (Scholes & Archer, 1997a).

Herbivory and fire have a somewhat analogous effect concerning triggering resprouting on grasses. However, although both stimulate grass regrowth, recurrent fires overall tend to shift the tree-grass balance towards grass dominance, whereas grazing has the opposite effect (Scholes & Archer, 1997a). The reasons for that are mainly twofold: grazing, by reducing the water use of grasses, tends to increase the survival rate of tree seedlings and small saplings and, arguably most importantly, by reducing burnable biomass, the fire risk and frequency also gets significantly reduced, therefore indirectly favoring tree recruitment. Browsing is thought to have a neutral to grass cover enhancing effect, depending on species involved and ecosystem. Interestingly it has also been observed that the same species of trees assume different phenotypical expressions contingent on the historical prevalence of fire or browsing. So overall, trait selection under historically more intense fire pressure tends to favor trees with tall and sparsely branched stems and swollen roots high in carbohydrate reserves, which are key for post-fire resprouting vigor. Whereas in ecosystems where grazing and browsing is prevalent over fire, individuals with cage like canopies have been selected instead (Archibald & Bond, 2003).

As mentioned earlier, although generally tree dominance comes at the detriment of grass growth and vice-versa, trees have been observed to have both an exclusion as well as facilitation effect upon grasses, which is highly site and species specific. Overall, grasses under tree canopies experience

reduced water stress - due to shading - and may also have more access to nutrients compared to grasses growing in between canopies due to the nutrient pump effect engendered by trees. Litterfall may also contribute to a higher nutrient availability underneath canopies while, at the same time, depending on factors such as amount and timing of litterfall as well as pH, may yield an overall grass growth inhibiting effect instead. Furthermore, it has been found that generally tree facilitation of grass growth appears to decrease with increasing rainfall, not surprisingly as water stress – which is negatively correlated with shading – becomes less critical (Scholes & Archer, 1997a). Conversely, grasses growing in-between canopies are expected to experience increased water stress, possibly higher nutrient limitation (depending on the local extent of the nutrient pump phenomenon), however will not experience any growth limitation due to shading. Thus, along a rainfall gradient, at the lower precipitation/higher aridity end, water stress should outweigh growth limitation by light, favoring grasses adapted to growing underneath tree canopies, whereas on the higher precipitation/lower aridity end, light limitation over growth may act as the primary bottleneck, in this case favoring grasses growing in-between canopy spaces. At the same time, this trend may not always be true, often depending on tree and grass species as well as soil characteristics. *In oak (Quercus douglasii) savannas in the western United States, herbaceous production is enhanced under tree canopies in drier regions but is reduced under tree canopies where annual rainfall exceeds 500 mm (McLaran & Bartolome, 1989). In drier regions of Kenya (450 mm annual rainfall), tree species (Acacia tortilis and Adansonia digitata) had a similar and positive influence on herbaceous production (95% higher under trees than in the open). However, on a more mesic site (750 mm annual rainfall), tree canopy enhancement of herbaceous productivity was substantially diminished and differed with tree species (52% higher under A. tortilis canopies than in the open, but only 18% higher under A. digitata). While these results support the hypothesis that facilitation is most likely to occur in stressful environments (Callaway, Ragan M., 1995), a comparison of 10 studies showed that enhancement or suppression of grass production by tree canopies was unrelated to annual rainfall (Mordelet & Menaut, 1995)(Scholes & Archer, 1997a).*

Besides or in addition to the primary influence of rainfall over tree-grass interactions, the net effect – facilitation vs inhibition - of tree growth over grasses has also found to be largely tree density dependent, so for instance, as trees grow and in-between canopy spaces shrink, an overall facilitation may shift towards net inhibition of herbaceous growth, highlighting the dynamic aspect of tree-grass interactions. *Because of the potentially positive effects of trees on grasses, herbaceous diversity and production may be greater where there are a few trees than where there are no trees, but the trend is reversed at high tree densities (Cameron et al., 1989) (Sciffres et al., 1982) (Stuart & Tainton & Barnard, 2010) (Scholes & Archer, 1997a)*

Last, tree-tree interactions have been regarded as predominantly competitive mostly via competition of belowground resources (water and nutrients) in dry regions. However different types of spatial distribution patterns also suggest some degree of facilitation taking place occasionally. *Savanna tree distribution can be over-dispersed (a quasi-regular spacing, suggesting competition), clumped (suggesting facilitation), or random...Competition between trees can occur in most open savannas but is influenced by topographic factors and is often counterbalanced by elements of facilitation, especially during the phase in which tree seedlings are established. (Scholes & Archer, 1997a)*

3.2. *Tree-grass interaction models:*

Different theories have been developed to explain tree-grass coexistence based on competitive interactions, differential resource use efficiency, different growth strategies, and differential response to disturbance, especially fire. (House et al., 2003) frames such theory by four conceptual models: niche separation, balanced competition, competitive exclusion, and multiple alternate states.

The assumption underlying the root-niche separation models is that plant communities in savanna systems are ultimately limited by moisture, which varies seasonally and limits growth. While grasses are more efficient in accessing soil water in the upper soil layers and during the growing season - due to overall higher fine root biomass - trees compensate for that disadvantage by exclusively accessing water from subsoil layers and thereby extending their growing season beyond that of grasses.

The *root-niche separation model by depth*, also known as Walter's two-layer hypothesis (Mueller-Dombois & Walter, 1971) understands that the relative partitioning between trees and grasses in savannas is largely modulated by abiotic factors such as soil types, and rainfall distribution, the reason for that being that such will ultimately determine the proportion of water reaching deeper soil layers to which only trees have access. So, for instance, sandier/coarser soils with some rainfall outside the grass growing season would favor trees more than grasses. It is important to note that, although differential ability to obtain resources due to varying root patterns in depth has been confirmed, it appears that trees still obtain most of their water and nutrients from upper soil layers where root systems of trees *and* grasses overlap (Scholes & Archer, 1997a).

Interannual *variation* of rainfall regarding absolute precipitation as well as distribution throughout the year is thought to enhance the overall balance between trees and grasses, by favoring trees in some years - i.e. more rainfall outside the growing season of grasses - and grasses in others - i.e. more frequent/smaller rainfall events (House et al., 2003). According to (Schenk & Jackson, 2002), *in general, spatial niche separation in root distributions appears to be more prevalent in arid systems where the bulk of precipitation falls during the non-growing season* (Sankaran et al., 2004). Although the ratio or dominance between trees and grasses has in some cases been found to be largely explained by their different abilities to obtain soil water, this model cannot explain the great tree-grass variation *within* a single climate-soil combination. (Scholes & Archer, 1997a)

Root-niche separation by phenology states that while grasses have a competitive advantage in accessing water and nutrients *during* the bulk of the growing season due to higher finer root biomass within the upper soil layers, trees have the ability to carry over stored resources from the previous growing season (nutrients and carbon stored within roots, which for going deeper, also allow for extended access to soil water), enabling them to extend their growing season beyond that one of grasses. In that sense: *we would predict dominance by trees wherever seasonality is strong, protracted, and predictable. In arid unpredictable environments dominated by small rainfall events, the opportunistic strategy of grasses would be favored* (Soriano & Sala, 1984)(Scholes & Archer, 1997a).

The *balanced competition model* is based on a few assumptions: 1) that intra-species competition outweighs inter-species competition, 2) that intra-species competition increases with plant density and

3) trees exhibit different degrees of vulnerability and dominance along their life stages. While the more competitive plant species (in this case adult trees) outcompetes the less competitive one (grasses), trees become self-limiting (due to intra-species competition) at a density inferior to the one required to completely eradicate the inferior competitor (grasses). In other words, in a scenario of limited disturbance (fire) and sufficient moisture, a savanna is expected to eventually transition to a woodland with very sparse grass cover, wherein tree density is now largely limited by tree-tree (intra-species) competition rather than by disturbance (Scholes & Archer, 1997b). As discussed earlier, while adult trees tend to outcompete grasses due to shading, young trees are outcompeted by grasses primarily owed to moisture limitation and fire, which frequently yields a balanced competition and population equilibrium. (House et al., 2003). In this model, rainfall would be the ultimate defining driver whether a system stays in a savanna-like state or shifts into a woodland. Meaning that beyond a certain rainfall threshold, tree recruitment increases non-linearly and the system shifts into a woodland, where tree growth is now limited by tree-tree competitive interactions instead (Sankaran et al., 2004).

The *competitive exclusion model* understands the spatial equilibrium between trees and grasses to be inherently unstable. A given savanna biome would be a snapshot within a transition to a more stable state, in which one of the competitors has gained upper hand. Thus, if drought as well as disturbance by fire is limited, a transition to a woodland would be unavoidable, while in the reverse scenario, an open grassland would be the ultimate consequence (House et al., 2003)

The *multiple stable states model*, states that tree-grass partitioning may assume different alternative stable states along a gradient of environmental variability. Perhaps the most dominant mechanism may be associated with fire. Within a certain annual rainfall variation range, there is a positive correlation between rainfall and fire frequency (specific to each ecosystem), favoring grass production with increasing rainfall, while beyond a certain annual rainfall threshold, the correlation between fire and rainfall becomes negative, at which point a rapid transition from savanna to woodland would be expected. (rainfall is assumed to be highly seasonal in this case, in order to allow for the seasonal drying out of biomass)

The multiple stable states model may give rise to a phenomenon or concept also known as hysteresis. Using the previous example, once a transition to a woodland has been achieved, a subsequent decrease in precipitation (which theoretically should now increase the correlation between fire and rainfall again) may not conversely result in a transition back to savanna, due to the (new) change in microclimate engendered by a largely closed canopy pattern – decreased wind, enhanced moisture, lower temperature and, most importantly, less easily burnable fuel and increased fire resistance. Alternatively, deforestation of a closed-canopy forest, by allowing the spread of more flammable grasses and due to a microclimate change, will likely intensify fire frequencies, thus preventing the system from returning to the original closed canopy state and possibly even enhancing the trend of tree loss (Archibald et al., 2018). In addition to the direct action of fire in undermining tree recruitment, intensification of the fire regime has in some cases been found to deplete nutrients and soil organic matter over time. Since grasses are better equipped to thrive on poor soil, an additional positive feedback loop can be established, triggered by either deforestation or drought and kept in a

low biomass/high fire frequency state, by limiting tree growth due to progressive nutrient depletion by fire (Wood & Bowman, 2012). *Transitions to alternate states may be accelerated if 'keystone species' establish and alter resource or disturbance regimes (D'Antonio & Vitousek, 1992) or if geophysical forces (e.g. wind, water erosion) initiate positive feedbacks (Schlesinger et al., 1990) (Archer & Stokes, 2000) (House et al., 2003).*

More recent so-called *demographic-bottleneck models* shift away from regarding the post-disturbance competitive interaction between savanna plant life forms as the main determinant of the tree-grass ratio. These models rather suggest that the differential influence of abiotic factors upon different tree life stages, ultimately determines whether or not trees are able to displace grasses over time. In that sense, while adult savanna trees are largely immune/adapted to local (historical) drought and fire events, at the seedling and sapling stage, drought and fire are the primary determinants limiting tree survival. A large proportion of seedlings – which tend to be present in higher numbers than saplings, thus the bottleneck – are killed by both drought and fire. In most savannas, drought is a more prevalent disturbance than fire, meaning drought acts as the main bottleneck for seedling survival. At the sapling stage – the survivors of drought – need to achieve a certain height as well as bark thickness in order to escape the flame zone and enhance their fire-resistance, respectively. The ratio of saplings able to escape the fire trap – which is largely a function of the interplay of fire frequency vs resource availability – will ultimately determine local tree recruitment rate.

In arid savannas the dominant bottleneck to tree recruitment is given by seedling survival due to drought. In contrast, in mesic savannas, it is rather fire frequency and intensity acting as the main bottleneck and thus determining the sapling survival rate. (Sankaran et al., 2004). Climate and precipitation seasonality emerge as primary modulators of such bottlenecks. For instance, while above average rainfall increases seedling survival in arid savannas, potentially favoring a subsequent shift towards an overall higher tree population, in mesic savannas it typically leads to proportionally higher burnable biomass (grasses more efficient in capitalizing from increased moisture during the growing season) with the net effect of topkilling a higher ratio of tree saplings, likely shifting the system towards increased C4 grass cover. Drought, on the other hand, would naturally increase seedling mortality, decreasing long-term tree recruitment in arid savannas, while, in mesic savannas, it would interestingly increase overall tree-recruitment as burnable biomass and thus fire frequency and intensity may be lowered (Bond, 2008).

All these models highlight various mechanisms that account for aspects of the interaction and relative dominance between trees and grasses. Presently it is believed that the long-term co-existence pattern between these plant communities may be less determined by different a priori abilities to obtain key resources, but rather by the interplay of abiotic factors such as climate and fire acting differently on growth and recruitment abilities of trees and grasses and, most importantly, with varying outcomes along tree life stages. So, for instance: *It is further useful to divorce the issue of co-existence of trees and grasses in the long term from the issue of resource partitioning in the short term, since the two may bear little relationship to one another outside of computer simulations. The dynamics of savannas, and probably many other ecosystems, are driven to a large degree by factors such as climate that*

originate outside the tree-grass system (Skarpe, 1992). The vegetation structure is therefore only to a small degree the result of the cumulative effect of competition for resources. Co-existence of trees and grass in this view is largely a result of the interaction of a variety of stressors and disturbances, acting differentially on trees and grass and patchily in time and space. Equilibrium niche theory is useful for understanding patterns of resource partitioning in between these stress periods. (Scholes & Archer, 1997a)

As suggested above, savanna plant community balance and interactions are highly defined by stressors and limitations acting differently upon different species. The limiting effect of one stressor may be magnified as it often implies or enhances limitations by a 2nd or even 3rd factor. Moreover, multifactor limitation does not act equally on different plant species, as their inherent abilities to shift physiological responses to stressors is largely genetically defined. For instance, limitations such as water do not have a linear effect on growth but interact with the ability of plants to absorb nutrients, which on their turn have a determining role on the photosynthetic capacity and therefore growth (Chapin et al., 1987). In that sense: *Nutrients are mineralized, transported to the root, and taken up only in the presence of water. Most of the observations advanced to suggest water is the main resource competed for by savanna vegetation (for instance, the near-linear relation between net primary production and annual rainfall) can apply equally to nutrients. A simplistic "law of the minimum" view of competition is not useful in this context. Multiple-factor limitation is the norm, either sequentially or simultaneously (Chapin et al., 1987) (Scholes & Archer, 1997a).*

In summary, resource partitioning is a useful concept in describing the co-existence of trees and grasses and influencing their relative ability to obtain resources given local abiotic constraints and climatic conditions. Resource partitioning varies dramatically along the life cycle of trees, yielding a dynamic and varying outcome with regards to the relative dominance between trees and grasses. Environmental factors such as fire regimes, precipitation and climate seasonality, soils, nutrient status, herbivory etc act differently on trees and grasses and imply in different magnitudes of stress/constraints along tree life cycle stages (Sankaran et al., 2004). In the absence of fire, or if fire intervals get extended for example due to more intense grazing, a savanna is expected to naturally reach its climatic potential and transition to a woodland with sparse or absent grass cover; while, conversely, there is an undeniable positive feedback between grass dominance and fire frequency – fire frequency being positively correlated to precipitation seasonality - keeping many savanna systems in a more flammable state. Tree seedlings are mostly limited by drought – often mediated by competition with grasses – while tree saplings are mostly limited by fire frequency - indirectly enhanced by grasses. *Tree-grass interactions in savannas cannot be predicted by a simple model. They include elements of competition and facilitation, varying complexly in both time and space. Coexistence is permitted by a combination of niche separation, stronger intra-life-form than inter-life-form competition toward the extremes of dominance, a balanced asymmetry of competition, and most importantly, frequent levelling disturbances, particularly fire...In reality, savanna structure is hierarchically constrained: by climate at regional-to-continental scales; by topographic effects on rainfall and landscape water redistribution, and by geomorphic effects on soil and plant-available water*

at landscape-to-regional scales; and finally by water redistribution and disturbance at local and patch scales (Coughenour & Ellis, 1993) (Scholes & Archer, 1997a).

3.3. Ecological thresholds:

Some of the patterns marked by interactions between abiotic factors such as fire, climate, soil types and hydrology with adaptive plant responses within a context of resource limitations, are of similar nature when comparing dynamics of tree-grass interactions *within* a savanna as well as transitions *between* savannas and forest. *The transition from savanna to forest shares many common elements with an analogous transition that occurs when an individual tree stem reaches a fire-resistant size and is no longer susceptible to topkill... both transitions mark a change from (1) a state maintained by regular fire to (2) a state that is largely uninfluenced by fire.* (Hoffmann et al., 2012)

Plant cover in xeric savannas is often dominated by grass species. Tree development/spread is less a function of frequent fire disturbances but rather due to climatic and hydrological constraints which act as a bottleneck for young tree survival. In other words, the development of tree communities is hindered or limited by resource limitation, typically drought and possibly enhanced by shallow soil with little available nutrients and low CEC. Mesic savannas, on the other hand, often occur under climatic conditions and associated to soil profiles comparable to seasonally dry tropical forests, and the decisive differentiating factor is fire frequency, which selects for different plant communities in these two climatically comparable biomes. In that sense tropical forests and mesic savannas can be seen as two different alternative states. As discussed in the alternative states model, fire suppression will enhance tree recruitment and likely lead to a transition to a more closed-canopy-like system, with amelioration of the microclimate and drastic reduction of its flammability and thus fire frequency. Conversely, a tropical forest may also shift to a more open canopy savanna-like-system due to extended and repeated droughts, triggering fires, or due to human interventions such as deforestation, shifting the system into a much more flammable state. Within these transitions, there are two essential changes that are worth characterizing conceptually: the *fire-resistance threshold* and the *fire-suppression threshold*. (Hoffmann et al., 2012) The fire resistance threshold relates to individual trees as they reach certain minimum height and bark thickness, which allows them to resist (not get topkilled) by local fire regimes. This is an important threshold as it will determine the fraction of tree saplings that make it to maturity at a given fire interval, and ultimately whether the system stays stable or whether the relative dominance of grasses or trees is shifted one way or another. The fire-suppression threshold, on the other hand is achieved when canopy closure sufficiently changes the microclimate (less wind, more moisture, lower temperatures) increasingly suppressing fire, by means of a positive feedback pattern that culminates in a closed forest, where growth is now no longer limited by fire frequency but rather likely due to tree-tree competition for resources and possibly even light. It's also worthwhile noting that, although typically within a transition from savanna to forest, the fire-resistance threshold needs to be achieved first, these two thresholds are essentially independent from each other, so for instance a fire-suppression threshold can be achieved without individual trees being fire-resistant. (Hoffmann et al., 2012)

Achieving the fire-resistance threshold is determined by the interplay of fire intensity and frequency and the attainment of a certain bark thickness as well as stem height and diameter of individual young trees. Bark thickness has been found to be the best predictor for fire resistance. *Based on data from 56 species obtained from 15 fire events (Fig. 2a), a bark thickness of 5.9 mm is needed to ensure a 50% chance of surviving a low-intensity fire (flame length < 2 m). For high-intensity burns (flame length > 2 m), bark thickness of 9.1 mm is required to reach this level of safety.* (Hoffmann et al., 2012)

The achievement of the fire-suppression threshold takes place due to a microclimate change resulting from canopy closure as well as a limitation or elimination of C4 grasses whose drying out is typically what consists of the main source for fires to ignite. Thus, the spatial extent of C4 grasses or conversely the relative canopy area occupied by trees have been identified as useful proxies indicating whether or not a system has achieved effective fire-suppression. *Based on data from savannas and forest in central Brazil* (Hoffmann et al., 2005) (Silva et al., 2008) (Geiger et al., 2011), *this threshold is reached when the leaf area index (LAI) of the overstorey reaches ~3.0. Alternately, (Archibald et al., 2009) found flammability to decline dramatically when tree cover exceeds 40%* (Hoffmann et al., 2012).

It's worthwhile noting that the quantification of these thresholds is useful for standardization purposes, however it may lead to over-simplifications when accessing the fire dynamics of individual ecosystems. So, for instance, a relatively open savanna that is grazed may have a higher fire resistance than proxies such as average bark thickness would otherwise suggest, or a relatively closed woodland may be less fire-proof than suggested by LAI indexes, if seasonality and duration of drought increase in a particular year.

Essentially, the achievement of either of these thresholds is determined by the interaction of fire frequency (negative correlation) and tree growth rate (positive correlation). Fire frequency is largely a function of climate and plant species - how much flammable biomass gets produced given certain climatic conditions. Tree growth (either to escape the fire trap or to promote fire suppression) is mostly a function of resource availability. Within a scenario of higher rainfall, richer soil and higher nutrient availability, a larger number of young trees have a higher chance of achieving the fire-resistance threshold for a given average fire regime. At the same time, especially when most of the rainfall takes place during the growing season of grasses, higher quantities of highly dry burnable biomass are produced, which in this case may enhance fire frequency and intensity, *as rainfall increases* (Archibald et al., 2010) (Hoffmann et al., 2012).

Historical fire regimes are thought to have selected well matched adaptive strategies in local plant communities, constituting one of the primary natural selection and speciation agents. Savanna trees, since they have historically been under selective pressure of relatively high fire incidence, invest a large fraction of carbon resources into extensive root systems with abundant carbohydrate reserves – enhancing resprouting vigor – and in the production of thick bark (main trait for fire-resistance), leaving less resources available for rapid above ground biomass accumulation (vertical growth). When topkilled, most forest species have very low - if any – resprouting ability, thin bark, and most of their carbon is allocated into vertical growth. Therefore, it stands to reason that the ease or likelihood for a system to achieve fire-resistance is mainly a function of the relative presence of savanna trees,

whereas it is a function of the density of forest trees - which are also typically shade tolerant - to achieve the fire-suppressive threshold. This, however, does not imply in either an exclusion of savanna trees in forests or in forest trees from savanna systems necessarily. *For those species with sufficient data, savanna species require from 3 to 24 years (median = 15) to accumulate 5.9 mm of bark, whereas forest species require from 16 to > 50 years (median = 31).* (Hoffmann et al., 2012)

In summary, it is the interplay of the different abiotic and biotic factors acting over tree recruitment, growth rates and canopy closure potential with fire frequency patterns that ultimately will determine in which direction – if any - a system will develop. The relative composition of a plant community at a given point in time is also of significant relevance as for example C4 grasses efficiently capitalize from resources available within the growing season and generate more fire by accumulating burnable biomass, while the local distribution and types of dominant tree species imply in different abilities to promote fire resistance and suppression. The balance between fire promoting and fire suppressive species is often a rather unstable one. Apparent stability over time is highly dependent on a certain combination of disturbance frequency, type, and magnitude (fires, droughts, herbivory), local resources (soil, rainfall) and plant functional traits. Furthermore, so called large infrequent disturbances (LIDs) (Fensham et al., 2009) (Bond, 2008) are often more significant in shifting community structure one way or another than *average* precipitation, drought and even fire, since, as discussed before, the population shift resulting from a surpassing of a threshold may not be reversed once conditions return to “normality”.

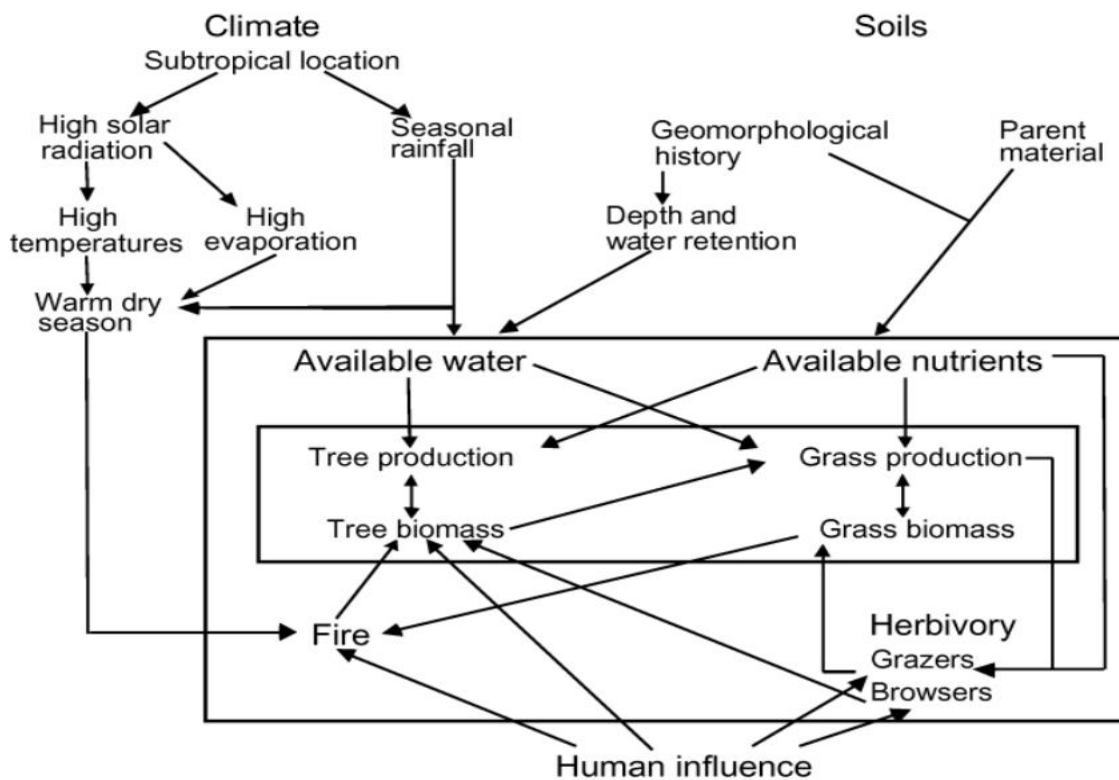


Figure 1: Key driving variables and feedbacks for mixed tree–grass systems (Scholes & Walker, 1993). Numerous factors interact to affect the abundance of grasses and woody vegetation in drylands. The balance between trees and grasses (innermost rectangle) can feed back to the ecosystem dynamics of water, nutrients, fire and herbivory (outer rectangle), which may in turn affect trees and grasses differently, creating feedback loops. The outside of the rectangle relates to extrinsic factors to the system and remain unaffected by the tree–nutrient–fire–herbivory feedbacks (House et al., 2003).

3.4. Atmosphere-vegetation feedback mechanisms:

Vegetative land cover and climate are intrinsically connected and influence each other at different magnitudes and within different time scales. Vegetation type and distribution have a complex effect over climate via biophysical as well as biogeochemical mechanisms, in some cases generating positive feedbacks between climate and land cover changes. In the next section we will describe the change of tropical forest cover with regards to their effects on climate and biogeochemistry, and the resulting feedbacks over plant communities. In that sense it is worthwhile noting that while in some cases a net effect of woody plant cover increase – natural bush and brush encroachment – is observed in tropical savanna systems, in many other cases a net reduction of tree cover results typically from human induced changes promoting deforestation and increased fire susceptibility. (Spracklen et al., 2018) identified that *most historical land cover change (LCC) has occurred in temperate regions with, until recently, less LCC in the tropics* (Hurt et al., 2011). *Rapid LCC has occurred in the past few decades, with 2.3 million km² of forest loss and 0.8 million km² of forest gain over the period 2000 to 2012, and the greatest rates of forest loss now occur in the tropics* (Hansen et al, 2013). To understand basic feedback mechanisms between land cover change and climate, we will briefly describe some of these key mechanisms next.

3.5. The effect of tree cover loss on local climate:

Tropical forests have the highest evapotranspiration rates of all terrestrial biomes due to low albedo, high leaf area index (LAI), high surface roughness length, and high rooting depth, all of which favor high rates of evapotranspiration one way or another. (Spracklen et al., 2018). Tropical forests also tend to have one of the lowest Bowen ratios (sensitive heat flux/latent heat flux) of terrestrial biomes, which is a direct effect of high evaporation rates and explains the average lower temperatures as well as temperature *variations* when compared to savanna or grasslands. (Spracklen et al., 2018). Loss of woody biomass in savannas reflects on climate by different biophysical as well as biogeochemical pathways. Albedo increase – resulting from tree cover loss – has a net cooling effect, since more energy is reflected as opposed to being absorbed, however the accompanied reduction of net solar energy received at the surface yields a reduction of the total energy available for evapotranspiration (Hoffmann & Jackson, 2000). Additionally, decrease of total surface roughness length, average rooting depth and LAI, has the combined effect of further diminishing total evapotranspiration, reducing the latent heat transport, yet conversely increasing the sensitive heat flux (increase of the Bowen ratio). Decreased evapotranspiration in turn leads to a reduced cloud cover – which may further increase incoming solar radiation – as well as reduced precipitation recycling (Spracklen et al., 2018). The overall drying out as well as warming of the atmosphere resulting from deforestation – due to the fact that trees are outcompeted by grasses as the climate gets drier and warmer - has the potential of establishing a positive feedback between tree loss and local climate change. Such a feedback spiral may shift the whole system to an alternative state, given that as these

trends advance, both progressively increasing drought as well as expected higher fire proneness may further inhibit original tree growth.

3.6. Biogenic emissions of non-methane hydrocarbons:

Non-methane hydrocarbons (NMHCs) are estimated to be over 90% of biogenic origin (naturally emitted by plants). (Hoffmann & Jackson, 2000). (Archer, Boutton, & Hibbard, 2001) found that most of the biogenic NMHC emissions are associated to evergreen slow growing shrubs as being largely a direct reflection of the buildup of chemical defenses to limit herbivory, being low for grasses as well as for fast growing trees. NMHC are of environmental as well as global energy budget concern due to their atmospheric chemistry which tends to increase the production of ozone, carbon monoxide and organic peroxides, while also reducing the net oxidative capacity of the atmosphere and thus likely increasing the residence time of greenhouse gases such as methane in the atmosphere. (Archer, Boutton, & Hibbard, 2001).

As mentioned earlier, the enhancement of the production of NMHCs is associated to the spread of slow growing evergreen shrubs, while being low for plants that invest resources in fast growth such as grasses as well as deciduous trees growing in moister and warm climates. Therefore, the natural phenomenon of woody plant encroachment which has been documented in many savanna ecosystems, appears to imply in a significant increase of the NMHC release, as the types of trees and shrubs at the forefront of woody plant encroachment are typically such that allocate a high fraction of resources for defense against herbivory – highly correlated to the production of NMHCs – in an aim of realizing a positive return on foliar investment by increasing leaf longevity (Archer, Boutton, Hibbard, 2001). According to these author`s field measurements, the production of isoprene – a NMHC *not* associated to defense – increased exponentially with temperature increase – from 20^oC – 40^oC – in a savanna biome in North Texas, suggesting that production of NMHCs is not only sensitive to land cover change but also to temperature change. Their model predicts that a doubling of CO₂ levels would also roughly double the emissions of NMHCs.

3.7. Influence of fire on local rainfall:

Research such as that of (Andreae et al., 2004) have studied the effects of smoke on cloud formation and precipitation. Atmospheric patterns above the warm ocean and above rainforests – “green ocean” (Andreae et al., 2004) – are fairly similar in its biophysical behavior and hydrological outcomes. In both cases there seems to be a positive feedback between low levels of cloud condensation nuclei (CCN) and frequent precipitation. Maritime as well as terrestrial *biogenic* CCN are conducive to forming large raindrops. Added to that, the fact that most radiation is transformed into latent heat as opposed to sensitive heat, generates slower updrafts, which gives cloud droplets more time to grow in size and precipitate earlier as well as at relatively low altitudes (Andreae et al., 2004). Each precipitation event, by washing off residual CCN and by promoting effective local cooling, keeps CCN as well as updrafts at low levels, with the net effect of frequent “warm rain” precipitation events with a relatively low chance of lightning.

In the event of fire, smoke produces a large amount of condensation nuclei, many of which have the ability/tendency to promote cloud drop nucleation, producing a higher density of small-sized droplets. Small size droplets is synonymous to larger precipitation intervals, such that, by delaying precipitation,

the conversion of more radiation into sensitive as opposed to latent heat increases the updraft magnitude and speed, forcing the air containing small droplets to higher and colder altitudes, where they lose latent heat via freezing, typically generating less frequent but more intense precipitation events often accompanied by hail storms and lightning (Andreae et al., 2004). *Smoke aerosol from vegetation fires reduces net radiation at the surface, increasing atmospheric heating and stabilizing the lower atmosphere* (Kolusu et al., 2015) (Zhang et al, 2009). *These changes can lead to 10% to 40% reduction in regional precipitation* (Hodnebrog et al., 2016) (Tosca et al, 2010) (Lee et al., 2014) (Spracklen et al., 2018) Thus, fire events, are conducive to less frequent but more intense precipitation events – which tends to increase the magnitude of erosion on land - as well as are more likely to trigger increased lightning, the last one being an important natural source for generating subsequent fire events.

3.8. Feedbacks between CO₂ increase and savanna plant communities:

Studies have shown that an increase in atmospheric CO₂ largely elicits the physiologic acclimation response of reducing stomatal conductance (Morrison & Gifford, 1983) (Polley et al., 1997) as well as the adaptation of stomatal density reduction (Woodward, 1987) across plant species and significantly modulated by moisture availability. This means that essentially the cost of water for photosynthesis is reduced, since at higher ambient CO₂ concentrations and within a scenario of some degree of moisture limitation, it is assumed that plants are able to fix the same amount of carbon, by “sacrificing” less water via transpiration, through stomatal aperture regulation. (Morrison & Gifford, 1983) *found that leaf conductance of 16, mostly C3 agricultural and horticultural species declined a mean 36% when grown at double the present CO₂ concentration. In our review of the stomatal responses of C4 plants to CO₂, conductance was reduced an average 34% across 16 observations and 29% across 12 species by an approximate doubling of the current CO₂ concentration* (Polley et al., 1997). (Woodward, 1987) found that an increase of atmospheric CO₂ levels of 21% caused an average decrease of stomatal density of 40% in the plant species analyzed.

In situations of *high* moisture availability and the *absence* of heat stress, higher CO₂ concentrations appear to elicit responses of total leaf area increase by C3 plants instead, however it was found that C4 plants` photosynthesis, leaf area and growth under high moisture conditions remain relatively unaffected by increased CO₂ availability (Morison and Gifford 1984b, Curtis et al. 1989, 1990, Polley et al. 1994, Dippery et al. 1995) (Polley et al., 1997).

C3 plants under high CO₂ concentrations *and* some degree of water stress, by regulation of stomatal conductance, are able to increase their water use efficiency, which typically increases the length of their growing season. Since savanna biomes are limited by water availability during a significant part of the growing season, an increase in atmospheric CO₂ concentration - via stomatal conductance regulation – typically reduces the overall transpiration rates, therefore increasing soil moisture for a longer period within an annual cycle. This phenomenon has important ecological consequences at the ecosystem level, since lower evapotranspiration rates imply in higher soil moisture content, and relatively small changes in the water balance of savannas, for instance, may induce considerable changes within plant community structures (Neilson, 1986) (Sala et al., 1992) (Polley et al., 1997). At the same time, an overall water use efficiency increase due to higher CO₂ levels may be partially offset by relative leaf temperature increase. This happens because lower transpiration rates of plants are expected to increase both leaf temperatures as well as the temperature of surrounding air due to

decreased evapotranspiration (increase of the Bowen ratio), with the effect of increasing the leaf-to-air vapor pressure deficit (Polley et al., 1997). In other words, higher CO₂ levels require less water to be transpired for the same photosynthetic gain (increases WUE), however as less water gets transpired, leaf temperatures increase, generating a negative feedback and partially offsetting the initial water use efficiency gain when/if ambient boundary layer temperatures rise, as that increases the water vapor pressure deficit or evaporative demand.

Trees seem to be more positively affected by higher soil moisture contents than C4 grasses, although this differential benefit changes along rainfall as well as soil quality (coarseness and depth) gradients. It is thought that to maximize tree growth benefit due to soil moisture conservation, some of the moisture needs to effectively reach deeper soil layers which is contingent both on rainfall distribution as well as total precipitation. So, for instance in arid savannas or such where most of the rainfall occurs during the growing season, the effect of differential tree growth stimulation over grass growth may be marginal. Last, assuming that plants with deeper rooting systems will overall be differentially benefited over others resulting from higher water use efficiencies due to increased CO₂ levels is probably an over-simplification, since temperature increases may offset the expected water use efficiency gains or increased moisture may shift the growth limiting factor to nitrogen availability in many cases, so the differential ability to obtain the latter one across local plant communities may increase in relevance instead.

In summary, higher atmospheric CO₂ levels have been found to increase the water use efficiency across plant species, with the net effect of increasing the soil moisture content for longer periods, which is critical for savanna ecosystems where plant growth is limited by moisture during a considerable part of the year.

3.9. Leaf size and total biomass modulation by atmospheric CO₂ levels, temperature and moisture

(Osborne et al., 2004) by studying palaeontologic records - analyzing an extensive dataset of 300 leaf fossil species ranging from the Devonian to the Mississippian - showed a strong correlation between atmospheric CO₂ levels and leaf sizes. Leaf fossils achieved their maximum size between 340 and 380 million years ago, which roughly coincides with a significant low level of atmospheric CO₂ and global climatic cooling (Osborne et al., 2004). The biophysical mechanism through which these climatic changes cause plants to develop larger leaves acts as follows: lower CO₂ levels trigger the physiological response of increased stomatal conductance (Polley et al., 1997) in addition to increased stomatal density (Woodward, 1987) in an effort of maintaining the photosynthetic capacity. A higher stomatal density and conductance implies in lower water use efficiency but enhanced cooling ability of plants. For those biomes where plants do not experience water stress, more efficient cooling abilities – based on higher water use - allow/select for larger leaves, which is also enhanced by the fact that lower CO₂ levels imply in lower global temperatures and thus reduced heat stress – which would otherwise have selected for smaller leaf sizes. In other words, a cooler climate with lower atmospheric CO₂ levels, induces the physiological responses of stomatal conductance and density increase which, while diminishing water use efficiency, improves cooling capacity in vascular plants. Limited or absent heat stress allows plants to increase their leaf size – *larger* leaves loose more water and are more likely to

overheat – which implies in an optimum combination of photosynthetic capacity (larger area and ability to capture sun light), and cooling, in environments *not* limited by moisture availability but likely limited by light.

Larger leaves are positively correlated with thicker twigs (Corner's rule) (Smith & Sperry & Adler, 2017) and overall increase the carbon fixing capacity or productivity provided there is no immediate local limitation of nutrients or water. *Larger leaves promote increases in maximum canopy size; they represent an optimal tradeoff between investment in woody supporting tissue and leaf area for photosynthetic carbon gain* (Westoby & Wright, 2003) (Beerling & Berner, 2005). Higher stomatal densities also appear to enhance the regulation efficiency of the fine-scale control of transpiration. Such fine scale regulation of transpiration allows for a maximized xylem length in trees, as it better protects them against cavitation (Tyree & Zimmermann, 2002) (Beerling & Berner, 2005). A longer xylem can sustain larger trees, again provided that water and nutrients are not limiting. Thus overall, higher stomatal densities and conductance are associated to higher water use or, conversely, lower water use efficiency. On sites where plant growth is not limited by water, increased cooling efficiency - due to higher water use – allows for larger leaves, which by enhancing or the photosynthetic capacity of plants (provided light limitation can be compensated for), increases the potential for net carbon fixation.

3.10. Feedbacks between terrestrial vascular plants and climate:

The atmospheric CO₂ level regulation is of primary importance to prevent both a runaway greenhouse as well as a runaway icehouse (Beerling & Berner, 2005). Weathering feedbacks, which are mediated by plants, determine the long-term carbon cycle. CO₂ is supplied to the atmosphere by volcanic activity and recycled back into the Earth's crust through the long-term carbonate-silicate rock weathering and sedimentation cycle. High atmospheric CO₂ contents cause the global climate to warm and, as a result, the global hydrological cycle also gets enhanced, both of which naturally magnify chemical rock weathering rates. The advent of terrestrial vascular plants enhanced the effectiveness of the atmospheric CO₂ and climate regulation by promoting chemical rock weathering at higher rates at greater atmospheric CO₂ concentrations. The latter happened via 2 main mechanisms: 1) in order to obtain nutrients to satisfy higher biomass growth as well as due to the precipitation recycling effect (ultimately increasing the contact time of water with mineral surfaces), vascular plant root systems weather rock at much higher rates - (Berner, 1998) estimated at an eightfold increase compared to rock covered by lichen or moss – with the net result of accelerating the inorganic carbonate-silicate weathering cycle. And 2), through the creation of a greater biomass as well as more recalcitrant types of reduced carbon compounds (i.e. lignin), total volume of organic carbon burial also gets enhanced. The magnification of chemical weathering by vascular terrestrial plants as well as the enhancement of organic carbon burial rates are both powerful negative feedbacks understood to have kept atmospheric CO₂ and climate varying within relatively narrow ranges across geologic time.

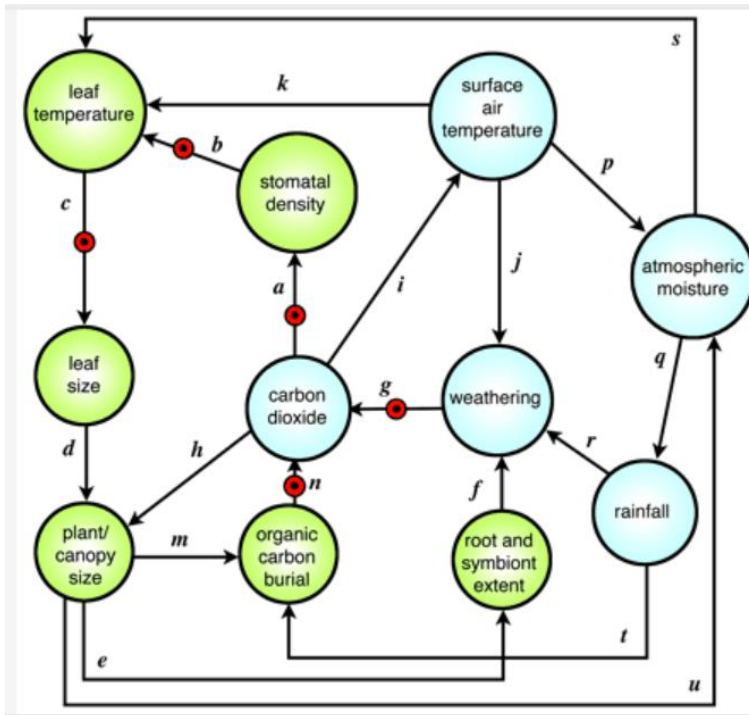


Figure 2: A systems analysis diagram of the geophysiological feedbacks between plants and atmospheric CO₂. It applies only when times of potential overheating of leaves due to high CO₂ levels may have occurred. Arrows originate at causes and end at effects. Arrows with bull's-eyes represent a negative response to a positive perturbation in the source circle. Arrows without bull's-eyes represent positive responses. Green circles represent primarily physiological plant responses or direct determinants and outcomes of such physiological changes, while blue circles represent abiotic determinants namely mechanisms that involve atmospheric processes. Letters adjacent to arrows designate paths followed by feedback loops. The time scales over which the paths operate are as follows: a, b, i, k, p, q, s, and u, 10⁰ to 10¹ years; c and d, 10¹ to 10³ years; f–h, j, m, n, r, and t, 10³ to 10⁶ years; e > 10⁶ years (Beerling & Berner, 2005). All feedback loops are negative, dampening an initial CO₂ increase. The exception are pathways that pass through the leaf temperature - leaf size effect.

On shorter timescales, the negative carbon fertilization feedback between atmospheric CO₂ and terrestrial biomass appears to be an important player (figure 2, pathway “h”), wherein global NPP and biomass is enhanced by increased atmospheric concentrations of CO₂. That in itself enhances the efficiency of atmospheric CO₂ regulation via the two previously mentioned atmospheric CO₂ drawdown mechanisms: increase in organic C burial rate (pathways h-m-n) as well as via magnification of chemical rock weathering due to larger roots (pathways h-e-f-g) and via increased precipitation recycling (pathway h-u-q-r-g). All these pathways are so-called negative feedback loops, which means they have a *stabilizing* effect over climate and atmospheric CO₂.

At the same time, the authors suggest 5 *positive* feedback pathways, all based on the fact that, along a certain temperature/atmospheric CO₂ level range, atmospheric CO₂ concentrations and total plant biomass may actually be *negatively* correlated. *All five pathways lead to positive feedbacks, whether CO₂ is rising or falling, but only if the paths at some stage involve very warm global climate states that could induce lethal overheating of leaves.* (Beerling & Berner, 2005). The reason for that is because an

increase in CO₂ levels, causes plants to respond with a decrease in stomatal density (Woodward, 1987) and in stomatal conductance (Polley et al., 1997), both of which decrease transpiration rates, resulting in an improved water use efficiency but reduced cooling efficiency (pathway a-b). Furthermore, an increase in atmospheric CO₂ levels also implies in an overall climatic warming (pathway i-k), with the added effect of increasing the leaf-to-air water vapor pressure deficit, and thus selecting for smaller leaves, in order to mitigate overheating. Smaller leaves imply in reduced photon capture capacity, which shifts away from the previously mentioned optimum balance, meaning - assuming a scenario of imminent heat stress - while water use efficiency is improved, reduced cooling capacity and carbon fixing capacity have the net effect of limiting overall plant biomass productivity (pathway c-d), compared to a lower CO₂/temperature scenario.

The resulting reduction in plant biomass implies in several positive (destabilizing) feedbacks on atmospheric CO₂ levels as it overall reduces the rate of organic carbon burial (pathway m-n) as well as chemical rock weathering rates. The latter happens via different mechanisms such as due to the fact that lower root biomass – moderated by hydrology - implies in reduced weathering rates due to a decrease of the contact time of water with un/partially weathered minerals (Wen et al., 2020) (pathways e-f-g ; u-q-r-g and u-q-t-n), and to a lesser extent since improved water use efficiency under high CO₂ levels should reduce terrestrial evapotranspiration rates and therefore limit the precipitation recycling effect, which, by reducing atmospheric moisture, directly acts in a manner of increasing the leaf-to-air water vapor deficit (heat stress) (pathway u-s).

It is important to note that positive and negative feedback loops typically take place simultaneously although often with different magnitudes and within different time frames. In that sense pathway a-b-c-d (positive feedback loop), which results from the physiological adaptation and acclimation of plants involving stomatal density and conductance as well as altering leaf size, ultimately establishing a negative correlation between atmospheric CO₂ levels and terrestrial biomass, may be limited, counter balanced, or even offset by pathway “h” (CO₂ fertilization) which implies in a negative (climate stabilizing) feedback mechanism.

Similarly, while pathway a-b-c-d-u (positive feedback) represents the fact that increased CO₂ levels, by increasing water use efficiency in plants and limiting evapotranspiration, have a limiting effect over the hydrological cycle (reduced precipitation recycling over continents), pathway i-p represents the fact that rising CO₂ enhances warming and therefore total precipitation on land (due to higher evaporation from the sea), and so implies in a negative feedback loop. Thus, if pathway i-p overrides pathway a-b-c-d-u, through mechanisms such as weathering rates and organic C burial, the hydrological cycle would in this case rather *limit* atmospheric CO₂ level extremes (pathways q-t-n and q-r-r).

3.11. C4 photosynthetic pathway origin, spread, and climatic determination and interactions:

The C4 photosynthetic pathway has evolved as a series of physiological adaptations in response to abiotic drivers, such as low CO₂ levels, drought, heat, salinity, amongst others, that in one way or another enhance photorespiration and carbon deficiency in plants. As we will see in subsequent sections, it appears to have had important evolutionary as well as biogeochemical implications during

Earth's history. Plants that have evolved the C₄ photosynthetic pathway contribute about 25% of the current global net primary productivity and represent a considerable fraction of crops consumed by humans (Sage, 2004). Its origin and spread are thought to be a result of a multivariable interaction between atmospheric CO₂, seasonality, temperature and aridity, and there is a strong historical negative correlation between atmospheric CO₂ levels and the relative dominance of C₄ plants (mostly grasses). The Evolution of this alternative photosynthetic pathway has independently occurred in a vast number of plant families and doesn't consist of a single biochemical pathway. *It is a series of biochemical and structural adjustments that have exploited phosphoenolpyruvate carboxylase (PEPCase) and other existing enzymes to concentrate CO₂ around Rubisco* (Sage, 2004). RUBISCO is the enzyme that catalyzes the entry of CO₂ into the photosynthetic metabolism by providing acceptor molecules and regulation of the pool sizes of photosynthetic intermediates (Sharkey, T.D., 1989). RUBISCO, however, is subject to both carboxylation – technically synonymous to carbon gain - as well as oxygenation. During oxygenation, a byproduct – phosphoglycolate – is produced which, for being toxic when accumulated, needs to be further metabolized, which is an energy *consuming* process, limiting the overall ability of the plant to obtain carbon. The oxygenation of RuBP plus the further metabolism of the toxic intermediate is termed photorespiration and the degree by which it takes place is governed by the ratio of CO₂ / O₂ that reaches RUBISCO (Sage, 2004). The CO₂ / O₂ ratio at the carboxylation/oxygenation site is both dependent on the given ambient CO₂ and O₂ partial pressures as well on the stomatal conductance. A higher stomatal conductance implies in a more efficient gas exchange favoring carboxylation, whereas a lower stomatal conductance conversely enhances the accumulation of oxygen, therefore favoring more photorespiration and limiting the overall photosynthetic efficiency.

The C₄ photosynthetic pathway has evolved as a CO₂ concentrating mechanism at the carboxylation/oxygenation site and implies in an additional energy investment – which makes it less competitive under scenarios where photorespiration is naturally low – while, at the same time, it increases the carbon gain and overall photosynthetic efficiency under scenarios of naturally high photorespiration, precisely by limiting that very process. In that sense, low CO₂ partial pressures and a high leaf-to-air water vapor pressure deficit – the latter one by limiting gas exchange via stomatal closure - would favor photorespiration and create a selective pressure for the C₄ photosynthetic pathway. *Instead of considering C₄ photosynthesis as a specific drought, salinity or low-CO₂ adaptation, it is better to think of it as an adaptation that compensates for high rates of photorespiration and carbon deficiency. In this context, any environmental factor that enhances photorespiration and reduces a positive carbon balance could potentially select for traits leading to C₄ photosynthesis. Heat, drought, salinity and low CO₂ are the most obvious factors, but others, such as flooding, could also stimulate photorespiration in certain situations.* (Sage, 2004). This multifactor determination of the relative efficiencies of the C₃ and C₄ photosynthetic pathways is highlighted by the fact that there are currently both highly well adapted C₃ plants to arid conditions as well as C₄ plants that thrive in wetlands (Sage, 2004).

The CO₂ compensation point is another useful concept and reflects the minimum CO₂ concentration requirements for an autotrophic process to occur (Sage, 2004). This point or threshold can be

understood as the ratio of CO_2/O_2 at which the net energy loss due to photorespiration equilibrates with the net gain due to photosynthesis. Plants exhibit varying carbon compensation points – essentially energy demands – along their life cycles. So, for instance at low CO_2 partial pressures, other drivers such as heat, drought or salinity – all of which trigger stomatal closure - may drive the CO_2/O_2 ratio at the carboxylation/oxygenation site below a plant's given CO_2 compensation point, which is what is thought has selected for the C4 carbon concentrating pathway at different times and for different plant families during the Paleozoic.

The appearance and spread of different lineages of C4 plants has invariably coincided with low atmospheric CO_2 levels. Nonetheless, a time mismatch on the order of tens of millions of years between historically low CO_2 levels and the spread of C4 grasses, suggest that, despite being the likely primary driver, low CO_2 levels alone cannot explain the massive expansion of C4 grasses (Beerling & Osborne, 2006). Therefore, low CO_2 levels must have acted in conjunction with other drivers to explain why low CO_2 periods not always coincided with C4 grass expansion. One such factor that could have tipped the balance towards enhanced competitiveness of C4 grasses – relative to C3 woody plants – could have been the increase of fire frequency as a result of increased precipitation seasonality like the onset of the Asian monsoon (J. E. Keeley & Rundel, 2003). Fire creates conditions that favor plants with rapid resprouting and regrowth strategies, for which grasses are well-known for, while increasing drought periods would particularly favor the C4 photosynthetic pathway. Increased grass cover also enhances the flammability of an ecosystem, suggesting a positive feedback between fire intensification and C4 grasses spread.

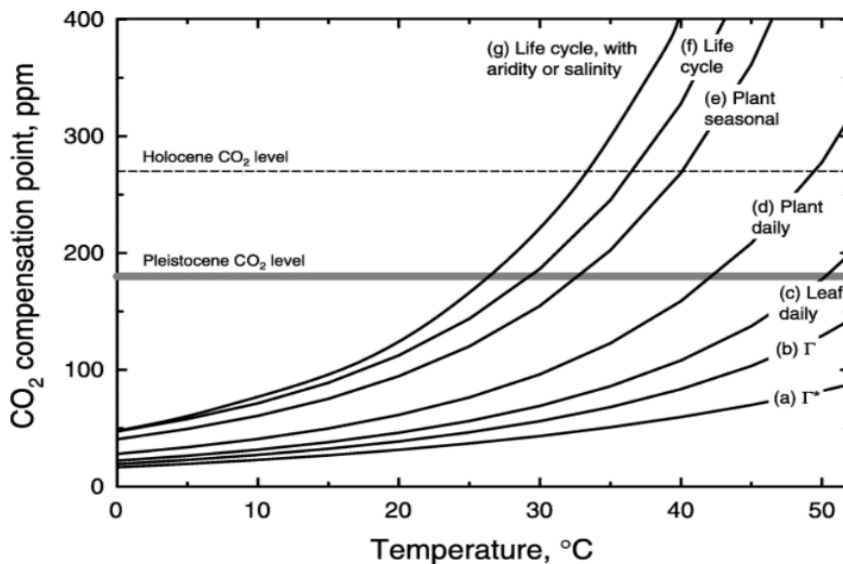


Figure 3: Potential relationships between temperature and the CO_2 compensation point of plants determined over different spatial and temporal scales (Sage, 2004). CO_2 compensation points for the rate of Rubisco carboxylation (Γ^*) and instantaneous net CO_2 assimilation rate (Γ) are based on measured data (Brooks & Farquhar, 1985; Sage et al., 1990). CO_2 compensation points at greater levels of complexity and time are educated guesses to demonstrate the potential effect (Sage, 2004). Carbon compensation points of plants are driven up either if the rate of photorespiration is increased (essentially more energy is required for a given carbon gain) – which can happen due to low CO_2 mixing rates, high

temperatures, low air moisture contents, salinity etc – or due to increased carbon demand by plants, for example during certain life cycle stages such as the setting of fruit, ripening and seeding. The grey line indicates atmospheric CO₂ levels corresponding to the late-Pleistocene; dashed lines are preindustrial Holocene levels of CO₂ that predominated over the past 10 000 yr. Adapted from (Sage, 2004). Portions of a curve above CO₂ lines indicate temperatures where a plant would be unable to meet its CO₂ requirement at a given CO₂ level (Sage, 2004).

3.12. Fire mediated feedbacks:

(Beerling & Osborne, 2006) suggest the fire-vegetation-climate feedback hypothesis as the explanation both for the conversion of forests into C₄ grass dominated savannas in the Miocene, as well as the reason for the ecological success of the savanna biome under current climatic conditions. Their hypothesis is based on a number of positive (self-enhancing) feedback mechanisms involving fire, the atmosphere and vegetation.

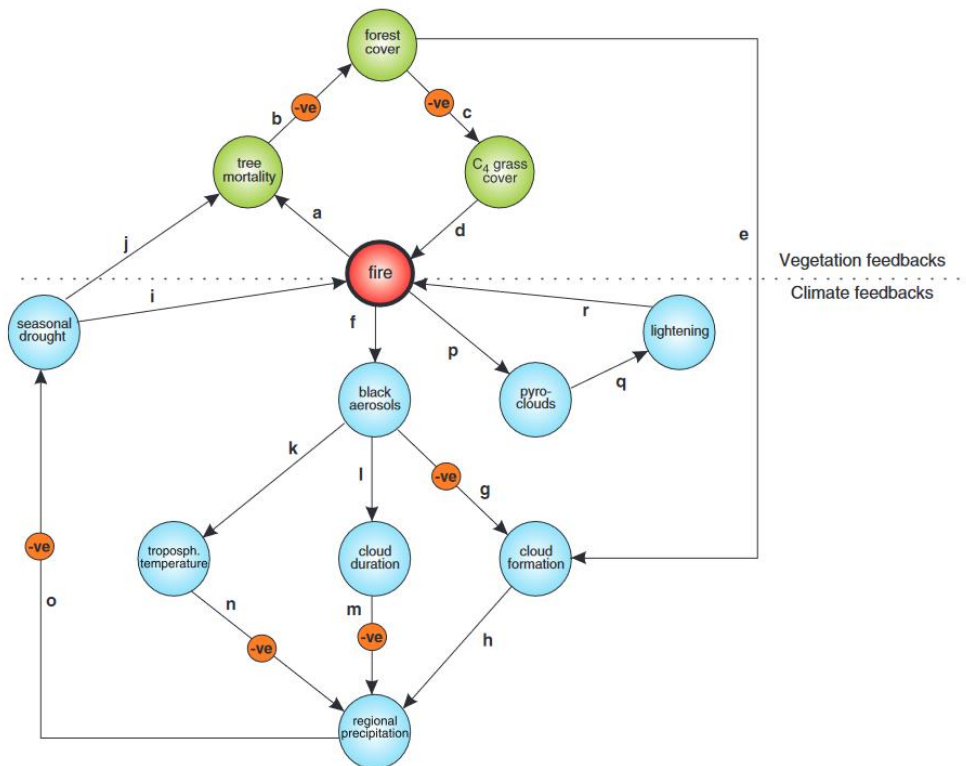


Figure 4: A systems analysis of fire–climate feedbacks. Arrows originate with causes and end at effects. Plain arrows indicate positive responses following an increase in the originating circle, and arrows marked with -ve symbol show negative responses. Closed loops with an even number of -ve labelled arrows or solely plain arrows are positive feedbacks, and those with an odd number of arrows with -ve labels are negative feedbacks (Beerling & Osborne, 2006).

As previously discussed, fire disturbance generates a competitive advantage of grass regrowth over tree regrowth, thus the magnitude of the positive feedback loop represented by pathway a-b-c-d in figure 4 reflects that feedback. In addition, forest cover directly enhances cloud formation, and the LAI of forests positively correlates with precipitation recycling, thus also with total precipitation (Hayden,

1998). In other words, increased deforestation leads to increased drought which both directly enhances tree mortality by reducing overall tree survival at the seedling stage, as well as by enhancing ecosystem flammability and fire frequency (pathways e-h-o-j and e-h-o-i-a) (Beerling & Osborne, 2006); two main mechanisms responsible for keeping forests in an alternative drier and more flammable state.

In addition to directly favoring rapid resprouters – in this case grasses over trees – fire also influences vegetation via a self-enhancing (more fire events producing) effect mediated by altered cloud formation as well as by changing local or even regional climate, depending on the magnitude of the fire event. The self-enhancing effect of fire represented by pathway p-q-r has been described by (Andreae et al., 2004) and acts via increased lightning events generated by high fire intensities. Black aerosols generated by fire also cause a greater heat absorbance at the troposphere, resulting in less energy reaching Earth’s surface (local or regional effect) limiting the hydrological cycle, causing both a decrease in total precipitation as well as decreasing its frequency (Spracklen et al., 2018) (all pathways between “f” and “o”, figure # 4).

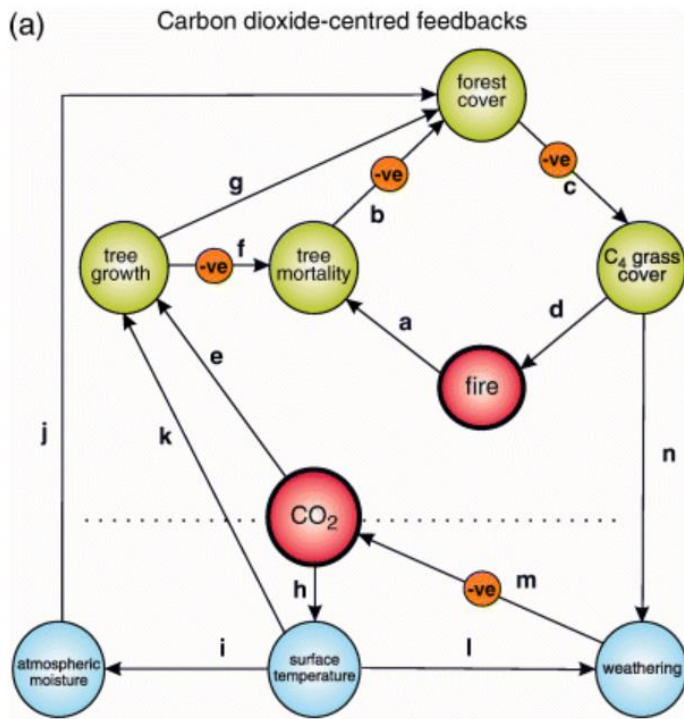


Figure 5: A systems analysis of fire–climate feedbacks. Arrows originate with causes and end at effects. Plain arrows indicate direct responses, and arrows marked with -ve symbol show inverse responses. Closed loops with an even number of -ve labelled arrows or solely plain arrows are positive feedbacks, and those with an odd number of arrows with -ve labels are negative feedbacks (Beerling & Osborne, 2006).

In figure 5, (Beerling & Osborne, 2006) expand their model to include further hypothesized feedbacks involving the long term carbon cycle. Low CO₂ levels during the Miocene implied in a direct competitive disadvantage for C₃ trees relative to C₄ grasses in savanna biomes (pathway “e”). In addition, low CO₂ levels also implied in a cooler drier climate which the authors assume to have further reduced tree growth. A global contraction of forests should have naturally reduced the biological weathering of carbonate-silicate rocks, the primary carbon sink within geologic time scales (Beerling & Berner, 2005). Nevertheless, C₄ grasses should have been able to compensate for the reduced weathering rates owed to a contraction in global tree cover, even suggesting a positive feedback between C₄ cover and global weathering rates. *However, the corresponding expansion of C₄ savannas may partially offset this effect (pathways e–g–c–n–m and h–k–g–c–n–m in figure 5) helping to ensure that atmospheric CO₂ remains low, although a cooler climate will slow rates of silicate rock weathering (pathway h–l–m). The strength of this feedback is also likely to depend on the extension of C₄ plants to high altitudes (Ehleringer & Cerling & Helliker, 1997) (Mora & Pratt, 2002), where rates of silicate weathering tend to be enhanced by high erosion rates and the uplift and exposure of fresh unweathered materials (Berner, 2004). Nevertheless, the C₄ savanna biome may act to maintain atmospheric CO₂ concentration close to the minimum so far observed (~180 ppm), allowing C₄ grasses to flourish at the expense of C₃ forests* ((Beerling & Osborne, 2006). If this last assumption (pathway “n” representing a positive feedback) is proven correct, then we would in fact have a mechanism involving the long term carbon cycle in a positive feedback, as C₄ plants, by being able to sustain high rock weathering rates, would have created an additional and long term acting mechanism capable of keeping atmospheric CO₂ levels at low concentrations for an extended period of time, which seems to be the most influential parameter determining C₄ grasses` competitive advantage. The authors conclude by suggesting additional feedback mechanisms between herbivory and savanna vegetation, where roughly grazing would favor tree cover, whereas browsing animals would favor grass cover.

3.13. Fire:

Fire has been a primary determinant in the history and evolution of land plants, and fossil records indicate that both share a common origin, in the late Silurian (He & Lamont, 2018). Today, (Bond et al., 2005) estimate that 40% of all terrestrial landmasses are fire prone. Fire, to occur, is dependent on burnable biomass, oxygen, and an ignition source, and is modulated by temperature and moisture contents of the atmosphere. Plants provide both: burnable biomass and oxygen, which highlights their intricate relationship. The extent of burnable biomass is determined by the interaction of abiotic factors – climate and precipitation – with vegetation growth and by the resulting evolutionary adaptations and innovations in land plants. In that sense the angiosperm revolution is thought to have significantly changed Earth`s fire regimes throughout its history. For instance, both in the Cretaceous as well as in the late Miocene, the dominance of low biomass but rapid growth types of angiosperms within a seasonal climate prone to drying out living plants as well as plant litter, have intensified the fire regimes during these periods. Conversely, the ability to form high biomass forests, tall and dense enough to shade out more flammable vegetation, has significantly reduced fire regimes. *Innovations leading to higher growth and reproductive rates, coupled with greater plasticity of form, produced the novel growth forms that created novel biomes and in turn triggered novel fire regimes (including no fire) and reshaped world vegetation. The extent of these novel biomes changed over time, in response*

not only to changing climate but also to changing O₂ and CO₂ content, fire activity, and, perhaps, large vertebrate herbivores. (Bond & Midgley, 2012).

Atmospheric oxygen contents are known to have fluctuated substantially throughout Earth's history, having been the most important abiotic factor over large time periods in determining fire regimes (Belcher et al., 2010), by influencing both the ease of a fire to get started and how hot it burns (He & Lamont, 2018). For plant biomass to catch and sustain fire, a minimum of 16% oxygen needs to be given (Belcher et al., 2010), and at around 19% O₂ mixing rates, ignitability increases non-linearly (He & Lamont, 2018). According to the same authors, in times of high atmospheric oxygen levels, oxygen contents have been the primary factor in determining fire regimes, whereas in times of low oxygen mixing rates, climate would take over the dominant role. High CO₂ levels have been associated to warm periods and increased tree branching, both of which enhances fire susceptibility. High CO₂ also tends to promote higher growth which may or may not enhance overall fire frequency, largely dependent on dominant vegetation species. Total precipitation seems to be less important than precipitation seasonality, where the combination of highly concentrated rainfall within a year followed by drought as well as high interannual variability are conducive to the highest fire frequencies and most intense fires. *For example, a long dry season every year creates fires at one- to five-year intervals in high rainfall areas of northern Australia that is dominated by the monsoon, which delivers ~1400 mm in four months followed by hot, dry weather for the rest of the year* (Oliveira & Wendland & Nearing, 2013) (He & Lamont, 2018).

Since oxygen levels only vary over much longer time periods, for present-day purposes we can assume it as a stable factor, and by doing so insight can be gained on how fire varies across other important gradients such as rainfall, productivity, temperature, latitude etc. In that sense (Pausas & Ribeiro, 2013) have analyzed fire probability along a global standing plant biomass or productivity gradient. They found that fire assumes what they named an *intermediate fire-productivity* pattern, meaning fire incidence appears to be highest at intermediate productivity type of biomes. They write: *The highest fire activity is not exactly in the middle (i.e. median) of the gradient but closer to the productive end than the arid end. This skewed distribution response may be the consequence of a threshold effect; i.e. increasing productivity increases fire activity up to a level (e.g. high moisture all year round) from which fire activity decreases drastically. In addition, this skewed distribution may also be driven by anthropogenic processes. For instance, deforestation of tropical rain forests in recent decades has increased fire weather and ignitions and thus the level of fire activity in these productive ecosystems that otherwise would rarely burn* (Uhl & Kauffman, 1990) (Siegert et al., 2001) (Pausas & Ribeiro, 2013). According to their hypothesis, modern fires are driven by a combination of burnable fuel and/or climate. For the higher productivity end of the spectrum, potentially burnable biomass is high, so the likelihood of fire is mainly a function of climatic variations, so for instance if drought increases in a given year, areas of high biomass dry out surpassing a local flammability threshold, thus rapidly increasing fire-proneness. On the other side of the spectrum, we find a very low biomass due to low productivity. In this case, fire is mostly driven by productivity, meaning if in a given year productivity increases – for example due to increased rainfall – the burnable biomass of this biome would increase accordingly and a plant biomass regulation by fire is expected.

One of the caveats of the global fire–productivity model is that it does not differentiate between different fire-type regimes such as surface and crown-fire regimes (J. Keeley et al., 2011). For instance, two ecosystems with similar productivity could have different fire types because of strong differences in fuel structure (Pausas & Keeley, 2009). A good example of how similar climatic conditions may create dissimilar fire regimes is given when comparing the fire regimes of north American and Eurasian boreal forests. In North America, the dominant conifer species maintain their branches along their trunks (favoring crown fires) and keep their seed banks on their branches (serotiny), only being released when fire reaches a certain height – examples of so called fire-adapted traits. Whereas in Eurasia, the dominant species shed their dead lower branches and also exhibit much thicker bark, which are examples of fire suppressing and fire-resistant traits, respectively. Therefore, it appears that occasionally very similar climatic and productive conditions generate substantially different fire regimes, given the evolutionary interplay of fire and plant adaptations (He & Lamont, 2018).

When it comes to future global implications, the intermediate fire-productivity hypothesis tells us that expected global warming will have a greater effect over the biomes located at the higher end of the productivity spectrum (high potentially burnable biomass regulated by climatic variations). *Consequently, tropical moist forests are the ecosystems most vulnerable to increased fire activity due to global warming (Cochrane, 2003) (Scholze et al, 2006) (Lewis et al., 2011) (Pausas & Ribeiro, 2013).*

Somewhat similar to the intermediate fire-productivity hypothesis, with regards to fire regimes influencing biodiversity a so called “intermediate-disturbance hypothesis has been suggested (Connell, 1978) (Huston, 2014) (He et al., 2019). So, for instance, while an increase in fire frequency may decrease species richness, for example because a reduced fire interval proves insufficient for resprouters to accumulate enough starch reserves within their root systems to survive a subsequent fire event, on the other hand if fire intervals are extended beyond a certain threshold, species that rely on fire for a certain part of their life cycle may disappear likewise. An increase in fire severity may have a similar effect, wiping out species whose fire resistance traits are incompatible with a certain degree of fire intensity. A somewhat complementary hypothesis, the pyrodiversity-biodiversity model states that a certain degree of variation within a fire regime maximizes the spatial and temporal heterogeneity – for example due to the effect of different parts within a biome being burned at different times as opposed to a more predictable burning pattern, or due to the effect that different fire intensities have varying effects regarding the post-burn nutrient release pattern, cycling and plant growth recovery time. An increased spatial heterogeneity proportionally increases niche diversification and thus is more conducive to a greater overall biodiversity. In reality, this pattern is not linear but rather “humped” as for instance some species (especially fauna) may decrease after a certain “minimum patchiness size” is surpassed. *Thus, the pyrodiversity-biodiversity relationship is likely to be humped, with the peak towards the upper end of the pyrodiversity gradient (He et al., 2019).* Overall, biodiversity is maximal at moderate levels of patch diversity, disturbance and fire severity over the landscape, and it appears that after a fire event there is an increase in biodiversity followed by a slow and steady decline, as the more dominant species outcompete those ones whose competitiveness relies on disturbance and its rather immediate aftermath (He & Lamont, 2018).

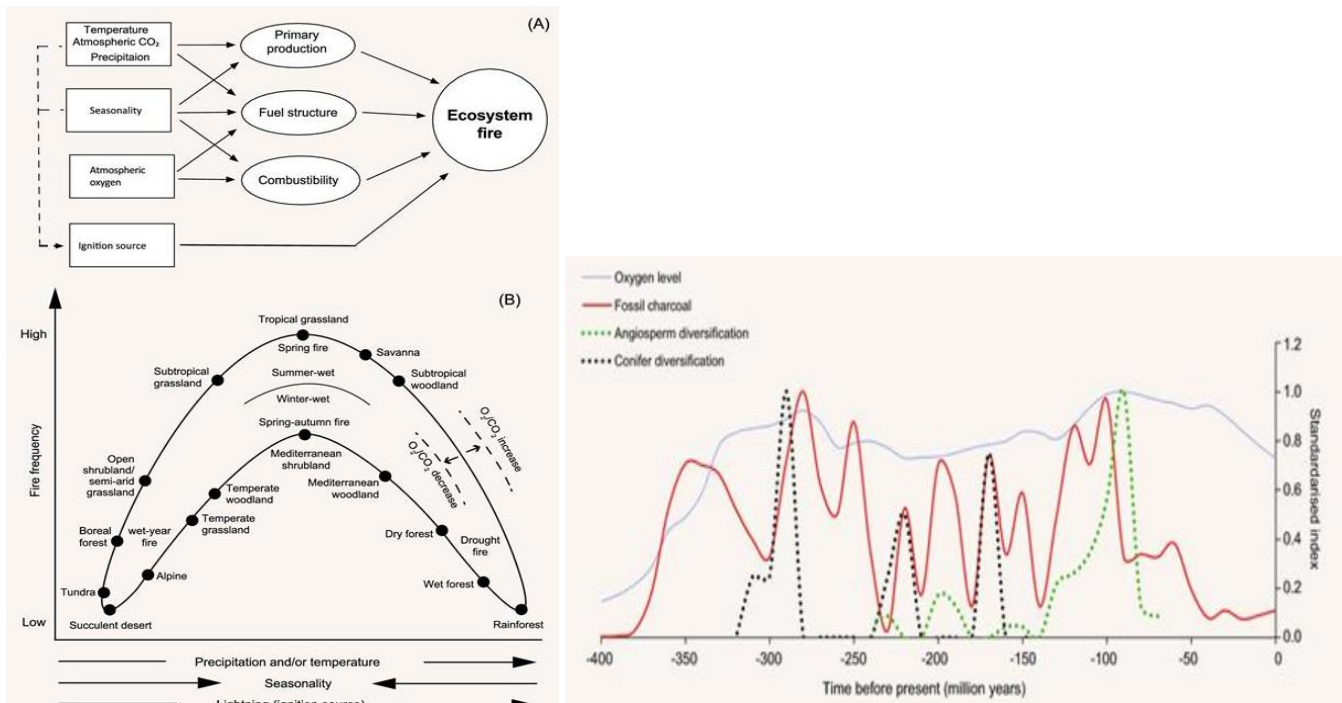


Figure 6: (left): Scheme of factors controlling fire as an ecosystem process. Sufficient primary production (a function of climate, nutrients and CO₂ level) as fuel is required to sustain a fire, but seasonally dry climates, in annual to decadal cycles, are required to remove moisture in green vegetation and convert it into combustible fuel. O₂ is essential for combustion; the level of O₂ in the atmosphere also influences the level of combustible fuel. Lightning, as the usual ignition source (prior to human activity), is also essential. The temporal and spatial structure of fuel determines the specific fire regime that shapes the evolution of plants. Major vegetation types, in the climate-fire frequency plane, along a gradient of increasing temperature and/or precipitation, fire frequency first increases and then decreases, along with seasonality in these climatic factors. Seasonality is a key ingredient to high fire frequency, allowing for fuel accumulation and subsequent drying. Historically, gradients of O₂ and CO₂ have also impacted on the position of the current boundaries of the fire regime 'boomerang' illustrated by the broken lines (He & Lamont, 2018).

Figure 7: (right): History of fluctuations in atmospheric O₂ and fossil charcoal over the last 400 million years and diversification of the major plant groups (conifers and angiosperms). Data sources: O₂ from; fossil charcoal from; diversification of conifers (origin of new families, both extant and extinct taxa) from; diversification of angiosperms (origin of new plant orders) from. Data were standardized to values between 0 and 1 to facilitate comparison using the formula (value - minimum)/(maximum - minimum) (He & Lamont, 2018).

3.14. Oxygen:

As previously mentioned, fire regimes have been identified as a central element in determining not only present day distribution and relative dominance of plant species in fire prone habitats, but has also exerted primary influence in promoting trait selection and speciation across plant communities (He et al., 2019). Understanding what the main determinants of present-day fire regimes are across landscapes is therefore of primary importance to gain insight about current and near-future interactions among plant species as well as large-scale changes in land cover. As mentioned earlier, atmospheric oxygen levels and climate constitute the main determinants of fire regimes (frequency and intensity). Climate tends to vary within much shorter time scales than oxygen levels do and it determines ecosystem flammability mostly via rainfall seasonality and temperature regimes (He &

Lamont, 2018). For the near future, given increasing CO₂ levels, an overall warming effect is expected – which should increase the potential for fire – as well as an increase in total global precipitation. Regarding the latter one, although a wetter climate overall reduces fire potential, this averaged effect may have a relatively low relevance or predictive power, as local and regional rainfall patterns override the latter one and may be difficult to predict, as they vary greatly across the globe. In the next section, we will describe recent theory about what constraints atmospheric oxygen level fluctuations over geologic time, and its effects over terrestrial vegetation.

Oxygen is produced by photosynthesis and consumed by organic matter oxidation – such as respiration, decomposition and fire - as well as oxidative rock weathering. The quantitative difference between photosynthesis and respiration (oxidation) is equal to the rate of organic carbon burial (plus reduced S burial, roughly) (Bernier & Canfield, 1989). Oxidative weathering is determined by the rate of uplift as well as by the rock type to be weathered, meaning the relative concentration of reduced carbon and pyrite (reduced sulfur) will ultimately determine the degree of oxidation (oxygen sink) associated to weathering. Conversely, the relative proportion of organic carbon and pyrite burial within the overall sedimentation process will also be key in the extent by which global sedimentation acts as an oxygen source (Bergman et al., 2004). According to the same authors, higher uplift rates increase both the oxidative weathering of rocks (oxygen sink) as well as overall sedimentation rates (oxygen source) and thus in and of itself constitutes a primary negative – atmospheric oxygen stabilizing – feedback over large time scales. This negative feedback mechanism is however unlikely to explain the narrow variations of atmospheric oxygen over geologic time, which are required for most life forms, and suggests a likely involvement of biota in the overall atmospheric oxygen regulation, especially given the fact that higher than present day oxygen levels have a rapidly depleting effect over most terrestrial life forms (Lenton & Watson, 2000).

In the model proposed by (Lenton & Watson, 2000)(see figure #9), the variation of organic carbon burial over time is the main determinant of oxygen mixing rates in the ocean. According to these authors, organic carbon burial is both sensitive to atmospheric oxygen concentrations directly, as well as via the influence of the latter on terrestrial biomass and weathering rates. According to Henry's law, dissolved oxygen is a direct function of atmospheric oxygen levels (and vice-versa), thus the degree of *anoxia* within the (deep) ocean (if any) is inversely correlated to the atmospheric oxygen level. The degree of anoxia influences the rate of organic carbon burial via multiple mechanisms. To understand how marine anoxia influences organic carbon burial, we should note that, according to (Lenton & Watson, 2000), organic carbon burial is a quadratic function of marine production which, although largely independent of anoxia (since marine production mostly happens on the surface ocean), is influenced indirectly by the latter one via the availability of nutrients such as phosphate and nitrate - which are typically limiting. The logic being that a greater availability of limiting nutrients increases marine production and thus also organic carbon burial.

Phosphate undergoes 3 main alternative avenues of sedimentation: it may associate to organic carbon, to iron or to calcium. The affinity of phosphate to iron is an inverse function of anoxia - anoxia is given by oxygen concentrations below 10% of its solubility, (Lenton & Watson, 2000); therefore a larger volume of anoxic ocean yields a higher availability of phosphate (due to decreased affinity to iron), resulting in a higher ratio of organic carbon that can potentially get buried per unit of (total marine)

phosphorus (Holland, 2006, 1994). In summary, a lowering of atmospheric oxygen concentration increases marine anoxia, which by increasing the availability of phosphate, enhances overall organic carbon burial rate, the ultimate atmospheric oxygen source (negative feedback). At the same time, an increase in anoxia drives up denitrification (nitrate being the “next best” electron acceptor once O₂ is depleted), thus a reduction in marine nitrate below Redfield ratios turns *nitrate* into the limiting nutrient, with the effect of limiting marine production and organic carbon burial. Therefore this last mechanism identified by (Lenton & Watson, 2000) acts as a positive feedback on atmospheric oxygen; however, when balanced with the previous one identified by (Holland, 2006, 1994), the net effect/outcome is understood to be of a *negative* feedback. Anoxia also directly influences the efficiency of organic carbon decomposition, especially because certain organic carbon compounds can only be decomposed in the presence of oxygen. Therefore, another positive feedback results from the direct inhibition of anoxia onto the carbon decomposition efficiency (Betts & Holland, 1991).

The above mechanisms show that *decreasing* levels of oxygen, by enhancing anoxia, effectively *increases* the net oxygen output via increased burial rates of organic carbon (and pyrite, which yields the same effect over oxygen). The reverse scenario of an increasing atmospheric oxygen level would have the opposite effect, as a less anoxic ocean overall reduces the burial of reduced C and S. However, once the ocean is fully oxic, a further increase in atmospheric oxygen levels cannot be further attenuated via the above-described mechanisms, which rely on an inverse relationship between anoxia and oxygen production. Therefore, in the absence of additional negative feedback mechanisms, nothing would prevent oxygen levels to keep rising, which would have an increasingly deleterious effect over most land biota.

Two such additional negative feedback mechanisms have been identified and included within a comprehensive model by (Lenton & Watson, 2000). Both these mechanisms act by changing the overall P availability, which, as we saw before, is key for determining the extent of organic C burial rates. Terrestrial plants and their associated biota (i.e. mycorrhizae) enhance rock weathering in an effort to obtain vital nutrients such as P. Weathering rates enhanced by vascular plants are thought to increase overall (global) weathering rates - compared a scenario of lichen or moss cover only - by at least one order of magnitude (Berner, 1998) (Ford Cochran & Berner, 1996) (Lenton & Watson, 2000). As we saw before, for all C3 plants, which represent the bulk of terrestrial biomass, photosynthetic efficiency is contingent on the CO₂/ O₂ ratio at the site of carboxylation/oxidation (RUBISCO). If oxygen mixing rates increase relative to CO₂ mixing rates, it becomes energetically decreasingly favorable for a C3 plant to obtain carbon (perform photosynthesis) approaching the point where the CO₂ compensation point is reached (Sage, 2004). This inhibition of photosynthesis due to increasing oxygen mixing rates (or decreasing CO₂ mixing rates) – also known as the Warburg effect (Lenton & Watson, 2000) – establishes a negative feedback mechanism between atmospheric O₂ levels and net global biomass production. The same authors also showed (see figure #8) that not only ecosystem flammability is positively correlated to atmospheric oxygen levels, but this relationship also experiences a considerable “dip” starting roughly around 21% mixing rate, which also happens to be the present day one. Therefore, in a gradual manner via the Warburg effect (only applicable to C3 plants) as well as “exponentially” via a flammability increase at/beyond 21% O₂ mixing rate, plant biomass assumes a negative correlation to O₂ levels, (see figure #8). Thus, an increase in oxygen levels *past* any degree of marine anoxia, is effectively attenuated via a reduction of terrestrial biomass, which for being directly

correlated to rock (and thus P) weathering rates, by reducing the total P availability both on land as well as in the ocean, effectively limit org C burial, the ultimate atmospheric oxygen source (Lenton & Watson, 2000).

In summary, a decrease in oxygen levels is effectively attenuated by marine negative feedbacks, resulting from the fact that oceanic anoxia is directly correlated with the efficiency of reduced C and S burial (oxygen source). This feedback mechanism is of more gradual nature, allowing oxygen levels to recover less readily, and is ineffective at high oxygen levels, where oceanic anoxia would be effectively precluded. An increase in oxygen levels, once all ocean turned oxic, cannot be further attenuated via marine mechanisms, instead negative feedbacks occur on land, where increased oxygen levels gradually enhance the cost of photosynthesis as well as “abruptly” enhance terrestrial biomass flammability. A reduced terrestrial biomass – resulting from an increase in the atmospheric oxygen levels - implies in reduced P weathering rates and availability, effectively diminishing the efficiency of organic carbon burial in the ocean. This last mechanism is assumed to act much more readily, only allowing an increase of oxygen levels beyond 21% at the expense of a very high reduction in total terrestrial biomass or contingent to a scenario of a significantly wetter climate. According to their model, an increase of atmospheric oxygen levels from 21% to 30% would have caused the global terrestrial biomass to have shrunk to merely 20% (one fifth) of present-day levels. According to their model, over geologic time, oxygen levels may have varied within a band of 18% to no more than 25% atmospheric mixing rate (Lenton & Watson, 2000).

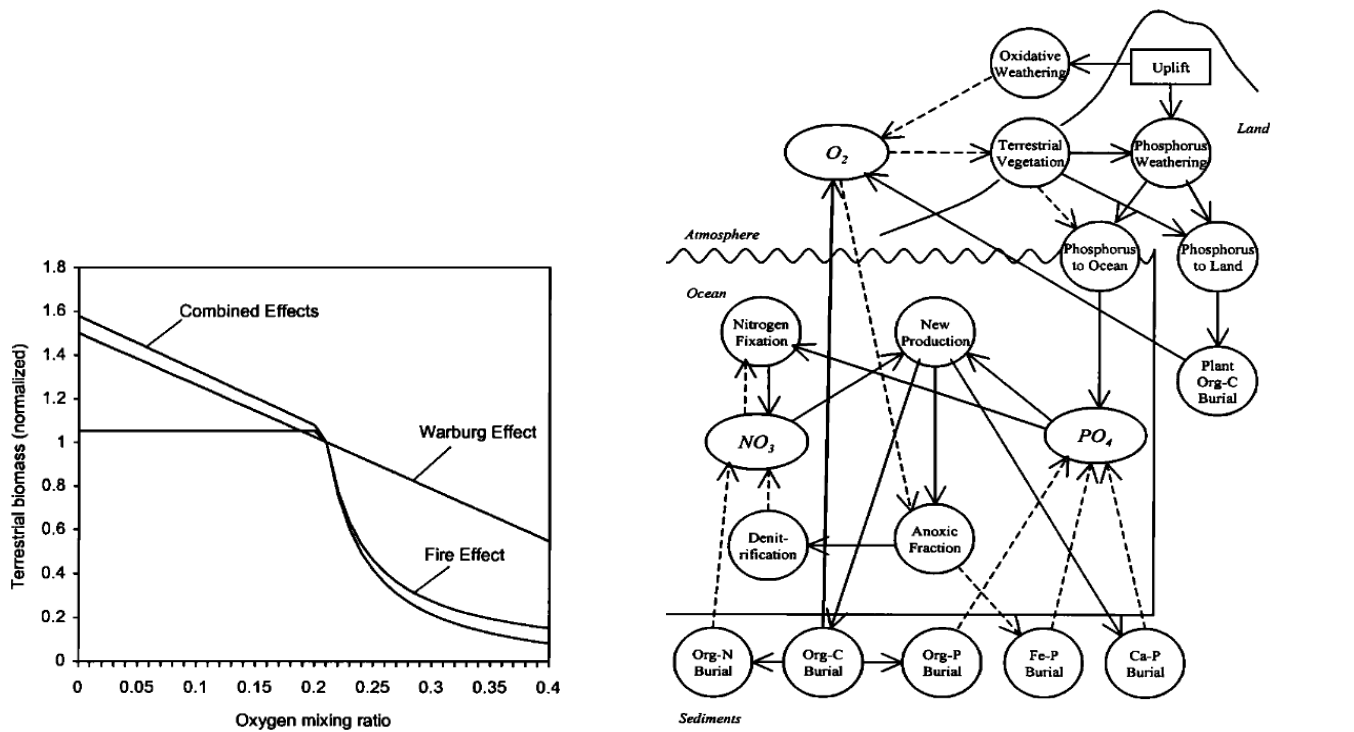


Figure 8: (left): Estimated dependence of land plant biomass on atmospheric oxygen mixing ratio showing the contributions of fire frequency and the Warburg effect (Lenton & Watson, 2000).

Figure 9: (right): Extended model. This includes the effects of oxygen mixing ratio on terrestrial vegetation via fire frequency and suppression of photosynthesis (the Warburg effect). Terrestrial vegetation can in turn affect the distribution of weathered phosphorus between the land and the ocean or directly alter phosphorus weathering (Lenton & Watson, 2000).

4. Discussion:

In this last section, we will discuss two of the earlier presented models that attempt to depict most significant forcings and relations among abiotic variables and adaptive responses of plant communities within fire prone ecosystems, as well as which suggest positive feedback loops capable of generating climate destabilizing effects likely to gain dominance in a context of a warming climate. Furthermore, we will briefly discuss the correlation between fire proneness and ecosystem productivity, and how a warming climate is expected to influence fire risk differently for ecosystems limited by dryness (largely too wet to burn) and those limited by productivity (not enough fuel continuity) (Resco de Dios, 2020). And last, given the fact that plant biomass regulation by fire is expected to increase under a warming climate, especially those types of fires where chances of containment dwindle, we briefly introduce the conditions – switches (Resco de Dios, 2020) – that need to be given for fire events to occur and mention common fire mitigation and management strategies, highlighting the somewhat antagonistic effect that they may exert upon fire risk dynamics, depending on local variables such as soil moisture, microclimate etc within a yearly cycle.

One of the motivations for this literature review was to understand where and to which extent reforestation, afforestation and other types of vegetation management in savanna systems with the goals of increasing the terrestrial carbon sink and ameliorate local microclimates can be a practical, feasible and desirable alternative, given natural constraints such as climatic trends and fire risk. In order to take informed decisions aligned with sustainable land management goals, this review highlights the importance of the acknowledgement of the high complexity of not only the dynamics among co-occurring species within Savanna biomes, but also the intricate relation between the unique conditions created by local and global abiotic factors – rainfall seasonality, climate, relative content of atmospheric gases, fire regimes, and soil – which ultimately determine local vegetative cover, while at the same vegetation cover itself exhibits non negligible effects onto these abiotic variables, by means of a variety of mechanisms such as precipitation recycling and cloud formation, albedo, non-methane hydrocarbons released, and by creating unique fire conditions.

Two comprehensive models representing positive and negative feedback mechanisms between vegetation, atmosphere and climate – roughly speaking – are the one proposed by (Beerling & Berner, 2005) where the central element is atmospheric CO₂ and a second model proposed by (Beerling & Osborne, 2006) where the central element is fire. Both models include “short term” mechanisms acting within years and decades as well as mechanisms acting within much longer time frames and typically involving the long-term carbon cycle.

The carbon cycle is of primary importance for the global energy budget and within large time scales the negative (stabilizing) feedbacks between CO₂ and vegetation tend to be the dominating ones. The fact that the carbonate-silicate rock weathering cycle is enhanced at higher atmospheric CO₂ concentrations is one reason for the prevalence of an overall negative feedback. We also saw that biological weathering enhances both the burial of reduced carbon as well as chemical rock weathering and thus the flux of nutrients to the ocean, boosting primary production and increasing the net carbon sink. While it is well known and accepted that higher CO₂ levels and a warmer climate tend to favor global biomass production on land via mechanisms such as lowering the cost of obtaining C, the enhancement of the hydrological cycle and in some cases also due to the increase of the growing season owed to a warmer climate, the model constructed by (Beerling & Berner, 2005) suggests that this positive correlation of higher CO₂ mixing rates and NPP may not always be the net global outcome. The reason for that is given by the fact that concomitant to the above-described mechanisms that enhance global primary productivity, a warming climate with higher CO₂ mixing rates tends to generate the net effect of increasing the leaf to air vapor pressure deficit due to warming itself as well as via reduction of stomatal conductance and by selecting for lower stomatal densities, within a large fraction of global terrestrial ecosystems. Thus, while water use efficiency is improved, this happens at the detriment of plants' cooling capacities, and in order to avoid overheating, a selective force for smaller leaves is created, diminishing the overall photosynthetic capacity of plants whose growth is largely seasonally limited by moisture. In other words, it appears that as climate warms, the terrestrial biomass enhancing mechanisms - increase of the growing season, lower cost to obtain C, etc - may at some point be outweighed by those that generate the opposite effect, as plants have to compromise their carbon fixing capacity in order to avoid overheating. Therefore, given the correlation of global NPP/global weathering rates and the global carbon sink highlighted earlier, if a warming climate reaches a threshold wherein subsequent warming *decreases* global productivity, rock weathering and org C burial, a positive - climate destabilizing – feedback could gain dominance.

The second model presented here, establishes fire as a central element (Beerling & Osborne, 2006). Essentially, we could divide this model in two “sub-models”, one involving “short term” mechanisms (figure #4) and one involving “long term” mechanisms (figure #5). The central or key assumption for the “long term mechanisms model” again is based on a *negative* correlation between atmospheric CO₂ levels and global weathering rates, although for a different reason than the one previously discussed. In this case, the spread of the grassland dominated savanna biome – assumed to be contingent both on low CO₂ mixing rates as well as sustained by increased fire activity – would, according to the authors, *not* imply in a reduction of overall rock weathering rates despite the decrease in the global area occupied by forests. Confirming the validity of this hypothesis would require further work especially because the assumptions made are of global scales and relate to millions of years past (Miocene).

Yet, one way to approach/validate this assumption is by comparing weathering rates of similar rock and soil types, within similar latitudes, climatic conditions and precipitation regimes but under different vegetative cover. Exactly that has been performed by (Wen et al., 2020) which compared weathering rates under woodland vs grassland cover using Ca²⁺ and DIC as proxies for rock weathering.

Under the same precipitation regime – the sites are in immediate vicinity of one another - they found that while 90% of the root biomass of grasses are within the upper 50cm of the soil profile and bio-pores have a predominantly horizontal orientation, only 50% of tree roots are within the 50 upper cm of soil, and not only do bio-pores reach deeper, but are also more vertically oriented. The overall effect found was that during and after precipitation events, a significantly higher volume of water percolates to deeper – more unweathered – soil/rock regions under a tree/woodland cover which, by increasing the residence time of acidified water due to root respiration with the mineral matrix, ultimately leads to higher carbonate dissolution rates, the local proxy for rock weathering. To put it in quantitative terms, when modelled for a 300-year time period, the weathering front advances twice as deep in the woodland soil compared to the grassland soil. Therefore, according to this study, tree biomass loss to grass cover would imply in a non-negligible *decrease* in local rock weathering rates, and if we assume that this trend is applicable across savanna and grassland regions, it should disconfirm the validity of the assumption represented in figure #5, pathway “n”.

Even if the hypothesis that a conversion from forests to grasslands would *not* imply in a reduction of rock weathering is at the very least questionable, the more short-term positive feedbacks between vegetation cover and fire frequency summarized by (Beerling & Osborne, 2006) seem to be anchored on more solid ground. Such feedbacks could roughly be divided in 3 categories. i) the positive feedback engendered due to the fact that C4 grasses are more efficient resprouters while also creating a higher volume of dry fuel at faster rates; ii) the positive feedback created when certain high-intensity fires dramatically increase the chance of subsequent fires ignited by lightning; and iii) the positive feedbacks via climate and precipitation change, namely the types of aerosols emitted by fires lead to an overall drying and cooling of the local climate, yielding more infrequent however stronger precipitation events. Other authors like (Wood & Bowman, 2012) suggested an additional fourth mechanism which is given by the fact that a more intense/frequent fire regime tends to enhance nutrient depletion – mostly N – which would favor C4 grasses over trees due to their higher photosynthetic N use efficiency.

All or a combination of some of the above-described positive feedbacks have been regarded as the mechanisms underlying transitions from tropical forest to savanna or from woodland to grassland, often triggered by human-caused deforestation. Thus, interestingly, for present day conditions, while some ecosystems are experiencing a natural increase in woody biomass, typically culminating in a more closed canopy type of biome accompanied by a change in the fire regime, other biomes – and the Amazon may be the most iconic within that 2nd category – are experiencing the reverse trend, which is massive woody biomass loss, typically anthropogenically triggered, however eventually entering a self-sustained “downward spiral” approaching an alternate drier state with decreased biodiversity and altered precipitation and fire regime.

Given the outlook of a warming climate and increasing atmospheric CO₂ levels, a natural question that arises is how do these trends may alter global occurrence and dynamics of wildfires, especially those within Mediterranean climate? To try to answer this question, it is worth noting how the likelihood as well as intensity and frequency of fire manifests itself as a function of ecosystem productivity. Overall, within a global range of fire prone ecosystems, such range can be understood as being placed between

two extremes, among which it is worthwhile to differentiate conceptually: On the one side we have ecosystems limited by productivity and on the other side, the ones limited by “dryness” (Resco de Dios, 2020). The systems limited by productivity are the ones located typically on the more arid end of the spectrum, aridity acting as the main – yet not the only - constraint for overall productivity. These systems typically do not accumulate enough biomass to create enough fuel continuity, so in most years, even if they burned, the resulting wildfire would likely be low in intensity and limited in its ability to spread widely. The possible exception for these types of low rainfall/productivity ecosystems are some arid grasslands, which due to the combination of readily creating dry/flammable biomass, sometimes even annually, and their extremely high post-fire recovery efficiency – leading to them outcompeting any potential plant species with more fire-suppressive characteristics – typically embody the systems with the highest fire frequency despite a comparatively low above ground biomass. A warming climate - at least in regions where rainfall does not increase proportionally - would be expected to increase environmental stress upon plant communities via heat and drought, therefore, ecosystems already limited by productivity may become even less productive under a warming climate. Thus, fire events should be expected to become less intense and possibly also less frequent in systems already limited by productivity.

On the other side, we have those systems – both within as well as outside Savanna biomes – that either have a fire regime with very great intervals in between fire events or such that have no natural history of fires, in other words, where fire is very rare and typically a result of human-induced disturbance such as deforestation. Most tropical and temperate forests can be described as ecosystems largely too wet to burn, as they tend to be characterized by very few open inter-canopy spaces and high transpiration rates, both of which limit sensitive heat production, as well as a very low ratio of dead (dry) fuel, if any. These forests are largely immune to natural wildfires as their level of dryness is insufficient or only dry enough during a very short period of time within a yearly cycle, to imply in a considerable fire risk. However, under a warming climate and under scenarios of high precipitation seasonality, the extent of time where forests enter a flammable (dry enough) state is expected to increase, which from a fire management perspective becomes especially challenging, since extensive areas previously too wet to burn, are now becoming fire prone for larger periods of time within a year and, if fire were to occur, the large amount of burnable biomass as well as fuel continuity has in many cases generated fires too great to be contained.

As we saw earlier, fires in and of itself cannot be regarded as a negative disturbance, as not only has it been shown that it is one of the main drivers of biodiversity in many global biomes, but plant evolution itself wouldn't have had occurred and culminated in today's plants without the “co-evolution” of plants and local fire regimes. Yet, as far as the protection of human life and property goes, wildfires have and need to be contained, avoided and managed as best as environmental constraints may allow. In order to better understand realistic and effective fire management strategies, we can draw from the work done by (Resco de Dios, 2020), that establishes 4 so called “switches” that need to be “turned on” for fire to occur. Switch or threshold #1 relates to the volume of above ground biomass per unit of area if you will, in other words, the productivity of a system. Very dry and warm regions of the world have the right climatic conditions for fire to occur, however, productivity is so low that if a fire were to

occur, the resulting spread and damage would likely be minimal as biomass and fuel continuity are too low. Switch or threshold #2 essentially relates to the dryness of the local biomass, so, as suggested earlier, most forests exhibit very large biomass per unit area, however the level of dryness is insufficient to pose a considerable fire risk during most if not the entire yearly cycle, on average years. Switch #3 relates to an ignition source, which can be both natural as well as human caused. And last, switch #4 relates to both the fuel characteristics as well as the environmental conditions at the event or shortly after ignition has occurred. In that sense, variables such as fuel ladder, fuel continuity, crown bulk density, fire suppressive vs fire enhancing traits of local flora, and likely most importantly, the ratio of dead/dry to live fuel need to be considered when it comes to fuel characteristics, while parameters such as topography, temperature, air moisture content, wind speed and direction are of equal importance in determining the ease of fire spread as well as chances of containment.

It turns out that as far as preventive fire management goes, threshold #4 appears to be the one with the highest management potential to avoid catastrophic wildfires. Practical actions for such may include forest thinning in order to reduce burnable biomass and improve water availability for the remaining stand, the breaking up of fuel ladders, targeted grazing to reduce the load of dry fuel, **and** the creation of strategic firebreaks. Limiting a potential ignition source may be only as effective as it is human caused; limiting overall productivity as well as the drying out of fuel may be less realistic especially within extensive “wild” areas.

Interestingly, many regions are *naturally* turning *more* fireproof – mainly those experiencing so called bush encroachment – which is also understood to be partially driven by increasing atmospheric CO₂ levels, as such increase would favor trees more than grasses. The explanation for this decreased fire proneness, is attributed both to the proportional reduction of vegetation that dries out rapidly such as grasses, as well as to a microclimate change. The latter one happens since a higher tree density diminishes wind speed by increasing total roughness length and most importantly increases the ratio of latent heat over sensitive heat, as more trees equal higher transpiration rates. This phenomenon appears to be at odds with for example the fire suppressive management action of thinning. Thinning naturally improves the below ground water availability for the remaining trees for a longer period within the dry season, thus delaying and/or diminishing the drying out process of live fuel and the creation of dead fuel, which is the main factor determining a system`s flammability.

In reality, both bush encroachment as well as thinning can have a fire enhancing as well as fire suppressing *net* outcome, which again highlights the complexity as well as multi factor nature of fuel dynamics. Bush encroachment does indeed “improve” the microclimate as described earlier, however only as long as vegetation is able to access groundwater at a rate sufficient to prevent it from drying out. While thinning, although it improves water availability for the remaining trees, tends to also “worsen” the microclimate and may also promote undergrowth which leads to the formation of fuel ladders. In summary, in ecosystems largely limited by moisture, productivity is ultimately mostly a result of the availability of groundwater, which plants will tap into promoting growth, and dry out if soil moisture isn`t replenished. Removing or preventing the buildup of dead fuel as well as breaking up fuel

continuity seem to be the most effective approach while aiming to prevent fire events too great to be contained.

5. Conclusion:

We live during a time in which the biosphere is undergoing relatively rapid changes, largely attributed to increases in the atmospheric CO₂ levels and resulting in warming of the global climate. Besides anthropogenic interventions, climatic changes are often at the root of what we see as large-scale changes in ecosystem structure, such as extinctions, displacements by invasives, woody plant encroachment, ecosystem degradation and desertification to name just a few. Not all these outcomes are necessarily negative, and some may even exhibit the secondary benefit of enhancing carbon fixation within terrestrial biomass. Others, like deforestation followed by natural disturbances in biomes like tropical forests, seem to trigger exclusively negative outcomes for the local climate, resources, and biodiversity. The potential to ameliorate local microclimates and draw “excessive” CO₂ from the atmosphere via afforestation or by allowing natural processes such as tree/bush encroachment to occur may sometimes be a sound and sensible aim, while in other cases may cause more long-term damage, whose likelihood appear to strongly correlate with the lack of prioritizing a well-adapted and diverse array of species. Preventing/limiting fire and fire spread, although it can hardly be argued against on the level of individual actions aimed to protect life and property, has had the net effect of creating a situation of a “biomass excess” or a “fire deficit” (Resco de Dios, 2020) in some parts of the world, given present-day oxygen levels and climate. The temporal and spatial action of drought may be exacerbated in its extent and intensity by a warming climate. In some cases, it may decrease fire risk by progressively drying out ecosystems already limited by productivity, while, in other cases, may trigger the flammability threshold/switch for very productive ecosystems, igniting extensive areas of historically non-flammable tropical as well as temperate forests - where species range from poorly to non-adapted to fire - and thus typically creating the right conditions for the types of fire events too great to be contained.

Free oxygen is essentially a product of (plant) life, and as such a given atmospheric content is essentially a reflection of the “former” plant productivity, which on its turn is largely determined by climate. The loop is closed as oxygen content feeds back onto terrestrial plant productivity, primarily by modulating plant biomass flammability as it interacts with local climate and secondarily by influencing the cost of photosynthesis for plants that use the C3 photosynthetic pathway. In addition, atmospheric O₂ levels determine the extent of oceanic anoxia, which on its turn influences the rate of the marine carbon sink, thus influencing climate on a larger time scale. As we saw at the end of the result section, there are highly responsive mechanisms which keep atmospheric oxygen fluctuations varying very slowly and within a relatively narrow band, namely marine mechanisms for low global oxygen levels and terrestrial mechanisms for high global oxygen levels. Given the fact that oxygen relative to CO₂ only varies very little both in magnitude and especially in time, current and near future variations in CO₂ levels may have a non-negligible effect over plant’s photosynthetic capacities. As CO₂

levels increase, the most obvious one may be the relative increase in the competitiveness of C3 plants relative to C4 plants, since the cost effectiveness of the C4 pathways decreases as CO₂ relative to O₂ increases. This assumption needs to be understood in the broadest way possible however, as for instance the extent of water limitation may shift the relative competitiveness of these 2 photosynthetic pathways. Additionally, increasing CO₂ mixing rates relative to O₂ should theoretically reduce the Warburg effect (see figure #8), thus – one could speculate - by relieving plant growth constraints via the more gradually acting mechanism, may conversely enhance the so called “fire deficit”, as a net increase in global terrestrial biomass especially in a scenario of also increasing rainfall seasonality and drought would be expected to proportionally increase regulation by fire.

Therefore, aiming for a reduction in fire frequency does not seem to be a feasible approach given the current likely already present “fire deficit”, nor is it necessarily desirable from an ecological perspective. A changing/warming climate may increase the fire deficit in some biomes, the potential for higher plant biomass in others or possibly even both the potential for more biomass as well as increased fire risk within the very same ecosystem, especially when rainfall seasonality increases. Therefore, sustainable and sound land management will have to be anchored in ongoing insights provided by advancements in the fields of fire ecology, atmospheric sciences, plant physiology, biogeochemistry amongst others.

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