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Projet de Fin d'Etudes

Woody encroachment impacts on soil properties

L'impact des ligneux sur les propriétés du sol

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2016-2017

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2017

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Le travail de recherche, dont l'objectif de base est d'acquérir une compétence méthodologique en matière de recherche, doit répondre à l'un des deux grands objectifs :

- Développer toute ou partie d'une méthode ou d'un outil nouveau permettant le traitement innovant d'un problème d'aménagement
- Approfondir les connaissances de base pour mieux affronter une question complexe en matière d'aménagement.

Afin de valoriser ce travail de recherche nous avons décidé de mettre en ligne sur la base du Système Universitaire de Documentation (SUDOC), les mémoires à partir de la mention bien.

REMERCIEMENTS

Nous tenons à remercier notre directrice de recherche, Séraphine Grellier, pour nous avoir encadré et donné tous les conseils dont nous avions eu besoin pour mener à bien ce PFE. Merci également d'avoir pris le temps de nous corriger tout au long de la rédaction du rapport.

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Review

Woody encroachment impacts on soil properties

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Abstract

During the last century, grasslands and savannahs across the world have been encroached by woody plants (Van Auken 2000, 2009). These landscapes are covering 40% of the land surface (Chapin, 2001 from Briggs et al., 2005).

Woody encroachment is generally perceived negatively resulting in degradation of the invaded ecosystem. Nevertheless, it can also benefit the environment. Therefore, it is important to understand the positive as well as the negative impacts on the biological, physical and chemical and properties.

Indeed, on one hand, by providing a micro climate beneath its canopy, trees or shrubs create "fertility islands". They bring up water, reload carbon and nutrients stocks, and increase soil life especially because litter is more abundant. On the other hand, trees and shrubs also alter hydraulic properties particularly by rising soil erosion.

Moreover, this study showed that the consequences on soil properties differ from various factors. For example, shrub species (leguminous vs non-leguminous), environmental conditions (climate such as temperature, rainfall and study location), the level of encroachment, resource competition and soil density are all factors that interact with each other and modify the consequences on soil properties that lead to differences between woody and herbaceous patches. Finally, this review revealed that scholars' opinions are well contrasted and the impacts of woody plants on soils cannot be treated as a whole, it differs and depends on the ecosystem. Due to its complexity this process still raises a lack of understanding and many interrogations that need to be further investigated.

Key words: encroachment, woody plant, shrub, shrubland, grassland, savannah, soil properties.

Introduction

During the last century, grasslands and savannahs across the world have been encroached by woody plants (Van Auken 2000, 2009). These landscapes are covering 40% of the land surface (Chapin, 2001 from Briggs et al., 2005). While grasslands (also called prairies) and savannahs are both characterized by grasses; savannahs are also covered by some trees and shrubs. In grasslands, the proportion of rainfall does not allow tree formation but is just enough to avoid creating a desert. That is why, most of the time, grasslands are located between deserts and forests (national geographic). In savannahs, the climate is quite different and can be defined as a dry and warm tropical climate. The dry season is long and without any rains, while the wet season is characterized by strong and daily rains for several months.

The proliferation of woody plants in arid and semi-arid areas has led to a change in vegetation structure. Indeed, these grazing areas are converted into savannahs, woodlands or shrublands (figure 1) (Allen et al., 2002, Van Auken, 2009, Eldridge et al. 2011). Furthermore, woody encroachment proliferation has been estimated by some researchers. Indeed, each year, it increases between 0.5% and 2% across the world (Archer et al., 1995).

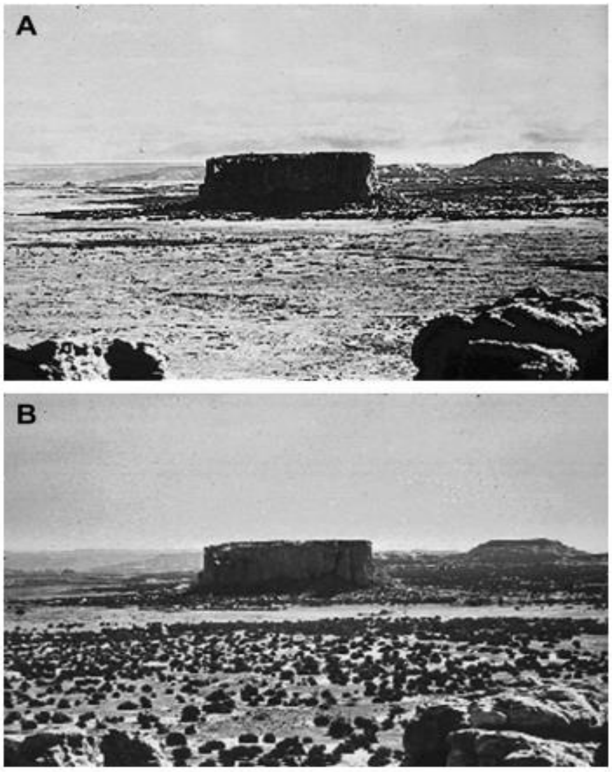


Figure 1: example of the encroachment of JUniperus species in semiarid grasslands (New Mexico)
Source: Van Auken, 2009; photo A: taken by Jackson in (1899), photo B: talen by H.E Malde (1977)

Woody plant encroachment has been widely studied and has been well documented since the last three decades (Van Auken 2009, Eldridge et al. 2011; Archer et al. 2001, Huxman et al. 2005). This phenomenon is driven by several factors such as global warming (climate change including atmospheric CO2), overgrazing, herbivory and the spread of seed by animals (Eldridge et al. 2011, Grellier 2011, D'Odorico et al. 2012, Van Auken, 2000). Invasion and encroachment have to be distinguished. Indeed, invasive species refer to species which have been introduced into an environment that is not its original environment. In other words, it refers to species which come from another area such as another continent (Van Auken, 2000, 2009; Grellier, 2011).

Among the many impacts of this process on ecosystems, this paper will focus more on the effects on soil properties. Indeed, it is mainly because of its capacity to store large quantities of carbon and therefore to have a "buffering effect" that is likely to play in climate change "(Buresi p4 from Lal, 2004). Despite this, woody plants are perceived negatively. However, they impact both positively and negatively the soil by changing its physical and chemical properties such as the modification of C and N cycles (Archer et al. 2001; etc.).

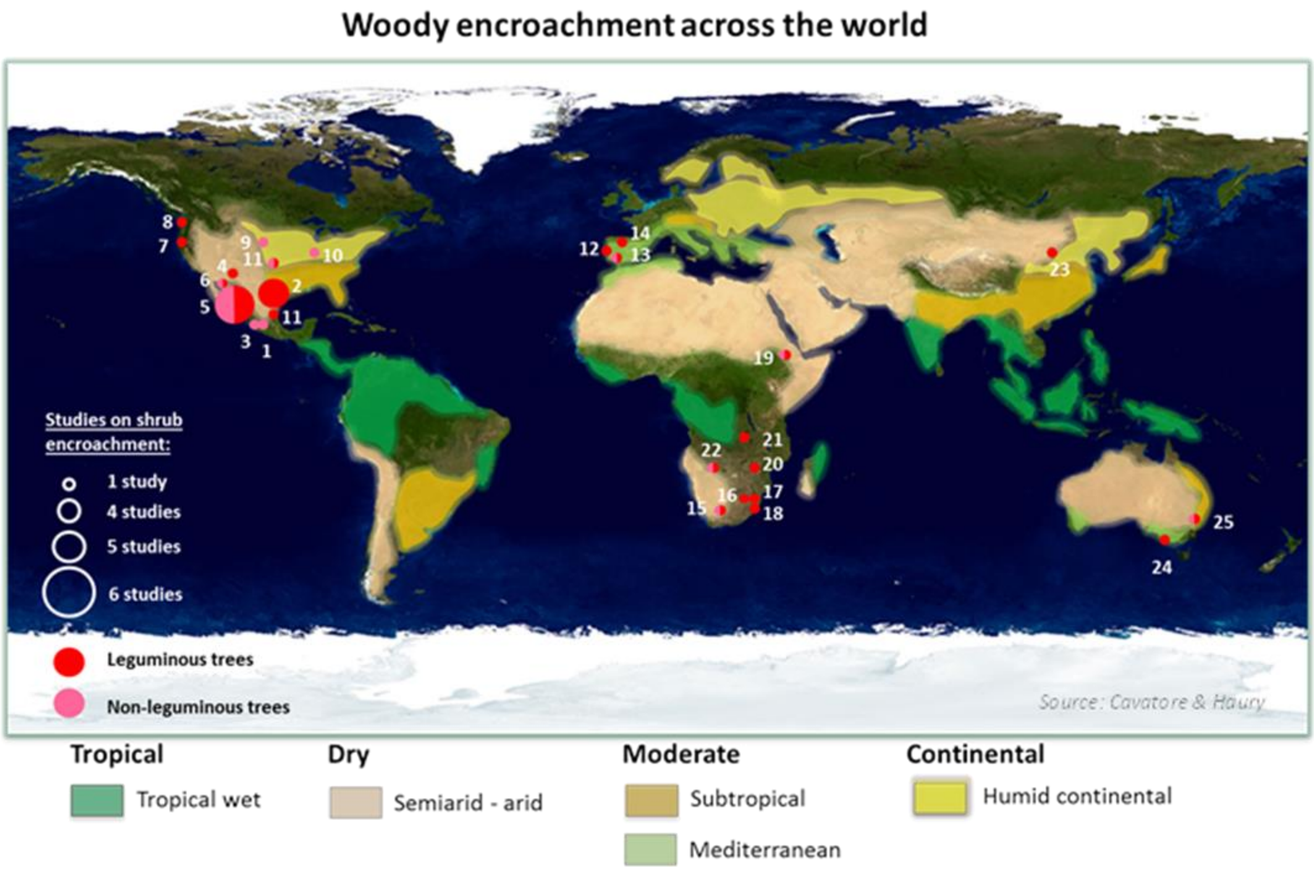
Finally, the purpose of this review is to enhance our understanding of the specific impacts of trees on soils in order to identify the main untreated points concerning this subject. To answer our main question: while woody plants are encroaching pastures and savannahs, are they impoverishing the ground and its environment? We decided to focus our work on three main questions: (i) what are the impacts of woody plants on soil life? (ii) What are their impacts on the water dynamics including erosion? (iii) Are biogeochemical cycles modified because of these trees? To answer these questions, this paper is divided as follows: first of all, it describes the consequences of woody plants on soil life, food webs and soil microbiology. Then, it outlines the impacts on water dynamics including soil erosion before ending with the consequences on carbon cycle, on nutrient cycle.

Method

Based on a theoretical approach, data were collected from a corpus of 45 Anglophone and scientific articles grouping a wide range of studies carried out on woody plants on all continents. Although the woody invasion is observed across the globe (plains of North America, Mediterranean basin, Australia, Southern Africa, Asia, (figure 2)), studies are unevenly distributed. Indeed, most of them have been realized in North America (Texas, Arizona), somewhat less in South Africa, mainly in pastures and savannahs and in arid, semi-arid and humid climatic conditions. Besides, more than half of the articles studied were conducted in dry conditions (semi-arid and arid environments) of North America.

In addition, this map also shows the proportion of studies which refers to leguminous and non-leguminous species. Indeed, the vast majority studied the encroachment of leguminous species.

Consequently, attention must be paid to the conclusions reached, for although these experiments deal with the same phenomenon, they have been carried out on different plants and different climates. Thus, the specific conditions and specificities of each ecosystem will be taken into account.



1. Larae tridentata
2. Prosopis glandulosa
3. Larrae & Bouteloua
4. Prosopis spp.
5. Prosopis velutina & sporobulus wrightii
6. Prosopis (mesquite), Larrae and Juniperus spp.
7. Juniperus virginiana
8. Cytisys scoparius L. Link
9. Cornus drummondii
10. Cornus drummondii
11. Prosopis, acacia, andropogon
12. Quercus
13. Cistus ladanifer et Retama sphaerocarpa
14. Stippa tenacissima
15. Acacia eriloba, A. haematoxylon, Boscia albitrunca, Rhigozum trichotonum & acacia melifera
16. Acacia spp

17. & 18. Acacia sieberiana
19. Maerua crassifolia, acacia nilotica, Ormocarpum trichocarpum, Grewia tenax, Lannea triphylla, G. villosa
20. Colophospermum mopane
21. Dichrostachys cinerea
22. Larrea tridentata, Bouteloua gracilis, prosopis glandulosa
23. Leguminous shrub
24. Mesquite
25. Eremophila sturtii, senna artemesioides, dodonaea viscosa, austrostipa spp., austrodanthonia spp., sclerolaena

Figure 2: woody encroachment across the world
Source: Cavatore & Haury

Part I – The soil: as life support for fauna and flora impacted by the woody plants

1-1 The soil: flora support

"Fertility islands"

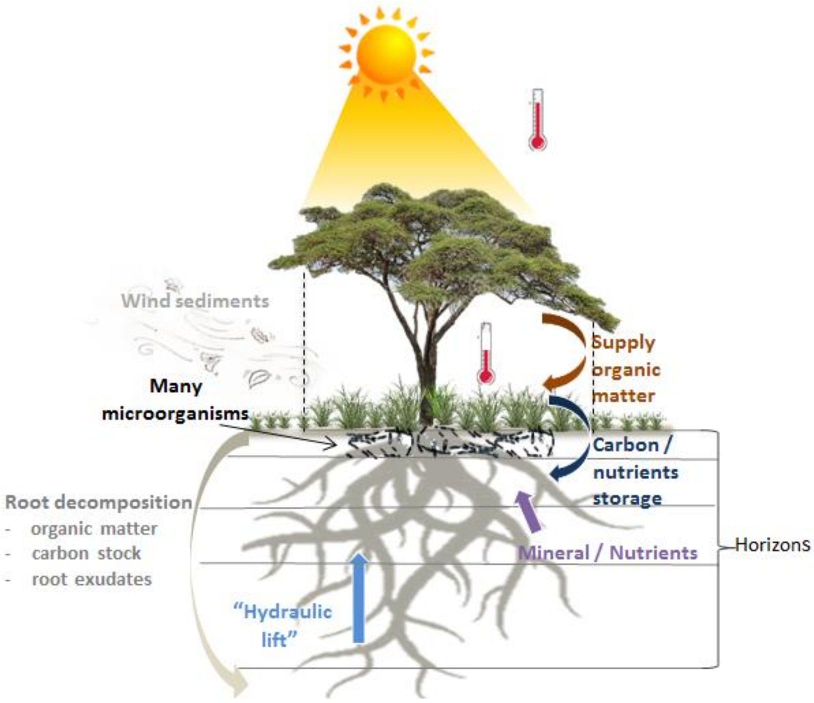


Figure 3: fertile Island beneath canopy
Source: Cavatore & Haury

Trees create a microclimate beneath the canopy. This is mainly because of a rise of evapotranspiration due to a higher leaf area index (Van Auken, 2009) and its foliage which provides shadows. Indeed, trees increase evapotranspiration (Scott et al., 2006). In other words, there is a difference of climate above and below trees mainly due to its foliage. Indeed, shadows provided by trees, lead to lower temperatures under canopy (compared to open grasslands) and better conditions for the activity of microorganisms. Moreover, the soil is strongly enriched with fungi, which retain more moisture in the soil and keep it moist and fertile (Price & Morgan, 2008; Belay et al., 2013). This moisture is partly provided by the phenomenon of "hydraulic lift" (Ludwig et al., 2003 from Buresi, p.5) whereby trees pump water from shallow to deeper soils. By carrying this water, tree releases some of it for the benefit of other nearby plants. There is also a greater intake of organic matter (Weltzin and Coughenour, 1990), an accumulation of nutrients, or wind deposits which are stopped by the canopy (Charley and West 1975, Schlesinger et al., 1990) (figure 3). Indeed, this canopy represents a physical barrier which leads to the accumulation of wind sediments on soil, just under the canopy (see part II for further information– erosion). Thus the aerial part of the tree makes available many beneficial resources to plants, microorganisms ... However, the underground part, inter alia; the root system should not be forgotten. It is also important to air the soil, to bring more organic matter and to store carbon when roots decompose and also to encourage the feeding of microorganisms through the root exudate.

Furthermore, as the woody grow, surface soil resources (e.g. accumulation of organic matter) are differently distributed and accumulate under the woody plant canopies and into the soil thanks to the root system. Also called resource islands, fertility islands or islands of fertility; these clusters of woody plants are known for concentrate different species of woody plants and resources (Bush and Van Auken, 1986, Archer et al., 1988, Schlesinger et al., 1990, Ravi et al., 2010). Soil resources are renewed in these fertile islands, making it privileged sites. Some researchers have found that these islands of fertility increase "carbon stocks and high levels of nitrogen that facilitate the relatively rapid decomposition of high-quality litter" (Cable et al., 2009, p.163), (for further details, see part III: carbon and nutrients).

Herbaceous cover

The consequences of woody plants on the vegetation cover are very controversial. Indeed, both negative and positive effects have be found on the vegetation cover biomass (Hoffman and Ashwell 2001, Lett and Knapp 2008, Eldridge et al., 2011; Ratajczak et al., 2012), or even neutral (Grellier et al.). For example, according to Mordelet and Menaut (1995), grass production

under tree canopies can be stimulated by almost 300% or deleted by more than 50%.

Several studies denounced the harmful effects of shrubs on the vegetation cover. As suggested by several researchers (Huenneke et al., 2002, Gillette and Pitchford, 2004, Briggs et al., 2005, Peco et al. 2006, Price and Morgan, 2008, Rivest et al., 2011, Mlambo, D. et al., 2005), encroachment is often linked to a decline in herbaceous cover, favouring the development of bare soils. Moreover, its foliage intercepts water which reduces the availability of water and thus decreases the herbaceous biomass while the soil moisture increases (Grellier, 2013). This argument was also supported by Selene (2008). Indeed, her study showed that woody encroachments decrease coverage of dominant C4 grass and species richness. This indicates that interspecific interactions induce significant changes in the stability of a specific community and may be the reason of a decline in biodiversity. Moreover, her results demonstrated that the invasion has effects on the community stability of the subdominant by making it less stable over time (increases species turnover rate).

In contrast with this argument, Tamrat et al. (2003) observed in south-western Ethiopia, a rise in the diversity and the richness of plant species because of the encroachment of woody plants. They also noted that the diversity, richness and uniformity of vascular plant species increased with the density of woody plants, probably due to increased spatial heterogeneity and improvement of the soil microclimate.

The inhibitory effects of woody plants, especially the effects of leguminous species on the growth of some neighbouring plants have been studied by several scientists (Walker and Vitousek 1991; Karen 2004; Soudzilovskaia et al. 2012). Despite an increase in nutrients, the impact of trees on plant communities can be influenced by other effects than the presence of N, but rather chemical or microbial (Karen, 2004).

In fact, herbaceous biomass is not only qualitatively improved (Treydte et al., 2007, Ravi et al., 2010) but also quantitatively (Burtt Davy, Keay & Brenan) under trees compared to inter-canopic spaces (Tiedemann and Klemmedson, 1977, Abule et al., 2005). Indeed, Norris et al. (2007) argued that the vegetation productivity would be about 2.5 times higher upstream of the forests of J. virginiana in comparison with open grasslands. Vegetation cover under trees is often green and uncovered during long dry periods compared to herbaceous plants in open areas. This could be explained by an environment rich in nutrients and more mesic than open areas (Mlambo, D. et al., 2005).

According to Grellier (2013), under some trees such as A. sieberiana, a toxic native species called Senecio inaequidens, develops and harms horses and cattle. She also noticed that the encroachment of A. sieberiana can cover the entire surface of grassland, reducing cattle access to pasture (Grellier 2013). Although shrubs provide food for grazers (Grellier, 2013), shrub encroachment reduces the profitability of grazing systems (Scholes and Archer, 1997) by decreasing the area of grazing (Smit 2004) and also the diversity of pastures into grasslands or savannahs (Briggs et al. 2005; Peco et al. 2006; Price and Morgan 2008; Rivest et al. 2011).

Note: the net aerial primary production (NAPP) is also higher than in non-invaded areas (Barger et al., 2011). However, NAPP appears to decrease in the most arid sites and grow in more temperate sites (Knapp et al., 2008), which means that there is a correlation with the rainfall regime. According to Barger et al. (2011), when the precipitations (P) are higher than 336mm per year, the aerial biomass increases by “0.7 g C m^{-2} yr^{-1} per each mm beyond 336 mm of rain” (Buresi p5). Although there is a significant increase in aerial biomass (Barger et al., 2011), root biomass is also increased under woody (Hollister et al., 2010), measured through soil organic carbon (SOC) (expanded in Part III).

1-2 The life of pedofauna

Soil communities and food webs

Shrub encroachment increases spatial heterogeneity, leading to a rise in soil fungal community variation and structural change

(Anthony et al., 2014). However, changes in the structure and dynamics of microbial populations have consequences on all ecosystem food webs. While some believe that the invasion generates an alteration of the biodiversity (Ravi et al., 2010); others argued that it produces a greater richness of populations, for example fungal and bacterial (Hollister et al.).

The biological soil properties are very impacted (Turnbull et al., 2010), because woody invasion makes soil resources and its properties more heterogeneous (Biederman and Boutton 2010).

As suggested by McCulley et al. (2004) and Shade & Hobbie (2005), soil microbial biomass would be more concentrated beneath trees because of the nice microclimate (described in the first part) (Springsti et al., 2010; McCulley). Moreover, clusters of woody trees create ecological niches with favourable conditions for the development of species (fungi, bacteria, etc.). However, researchers have also reported that shrub encroachment has negative impacts on soil life because it decreases soil respiration, (particularly in mesic grasslands McCarron et al., 2003), reduces the diversity of fungi and modify both microbial biomass and activity (Van Auken, 2009, Eldridge et al., 2013, He et al., 2010 Lett and Knapp, 2005).

Indeed, a more abundant aerial or underground litter (Archer et al., Hibbard et al., 2001) promotes surface microbial life (McCulley et al., 2004). Furthermore, as there is a high carbon and nitrogen stocks under shrubs (due to the deposition of high quality litter on the soil surface), there is a large microbial communities in the soil (Cable et al., 2009). Some trees such as mesquites seem to increase the amount of microbes by almost 3 times in the superficial layers compared to the grass and bare microsites (Cable et al., 2009).

Jackson et al. (2002, p. 625) reported that this loss of species richness could be explained by the "loss of root feeding species". At the same time, Biederman and Boutton (2009) hypothesized that “the nature of under-woody plants limited root parasites” which explains the change in the structure of the community despite identical biomass and specific richness” (Buresi, p9).

It can be noted that the interactions between the ecological niches and the species populations are dynamic. These interactions can lead to "positive feedback" (Buresi, p10). For example, by creating galleries, termites which are more present under shrubs (Turnbull et al., 2010), contribute to the mechanical fragmentation of the litter for the benefit of microorganisms.

In conclusion, although woody can be privileged habitat for microbiology, it “can alter the ecological equilibrium and even destroy the ecosystem as a whole” (Buresi, p10).

1.3 A short conclusion of the effects of woody encroachment on herbaceous cover and on pedofauna

Effects of woody encroachment on herbaceous cover			
Parameters	**Positive effects**	**Negative effects**	**Total**
climate	8	9	17
arid – semi arid	7	4	11
mesic – (sub) humid	1	0	1
(sub)tropical	0	2	2
mediterranean	0	3	3
Pedoclimax	10	10	17
grassland/prairie	4	5	9
Woodland /shrubland	0	4	4
savannah	4	0	4
desert	2	1	3
Woody species	8	8	16
leguminous	5	3	8
non-leguminous	3	5	8

Table 1, source: Cavatore & Haury

The graph above shows that the effects of wood invasion tend to be positive in arid/semi-arid environments (a rise in plant biomass). Indeed, the tree creates a micro climate under its canopy. Nevertheless, it is not possible to determine in which pedoclimax woody encroachment improves or alters the properties of the soil because there is no great difference.

Finally, the same is true for woody species. In fact, we are not able to say whether legumes or non-legumes have a positive or negative impact on the herbaceous cover. Thus, it would be interesting to carry out more experiments in order to be able to identify a trend.

Effects of woody encroachment on pedofauna			
Parameters	**Positive effects**	**Negative effects**	**Total**
climate	4	7	11
arid – semi arid	2	5	7
mesic – (sub) humid	1	0	1
(sub)tropical	1	1	2
continental	0	1	1
mediterranean	0	0	0
Pedoclimax	4	10	14
grassland/prairie	2	6	8
Woodland /shrubland	1	1	2
savannah	0	1	1
desert	1	2	3
Woody species	4	6	10
leguminous	4	4	8
non-leguminous	0	2	2

Table 2, source: Cavatore, Haury

The 2nd graph which reports the effects on the pedofauna, shows that woody encroachment tends to affect it negatively, especially in arid/ semi-arid and also mainly in the grassland / prairie. With an equal number of studies that have found positive and negative effects, it is therefore not possible to assess whether legumes or non-legumes have a positive or negative impact. It could be interesting to further investigate the impacts of woody encroachment on pedofauna with leguminous and non-leguminous.

1-4 Towards a deeper understanding of untreated/uncovered questions

As seen previously, numerous studies have been conducted in order to better understand the effect of woody plant on soil. The opinions are very mixed and we cannot assert that this phenomenon has overall positive or negative effects because many factors must be taken into consideration. Indeed, these islands of fertility can both enhance or decline the soil life. For example, these huge different points of views depend on the location of the studied sites (Eldridge et al., 2013), the level of encroachment, the climate (Knapp et al., 2008b), the composition of woody species can influence the outcome of ecosystem responses to the encroachment of woody plants.

This study revealed that future studies should try to answer the following questions:

- For example, Mlambo et al. (2005) raised an interesting point concerning the organic matter under canopy. Indeed, the amount of litter input and decomposition rate between "tree interspaces" and under trees could be further investigated.

- How interactions (both biotic and abiotic) affect the structure and composition of plant communities to woody encroachment? (Hai-yang Zhang, 2016)

- Further studies should be conducted in order to know how grazing interacts with the catena? (E.g., Belsky et al., 1993 ; Abule et al., 2005 ; Mbatha and Ward, 2010 ; Dunne et al., 2011)

- Information concerning soil respiration are well contrasted and mainly depends on climate. Indeed, in mesic conditions, woody encroachment decreases soil respiration (McCarron et al., 2003), whereas it increases it in subtropical environment (Archer, 2000). It could be interesting to further experiment it in dry conditions. Are the impacts on soil respiration are similar to mesic or subtropical environments?

- Finally, others studies should focus on the correlation between "toxic sub-canopy species" and the increase of Acacias' encroachment (Grellier, 2013).

Part II- Woody plants and water dynamics at different scales

2.1 Water resources

Different climate conditions are changing the soil water balance

By invading grasslands, shrubs impact water cycle and resources. These changes depend on climate conditions. Moreover, trees intercept rainwater which may be rapidly evaporated in arid and semi-arid environments (Wilcox et al., 2003). Thus, the water does not fall on land, which decreases the amount of water reaching the ground and considerably declines groundwater recharge (Archer, 2010; Parizek et al., 2002; Grellier, 2014).

Trees also provide shade. Therefore, it creates a microclimate under trees also called islands of fertility, decreasing temperature and evapotranspiration (Belsky et al, 1989; Vetaas, 1992; Grellier, 2014). In humid climates, trees increase both transpiration and interception (Jarvis and McNaughton, 1986; Crockford and Richardson 2000; Huxman, 2005). The rise of transpiration induces a high evapotranspiration. (Huxman et al., 2005). In fact, as mentioned in some studies, trees increase evapotranspiration (Scott et al., 2006), but it depends on the climate. Besides, we can notice higher evapotranspiration in studies concerning mesic areas than in arid areas (figure 4).

Moreover, according to Grellier et al. (2011) in South Africa, "gully head erosion" and surface water runoff were not well correlated. This argument is supported by Imeson and Kwaad (1980), who denounced that gully erosion can be generated by subsurface runoff.

Is there a correlation between water infiltration and erosion?

Infiltration is higher under trees compared to bare soils (Dye and Walker, 1980, Eldridge et al., 2011). In fact, stemflow can increase infiltration (Dunkerley, 2002; Liang et al., 2009). The water flows down the stem and reach a greater depth by flowing along trees' roots. This can also be explained by the presence of bigger macro pores in soils under the canopy (Dye and Walker, 1980). In few cases, by increasing the amount of subsurface water under the canopy, infiltration leads to erosion (Sonnenveld et al., 2005 in Grellier, 2011).

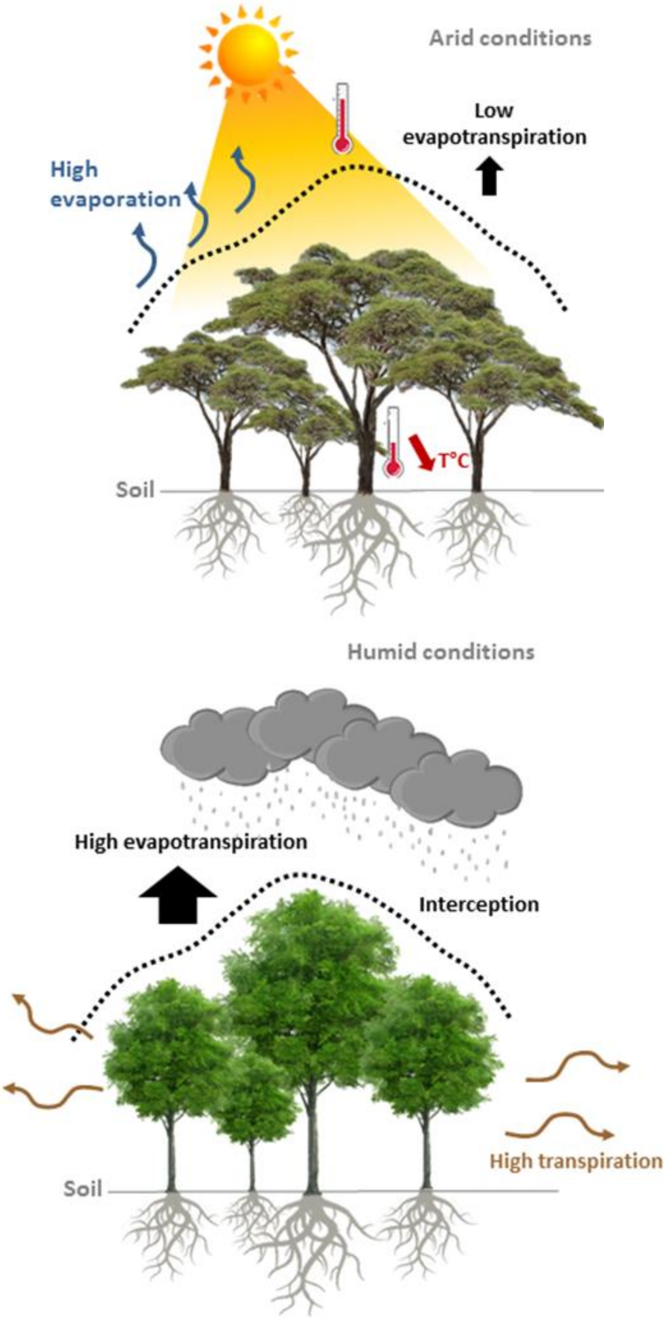


Figure 4: Water cycle in different conditions
Source: Cavatore & Haury

Inspired from: Belsky et al., 1989; Vetaas, 1992; Wilcox et al., 2003; Grellier et al., 2014 (arid conditions) & Jarvis and McNaughton, 1986; Crockford and Richardson, 2000; Huxman et al., 2005

2.2 Erosion

Erosion at tree scale: water runoff often leads to soil erosion

Woody plants are known for impacting water runoff. Indeed, the change in grass cover caused by encroachment can foster water surface runoff (Parizek et al., 2002; Huxman et al., 2005). Beside, trees play a key role in erosion (Parizek et al., 2002; Huxman et al., 2005; Grellier et al., 2014; Buresi, 2014). Indeed, they argued that by increasing water runoff, woody plant encroachments induce erosion processes. Moreover, the impacts of shrub encroachment on the vegetation cover are well contrasted. On one hand, the microclimate under canopy created in particular by the shadows of trees, can benefit some plants (Archer, 1997); but on the other hand, it can also create a decline in the existing vegetation cover near the shrubs (Petersen et Stringham, 2008; Puttock et al., 2013 in Buresi). These differences depend on where the encroachment takes place. For example, on bare soils, shrub encroachment can benefit soil properties, in herbaceous areas; it can lead to a decline of the neighbouring plant species.

Therefore, there is a high topographic difference between shrub islands and the surrounding bare soils. This gap dramatically alters water flows (Parizek et al., 2002). Indeed, the changes in grass cover (the rise of bare soils and the decline of vegetation cover) influence erosion (Parsons et al., 1996; Schlesinger et al., 1999; Wainwright et al., 2000; Li et al., 2007; Li et al., 2008). Other studies found that, by increasing spatial heterogeneity, it also leads to erosion (Turnbull et al., 2010 in Buresi, 2014).

As suggested by Grellier (2011) and Podwojewski (2011; 2014), erosion processes are driven by tree species but also by some other factors which influence this phenomenon such as the vegetation cover, slopes, rainfall (Bouchnak et al., 2009) and soil aggregate stability (see the next part: erosion at the catchment scale). For example, Grellier (2014) denounced that acacias increased gully erosion in grassland (in South Africa). In contrast with this argument, as mentioned in Podwojewski's study (2014); Bochet et al. (2006) and Cerdà (1999), found that vegetation cover does not particularly induce erosion.

Previous studies also found that in different areas, thanks to the litter below trees and the vegetation cover just under these islands of trees, the soil can be protected from water runoff that leads to erosion (Descroix et al., 2001 in Grellier, 2011; Graf, 1979; Munoz-Roblez et al., 2010; Piersen et al., 2010). Indeed, in comparison with bare soils, these plants intercept water thanks to their foliage and their roots (Archibold et al., 2013).

In semiarid grasslands, a sediment layer takes shape under canopy. Therefore, this soil crust increases water runoffs and finally, it leads to erosion processes (Petersen and Stringham, 2008 in Grellier, 2011; Buresi, 2014). Finally, trees impact both surface and subsurface water (Liang et al., 2009; Huxman et al., 2005), because the soil crust (which is under trees) reduces the water infiltration in the ground (figure 5).

Nevertheless, other scholars like Grellier (2014) found different results in a sub humid grassland in South Africa. Indeed, according to this study, surface runoffs were not the main erosion process. In this kind of area, erosion is more likely driven by sub surface runoffs.

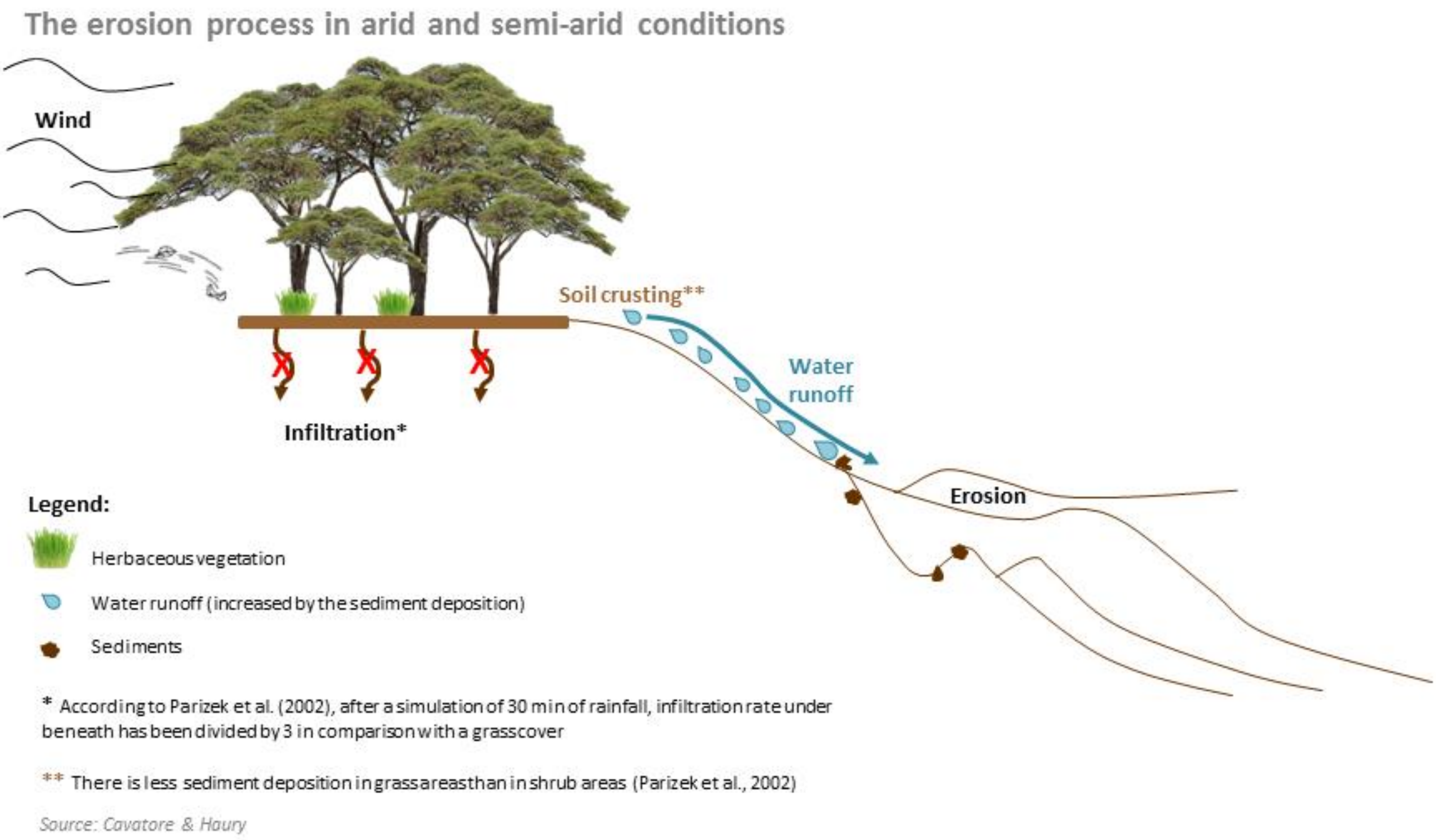


Figure 5: the erosion process in arid and semi-arid conditions
Source: Cavatore & Haury

Erosion at the catchment scale

The previous part showed that shrub encroachment plays a key role in erosion process at the tree scale. As mentioned earlier, woody encroachment and vegetation cover induce erosion process. For example, Grellier et al. (2012) noticed a correlation between the invasion of acacia and gully erosion in sub-humid grasslands of South-Africa. Indeed, there was a rise of 3.9% of gully area from 1945 to 2009. At the same time, this period was known an encroachment of the catchment since 1985.

Nevertheless, at this catchment scale, further parameters have to be taken into considerations such as rainfall, slope, drainage and soil aggregate stability (Bouchnak et al., 2009, Munoz-Robles et al., 2010; Manjoro et al. (2012), Grellier et al., 2012; Podwojewski, 2014).

For example, in the case of Grellier et al. (2012), encroachment of acacias increased from 1945 to 2009 but has known an amazing growth since 1985. At the same time, there was a rise of rainfall (the average increased by 200mm/y with a change from 752 mm/y to 906mm/y). Finally, some studies (Ansley et al., 2001; Sankaran et al., 2005; Widenmaier and Strong, 2010; Grellier et al., 2012) found a strong correlation between rainfall and erosion. Indeed, increasing rainfalls lead to a rise in tree population. However, other studies such as Goslee et al. (2003) disagree with this argument.

In humid or sub-humid areas, the gully retreat is higher than in dry areas. Indeed, after long period of rainfall, there is a collapse/detachment of aggregates, blocks, driven by shrinking and swelling (De Pley, 1974, in Grellier et al., 2012). These blocks come from a surface which is after the collapse without vegetation and as mentioned earlier; vegetation cover can protect the soil. Thus, it can easily lead to a deposit of sediment downstream (Podwojewski et al. in Grellier et al., 2012).

Slope steepness also impacts erosion. As observed by Manjoro et al. (2012), slopes between 5 and 9° significantly raise erosion.

The vegetation cover is also an important parameter because grass under trees both protects the soil from raindrop that leads to

splash erosion and reduce surface runoff too (Podwojewski et al., 2014). Podwojewski et al. (2014) noticed that there is a low soil aggregate stability beneath trees compared to open areas.

2.3 A short conclusion of the effects of woody encroachment on the erosion process

Erosion process

Effects of woody encroachment on erosion				
Parameters	Positive effects[1]	Negative effects[2]	Neutral effects	Total
climate				
arid – semi arid	0	3	0	3
temperate	0	0	0	0
mesic – (sub) humid	0	2	0	2
(sub)tropical	0	1	0	1
Pedoclimax				
grassland/prairie	0	6	0	6
Woodland /shrubland	0	0	0	0
savannah	0	0	0	0
desert	0	0	0	0
Woody species				4
leguminous	0	2	0	2
non-leguminous	0	2	0	

[1] Positive: protection from erosion
[2] Negative: erosion

Table 3, source: Cavatore & Haury

Generally, on the tree and watershed scales, in all conditions, shrub encroachment leads to soil erosion. Nevertheless, this phenomenon is significantly notable in dry and mesic conditions. Furthermore, the same trend is observed in grasslands. Moreover, the impact of tree encroachment on erosion process could be studied in different areas such as woodlands, shrublands, savannahs and desert if it is possible because for now, the results are poor concerning these areas.

The table also showed that the erosion process does not really depend on the woody specie because both leguminous and non-leguminous generate erosion. However, more studies on this subject could check the visible tendency through this table.

Besides, the soil aggregate stability is lower upstream. Thus, it favours a formation of a crust which will generate surface and therefore surface erosion.

Finally, few studies have focused their work at the catchment scale. Nevertheless, those who did it demonstrated that at this scale; the slope, the vegetation cover and the stability of aggregate are decisive in the erosion process. Nevertheless, experiences could be done at the catchment scale, in order to get more details.

2.4 Towards a deeper understanding of uncovered questions

By studying these articles, we found that views concerning the impacts of shrub encroachment on the erosion process remain quite contrasted. For example, for some scholars, trees create a barrier which suit to waterproof soils from raindrops and reduce soil erosion, but for some others, the reverse occurs. These differences mainly depend on climate conditions, vegetation cover and tree species.

Indeed, these islands of trees favour an accumulation of wind deposition. This deposition creates a crust generating water runoffs and consequently soil erosion (especially in arid and semi-arid climates).

These articles also revealed that erosion can be caused by both surface and subsurface runoffs.

Furthermore, some questions still remain without answers. Therefore, we consider it is necessary to further investigate the following questions:

- Do soil structural properties influence infiltration and therefore the erosion process? For example, woody encroachment on clay or loam soils can be different. Moreover, a change in soil density can decline the water infiltration in the soil and as seen previously, it leads to water runoff and erosion.

- Do some woody plant species plants affect more erosion? The idea would be to further study and experiment the impacts of woody species with different root system in order to see if they impact erosion by the same way. It could also be interesting to study if the impacts are similar when the invasion concerns several or a single tree.

- How woody plants impact the soil stability?

- Are there other drivers such as termite mounds which can influence subsurface drainage systems and lead to erosion?

- Few recent studies studied erosion process at the watershed scale. It could be interesting to further investigate the impacts of woody encroachment on erosion at this scale.

Part III- Biogeochemical cycle: carbon and nutrient pools

As seen in the previous section, because of its physiology and the microclimate that remains under its canopy, tree can alter interactions between soil surface and atmosphere. Thus, it modifies the biogeochemical cycle of the soil (Schlesinger et al 1990; Graetz 1991; Bonan 1997; Archer 2000; Huxman et al. 2005; Maestre et al. 2009).

Cumulative plant productivity and nutrient availability in the rhizosphere are key factors in maintaining ecosystems (Phillips et al., 2011, Dijkstra et al., 2013). Studies agree that the priming effect of the rhizosphere can help the decomposition of soil organic matter (SOM). According to many researchers (Wand et al., 1999, Morgan et al., 2004, Pendall et al., 2004a Parton et al., 2007, Phillips et al., 2011, Nie et al. 2013 a) and recently Ming Nie in 2016, the elevated CO2 (eCO2) has a positive effect on the growth of plant biomass, increases the storage of plant nitrogen as well as a marked increase in total decomposition of SOM.

3.1 C stocks changes

Soil Carbon

The impacts of woody encroachment on C cycle are contrasted. While some studies denounced that there is greater concentration (sequestration) of carbon under trees than in herbaceous patches (Boutton et al., 2009; Cable et al., 2009, Saintilan et al., 2015; Podwojewski et al., 2014; Eldridge et al., 2011, Hibbart et al., 2001); some others totally disagree with this argument (Schlesinger et al., 1996; McCarron et al., 2003).

Some studies showed that the rise of net primary productivity (by 3 for Norris et al., 2001a; Smith and Johnson 2003; Norris et al., 2007 or by 10 for Archer et al., 2000) leads to an increase in C storage (McKinley and Blair, 2008). In Li et al. (2005) and Boutton' s view (2009), the soil organic carbon (SOC) increases as trees encroached. For example, between 0 and 15 cm, the SOC was about 200% according to Liao & Boutton (2008) while it was 100% for McCulley et al. (2004) for the first 20 cm. This argument was also supported by Jackson et al. (2002) who expressed that wooded grasslands significantly increase C stock (these results reflect the analyses of 115 different studies). This percentage change is partly due to the climate but also to the soil density, according to Barger et al. (2011). The lower is the density; the greater is the carbon storage in the soil. Carbon stocks would increase significantly as a result of the woody invasion (Boutton et al., 2009), regardless of woody species (Barger et al., 2011).

Nevertheless, McCarron et al. (2003), Coetsee et al. (2013) and Belay et al. (2013) exposed that there is no changes in SOC before and after the encroachment (from Buresi).

Furthermore, according to some researchers, woody plant does not impact negatively the environment because the primary production does not change with or without the encroachment. Nevertheless, it is more complicated. Indeed, in semi-arid and humid areas (precipitations (P)>336mm) of the southwestern United States, both C sequestration above the ground and SOC gains have been observed. Nevertheless, the trend was totally different in arid areas (P<336mm). Indeed, there was a high decrease of 6,200 g C m-2 according to Barger et al. (2011) in Podwojewski's work (2017). To contrast with this argument, Jackson et al. (2002) found the opposite in a meta-analysis.

Many factors also influence the quantity of carbon into soil including the climate (Li et al. 2015; Jackson et al., 2002). In fact, some researchers argued that the carbon stocks in the soil increase in arid areas (Jackson et al., 2002; Blaser et al., 2014; Eldridge et al., 2011) and decrease in humid areas (Jackson et al., 2002). However, Li et al. (2015) distinguished the consequences on soils in sub-humid and semi-arid conditions. Indeed, compared to dry and sub-humid areas, in semi-arid and humid areas, the

quantity of carbon storage in the ground considerably increases (Li et al., 2015).

C/N Ratio

On one hand, some studies (Biederman et Boutton 2010; Grellier et al., 2013; Podwojewski 2014) denounced that there is a high level of C/N under shrubs which means that there is not enough nitrogen to allow the decomposition of carbon but on the other hand, Hudak (2003) and Blaser et al. (2014) showed that C/N ratio decreased as woody encroached.

3.2 Nutrients

As seen previously in the part I, "fertile islands" generate an accumulation of litter, SOC and high concentration of nitrogen (Archer, 2000). This concentration of nutrient depends also on various factors such as wind, water, animals (Belsky et al., 1989; Weltz et al., 1998; Okin & Gillette, 2001), soil moisture, temperature, pH or soil cation exchange (Marschmer, 1995).

Nitrogen stocks changes

As for carbon, the consequences on nitrogen are contrasted. While some showed that the N storage is higher under canopy (Archer, 2000; Hibbart et al., 2001; Blaser et al., 2014; Belsky et al., 1993, Abule et al., 2005, Ludwig et al., 2004, Treydte et al., 2007, Jessica 2009; Throop et al., 2008); some others found that it does not differ in sub-humid environment of Africa (Podwojewski et al., 2014; Grellier et al., 2013). To support this argument, Maestre et al. (2009, p.936) denounced that the quantity of "organic C, total N and the potential N mineralization" in the soil, raised by woody plants can both be observed both beneath trees and in bare soils. In the same way, some other studies (Karen 2004; Duncan C 2008; Anthony et al. 2014) showed that shrub encroachments induce a greater N- mineralization, nitrification rate and a better soil respiration (Raich and Schlesinger, 1992). It is about 44% increase in N compared to grasslands according to Tiedemann and Klemmedson (2000).

Some studies also revealed that the impacts of woody plants on N storage depend on climate conditions (Jackson et al., 2002) or on shrub encroachment (Zhang et al., 2016). Indeed, there was a rise between 50-150% in nitrogen storage in the shallow soils (30 cm) (Boutton and Liao, 2010). Moreover, trees increase both N stocks and N mineralisation in dry areas (Blaser et al., 2014; Eldridge et al., 2011).

Furthermore, other factors induce changes in N stocks such as tree size (according Ludwig et al. (2004) and Treydte et al. (2007) there is higher nitrogen under bigger trees than smaller trees). Besides, tree species such as leguminous trees and more especially acacias enhance the nitrogen content in the soil (Wiegand et al. 2005; Treydte et al. 2007). Indeed, these kinds of woody plant are nitrogen-fixing (Eldridge et al. 2011, Knapp et al 2008, Boutton and Liao 2010, Kambatuku et al., 2011; Belay et al., 2013). In other words, they are able to fix more easily nitrogen than non-leguminous species that is why tree litter is generally rich in nitrogen and rapidly decomposable (Hibbard et al., 2001). It also means that woody shrubs provide N to the ecosystem (Carlsson and Huss-Danell 2003). Indeed, leguminous species transfer nutrients to non-leguminous species (Sierra and Nygren 2006). On one hand, it can benefit the vegetation cover because nitrogen allows plant growth but on the other hand these exchanges can disturb "the natural competitive balance among neighboring native grasses" (Wedin and Tilman 1993; Hellmann et al. 2011; Soudzilovskaia et al. 2012 in Zhang et al., 2016, p.1214).

Phosphor changes

Phosphor cycle is also modified by legumes (Blaser et al., 2014). Several researchers have found that phosphatase production is 3 times higher beneath trees (Houlton et al., 2008; Blaser et al., 2014; Ludwig et al., 2004; Sitters et al., 2013). The legumes thus have a not insignificant advantage which allows it to develop in a nutrient-poor environment (nitrogen, phosphor ...), (Houltonet, 2008).

Others nutrients in form of ions

In most of the cases, woody encroachment impacts the concentration of ions into soil. For example, some researchers remarked that K+, Ca2+, Na+, No3-, PO4, Cl and Mg2+ were more important under shrubs (especially under acacias) than in herbaceous patches (Belsky et al., 1993; Schlesinger et al. 1996; Cable et al. 2009; Hibbart et al., 2001; Trinogga, 2010; Grellier, 2011; Rolo 2012). They explained that thanks to the capacity of their roots, trees pump nutrients and redistribute them over ground through litter input (Vejre and Hoppe, 1998; Vanlauwe et al., 2005). Belsky et al. (1993) found that in savannahs, isolated acacias tend to decline the amount of exchangeable Mg2+ while Grellier (2011) found the opposite.

Trinogga (2010) and Grellier (2014) revealed that the cation exchange capacity (CEC) is higher under acacias. This rise in CEC is caused by the litter which alters the chemical properties and increases cations such as Ca2+ and Mg2+ (Trinogga, 2010; Grellier, 2014).

Concerning pH level, a study revealed that under woody trees, pH was pretty acidic than in open grasslands. It can be explained by the higher oxidation of anion because of an important input of organic matter (Whitford, 1992; Mlambo, D.et al. 2005; Eldridge et al., 2011).

Some researchers supported the negative effects of woody encroachment on nutrient distribution (Barnes and Archer, 1999; Cubera and Moreno, 2007). Indeed, in a semi-arid savannah, shrubs can reduce nutrient inputs to neighbouring plants by competing with native species for soil resources (Meyer et al., 2008; Everard et al. 2010). To contrast with this argument, in the same climate but in grasslands, woody encroachment improves the concentration of nutrients and increases the spatial heterogeneity of soil resource (Jessica et al., 2009).

Finally a meta-analysis realized in semi-arid climate, demonstrated that woody encroachment significantly affected the biochemical cycle in soil by causing: "lowered pH, increased C, N, exchangeable soil C, available P and potential mineralization of N" (Eldridge et al., 2011 in Buresi, p8). Another study found that woody plants in savannah "have a lower bulk density, contain more root biomass, have higher concentrations of SOC and total N (TN) and have a greater rates of respiration and N-mineralization and nitric oxide (NO) emission" in a subtropical climate (Archer, 2000, p8). By increasing NO emission, it can provoke acid rain. Consequently, the invasion of woody plants has a strong impact on the biochemical cycles of the soil.

3.3 A short conclusion of the effects of woody encroachment on biogeochemical cycles

C-cycle

Effects of woody encroachment on C cycle				
Parameters	**Positive effects**	**Negative effects**	**Neutral effects**	**Total**
climate				
arid – semi arid	4	1	0	5
mesic – (sub) humid	2	2	1	5
(sub)tropical	4	0	0	4
mediterranean	0	0	0	0
Pedoclimax	8	4	1	13
grassland/prairie	5	2	1	8
Woodland /shrubland	2	0	0	2
savannah	1	2	0	3
desert	0	0	0	0
Woody species	8	2	2	12
leguminous	6	0	0	6
non-leguminous	2	2	2	6

Table 4, source: Cavatore & Haury

In sum, the chart below identifies that changes in carbon concentration under trees and into the soil are driven by several factors such as climate, pedoclimax and woody specie. Indeed, in general, with arid, semi-arid or subtropical climate, woody invasion provides more favourable conditions for carbon accumulation both under trees and in the soil. Nevertheless, it can also be seen that grasslands, unlike savannahs facilitate these positive effects on carbon cycle. Finally, by comparing the impacts of both leguminous and non-leguminous species on the C-cycle, it can be

seen that leguminous trees impact positively the C-cycle.

Moreover, it could be interesting to further investigate the impacts of woody encroachment on C-cycle with non-leguminous species. Indeed, for now, it is difficult to say if these species positively or negatively impacts C-cycle (see the table).

Finally, more studies in Mediterranean and humid conditions could be useful. In fact, the table demonstrates that in these conditions, it is difficult to establish a correlation between woody encroachment and C-cycle.

N-stocks

Effects of woody encroachment on N stocks				
Parameters	Positive effects	Negative effects	Neutral effects	Total
climate	23	2	3	28
arid – semi arid	12	1	0	13
mesic – (sub) humid	5	0	2	7
(sub)tropical	6	0	0	6
mediterranean	0	1	1	2
Pedoclimax	21	1	3	25
grassland/prairie	7	1	3	11
Woodland /shrubland	1	0	0	1
savannah	12	0	0	12
desert	1	0	0	1
Woody species	23	3	3	29
leguminous	18	3	2	23
non-leguminous	5	0	1	6

Table 5, source: Cavatore & Haury

For the effects on the nitrogen stock, it can be seen that a large part of the studies shows a positive effect (i.e. woody encroachment contributes to the supply of nitrogen). These effects are particularly prevalent in arid semi-arid environments but also in (sub) tropical environments and in savannahs and grasslands. Finally, it can be argued that leguminous trees play an important positive role in increasing N stocks. This is due to the ability of this type of plant to easily capture nitrogen.

Cation exchange capacity

Effects of woody encroachment on CEC				
Parameters	Positive effects	Negative effects	Neutral effects	Total
climate				2
arid – semi arid	0	0	0	0
temperate	0	0	0	0
mesic –(sub)humid	1	0	0	1
(sub)tropical	1	0	0	1
mediterranean	0	0	0	0
Pedoclimax				1
grassland/prairie	1	0	0	1
Woodland /shrubland	0	0	0	0
savannah	0	0	0	0
desert	0	0	0	0
Woody species				2
leguminous	2	0	0	2
non-leguminous	0	0	0	0

Table 6, source: Cavatore & Haury

Once again, there are not enough studies on this subject. Therefore, a general conclusion concerning the effects of trees on CEC in different environments (different climates in several areas) is impossible. Nevertheless, this table shows a trend concerning tree species. In fact, it would appear that leguminous species promote cation exchange capacity. Moreover, it is difficult to reach a conclusion about non-leguminous trees.

Ions

Concerning ions, the table below reveals that more studies concerning ions should be done in all areas with different climate and with different woody species. Indeed, a comparison of only 8 studies is not enough to have a conclusion. Concerning the climate, there is no one which is better than the others for ions (a high concentration under shrubs). However, this table shows that all climate and especially temperate and Mediterranean should be further analyzed. The same conclusion can be said concerning the pedoclimax because the effects of woody encroachment on ions are not significant in

grasslands, woodlands, savannahs or deserts according to this table. Finally, it also shows that leguminous trees positively impact ion concentration; this is probably because of their properties.

Effects of woody encroachment on ion			
Parameters	**Positive effects**	**Negative effects**	**Total**
climate			6
arid - semi arid	3	0	3
temperate	0	0	0
mesic – (sub) humid	2	0	2
(sub)tropical	3	1	4
mediterranean	1	0	1
Pedoclimax			8
grassland/prairie	2	0	2
woodland/shrubland	2	0	2
savannah	2	1	3
desert	1	0	1
Woody species			10
leguminous	6	1	7
non-leguminous	3	0	3

Table 7, source: Cavatore & Haury

3.4 Towards a deeper understanding of uncovered questions

Most of the studies showed that the SOC is higher under trees. Changes in SOC may be due to environment conditions (temperature/climate), tree species but also to other factors such as soil bulk density that should be better explorer.

- Some studies show very large variations in SOC “from a loss of 6200 to gains of 2700 g C m -2 after encroachment "(Barger et al., 2011), Buresi p7). However, reasons for these changes are not well understood (McCulley et al., 2004; Liu et al., 2011), they deserve to be clarified.

- Moreover, in the future, it would be useful to see how the C stock evolves on the basis of the woody plant species in the same climate conditions.

- Studies also noticed that tree size could induce changes in N soil concentration (Ludwig et al., 2004; Treydte et al., 2007). Nonetheless, it could be interesting to experiment if this argument is true for all shrub species.

- This report also revealed that woody encroachment impacts C and N stocks. However, few studies have been experimented in deep soils. In fact, most of the studies made experimentations on shallow soils (<20cm). It could be useful to answer the following question: How woody encroachment impacts C stocks in deeper soils? (Blaser et al., 2014) and N stocks in deeper soils ?

Conclusion

This review aimed to enhance the understanding of woody encroachment on soil properties and to summarize the main consequences of shrub encroachment on soils. As seen previously, the consequences of woody encroachment on soil properties have been widely investigated. Indeed, woody plants impact biological (vegetation cover, respiration), physical (water dynamics including soil erosion) and chemical (C and N stocks, other nutrient pools, pH) soil properties.

Moreover, this study showed that the consequence on soil properties differs from various factors. For example, shrub species (leguminous vs non-leguminous), environmental conditions (climate: temperature, rainfall; study location), the level of encroachment, resource competition and soil density are all factors that interact with each other and modify the consequences on soil properties that leads to differences between woody and herbaceous patches (appendix 1).

To answer our main question concerning the soil enrichment or soil depletion, we cannot claim that the woody encroachment phenomenon has overall positive or negative effects on soil. Of course in some conditions, it impoverishes the soil but in some others, it enriches it. For example, the respiration rate decreases in mesic areas (McCarron et al., 2003) but increases in subtropical areas (Archer et al., 2000). Another example could be concerning the vegetation cover. Indeed, while some denounced that vegetation cover was stimulated beneath trees (Mordelet and Menaut; 1995), some others showed the opposite (i.e. it leads to the decline of the vegetation cover and the expansion of bare soils (Huenneke et al., 2002, Gillette and Pitchford, 2004, Briggs et al., 2005, Peco et al. 2006, Price and Morgan, 2008, Rivest et al., 2011, Mlambo, D. et al., 2005)). Finally, this review revealed that scholars' opinions are well contrasted and the impacts of woody plants on soils cannot be treated universally/as a whole, it differs and depends on the ecosystem.

Acknowledgments

We thank Séraphine Grellier for accompanying us throughout our study and for reading this manuscript. Her helpful comments and advices enabled us to achieve this review.

Appendix

Parameter	Community Type: Herbaceous	Community Type: Woody Plant
ANPP (Mg ha^{-1} y^{-1})^a	1.9 - 3.4	5.1 - 6.0
Bulk Density (g cm^{-3})^a	1.4 ± 0.01	1.1 ± 0.04
% Clay^a	20 ± 0.7	20 ± 1
Fine Roots (g m^{-2})^a	100 - 175	400 - 700
Coarse Roots (g m^{-2})^a	100 - 400	400 - 1,100
Organic C^a: %	0.84 ± 0.05	2.2 ± 0.23
g m^{-2}	1165 ± 67	2352 ± 276
Potential C mineralization (mg C kg^{-1} soil day^{-1})^b	7.3 ± 5.7	15.5 ± 6.8
Soil Respiration (mg CO_2 m^{-2} y^{-1})^b	611 ± 83	730 ± 67
Q_{10} Values for *in situ* soil respiration^b	1.2	1.4, 2.7
Total N^a: %	0.07 ± 0.00	0.18 ± 0.02
g m^{-2}	91 ± 6	192 ± 20
N-mineralization^a: g N m^{-2} y^{-1}	6 ± 1	22 ± 2
µg N g^{-1} y^{-1}	42 ± 5	200 ± 18
NO flux (ng NO-N cm^{-2} h^{-1})^c		
Dry soil	0.2 ± 0.07	2.8 ± 0.25
Wet soil	1.1 ± 0.11	16.2 ± 2.03

Table 8: A comparison of different parameters (aboveground net primary productivity, organic carbon, nitrogen pools, etc.) between herbaceous and woody plants patches in a "sandy loam upland" at la Copita, Texas, USA.

Source: Archer et al., 2000

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Woody encroachment impacts on soil properties
L'impact des ligneux sur les propriétés du sol

Résumé:

Au cours des dernières décennies, les ligneux ont envahi les pâturages et savanes (Van Auken, 2000, 2009). Pâturages et savanes représentent 40% des paysages (Chapin, 2001 from Briggs et al., 2005).

La multiplication des ligneux dans ces types de milieux (prairies et savanes) a souvent été perçue comme néfaste à l'écosystème, mais elle peut également être bénéfique pour l'environnement. Comprendre l'ensemble de ces impacts, aussi bien positifs que négatifs sur le sol (propriétés biologique, physique et chimique) est une nécessité.

En envahissant ces milieux, les ligneux, surnommés aussi « ilots de fertilités » créent un microclimat sous la canopée, favorable ou non aux espèces natives. Ces arbres modifient également les stockages du carbone, de l'azote et d'autres nutriments dans le sol. Toutefois, ils peuvent également entrainer une accumulation de dépôts sédimentaires sous la canopée, et créer une 'croute' sensible à l'écoulement de surface et entrainant par conséquent l'érosion des sols.

Cette étude a révélé que les conséquences sur les propriétés du sol dépendent de nombreux facteurs comme l'espèce du ligneux (espèce légumineuse ou non-légumineuse), des conditions environnementales (climat dont la température et les précipitations, site de l'étude), le degré d'invasion, la compétition pour les ressources du sol et la densité du sol.

Enfin, cette revue a aussi montré que les avis restent controversés quant aux impacts des ligneux sur les propriétés du sol. Les conséquences de l'invasion de ces arbres sur le sol ne peuvent pas être traitées comme une généralité. En effet, elles dépendent de divers facteurs dont l'écosystème dans lequel l'empiètement des ligneux intervient.

Mots clés : invasion, ligneux, prairies, savanes, propriétés du sol, empiétement du sol.