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The rooting patterns of woody and herbaceous plants in a savanna; are they complementary or in competition?

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Summary

Root patterns of three woody plants are described in relation to water profiles and average root depth of annual species on three contrasted soil types along a toposequence in a watershed of northern Cameroon. This watershed is in a Sudano-Sahelian savanna where mean annual precipitation is 800 mm, entirely restricted to the period May–June to September–October. Results show great variations of root structure of woody plants according to the distribution of water in the soil during one year. Consequently, under the same climatic conditions, soil depths exploited by woody plants and herbaceous plants can either be the same or not. In the most degraded soils, water does not infiltrate deeply and roots of the two components of savanna are limited to the upper horizons. On the other types of soil, root distribution depends on the soil profile.

Key words: Cameroon, root, savanna, soil, water resources

Résumé

La structure racinaire de trois arbres ou arbustes est décrite, en liaison avec quelques profils hydriques et la profondeur racinaire moyenne des plantes annuelles, sur trois types de sol aux caractéristiques hydriques très contrastées et situés le long d'une toposéquence d'un bassin versant du Nord-Cameroun. Le bassin versant est localisé dans une savane soudano-sahélienne où la pluviosité annuelle moyenne est de 800 mm répartis entre mai–juin et septembre–octobre. Les résultats montrent une forte variation de la structure racinaire des plantes ligneuses en liaison avec la répartition de l'eau dans le sol au cours de l'année. Sous les mêmes conditions climatiques, la profondeur de sol exploitée par les espèces ligneuses et les espèces herbacées peut être ou non la même. Sur les sols les plus dégradés, elle est la même, dans les horizons de surface, à cause de la très faible infiltration de l'eau dans ces sols. Sur les autres types de sol, la répartition des racines dépend du profil pédologique.

Introduction

The nomenclature in this paper follows Hutchinson & Dalziel (1954–72). The overriding factor giving rise to vegetation structure in African savannas is the soil water balance (Walter, 1971; Walker, 1981; Walker & Noy-Meir, 1982). Walter (1971) argued that in semi-arid savannas with free drainage, the existence

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of a more or less stable mixture of grasses and woody plants is due to a complementarity between the rooting zones of perennial grasses and woody plants. Grasses root only in the upper soil layer and are superior competitors in that horizon. Adult woody plants have deeper roots and thereby avoid competition with grasses. Based on this hypothesis, models were developed by Walker (1981), Walker *et al.* (1981), Walker & Noy-Meir (1982) and Knoop & Walker (1985) that describe the dynamic equilibrium between the two principal savanna components in relation to vertical distribution of the water resource, and competition between grasses and woody plants for available soil water. The present study was carried out to test the assumption of a two-layer rooting zone in the Sudano-Sahelian savannas of northern Cameroon. A phenological study has shown previously, on all three stations used in this study, that populations of *Acacia seyal* Del. and *Acacia hockii* De Wild actively grew over a longer period than the rainy season while *Lannea humilis* (Oliv.) Engl. grew only during the rainy season, from June to September, as the major herbaceous species (Seghieri, 1990; Seghieri *et al.*, 1995). The study analyses if the phenological differences might be related to the differences in root development and/or in soil water infiltration. The woody root patterns of adult individuals of *Acacia seyal, Lannea humilis* and *Acacia hockii*, were observed in three types of soil in relation to the annual vertical distribution of available soil water and in relation to the depth of annual plant roots. In semi-arid savannas, the topography and soil surface conditions are responsible for rainfall redistribution (Casenave & Valentin, 1992). Hydrological functioning of the soils is a determining factor for the redistributed water use by vegetation. The root development determines the soil depth and volume exploited by plants. Many studies have demonstrated that the edaphic environment is a primary effector as well as affecter of root growth and therefore whole plant growth and development (Zobel, 1989). The analysis of root development in relation to the hydrological functioning of soils is essential to take into account the heterogeneity of savannas conditions in general models.

Study area

The studied savannas receive an average of 600–800 mm of annual rainfall, spread from June to September. July and August are the wettest months. Sites were located in a small watershed, 30 km south of Maroua in the Diamaré plain. The herbaceous stratum is composed of annual grass communities and woody species are fallow plants (mainly Combretaceae and *Acacia* ssp.). In this region, a high spatial variability of soil water properties exists and free drainage is not common (Seiny-Boukar, 1990).

Three stations were studied. One is on typical vertisol. A second is on highly degraded vertisol known locally as 'hardé'; these two stations are located on the lower slopes. The third one, on sandy-clay ferruginous soil, is located on an upper slope.

Typical vertisol is a clayey soil. It contains 40–45% of smectite in the overall profile. The surface of the soil presents deep shrinkage cracks during the dry season. The infiltration is good at the beginning of the rainy season but runoff increases as soil becomes saturated (Masse, 1992). Tree cover is between 20% and 30%, and the dominant species *Acacia seyal* represents 70% of the woody cover on this type of soil (Seghieri, 1990). Herbaceous cover is abundant (up to 90%).

'Hardé' has widespread surface overcrusting which greatly reduces its permeability. The upper layer (0–20 cm) texture is sandy-silt. It arises from the typical vertisol by anthropic degradation (Seiny-Boukar, 1990). Woody and herbaceous cover is sparse and patchy (5–7%). *Lannea humilis* is typically an indicator of the most degraded areas on the watershed.

Ferruginous soil has outcrops of underlying ironstone cuirass and scattered ferruginized gravel on the surface. The cuirass, which can be very thick, indicates that it is a very old soil formed under a wetter climate than at present (Seiny-Boukar, 1990). Indeed, in a wet enough tropical climate, ferruginous pedogenesis brings about a strong release of thermite or iron hydroxide. Accumulated in horizons, it can harden in cuirass which is very slowly destroyed, either in the surface layer by vegetation influence, or through all its thickness by mechanical action after water has taken off the underlying strata (Aubert & Boulaine, 1980). This soil is sandy in the first 40 cm (8–13% clay) and sandy-clayey deeper down (20–28% clay). The ligneous cover is the most important (40–50%) and the most diversified. Herbaceous cover is between 50% and 70% during the rainy season.

Methods

The study was conducted in 1986. Soil moisture was measured with a neutronic humidimeter (Solo 20 and one access per station) at 5–8 m from each shrub. Moisture contents exceeding $-1{\cdot}6$ MPa (pF 4.2) were considered to provide available water to the plants. The method of root extraction used here was limited to roots comprising the architectural system. Architectural root development results only from the depth and volume reached by infiltrated water during every rainy season in a given soil type. It does not depend on the seasonal variations of the soil water content. Therefore, only the tendency of the seasonal variation of soil water content (four dates) is used.

A root profile of one tree per station was carried out. The shrubs studied were adult individuals of *Acacia seyal* on vertisol, *Lannea humilis* on 'Hardé' and *Acacia hockii* on ferruginous soil. A pit of 2 m diameter was dug around each woody individual and roots were carefully extracted to a depth of 1·5 m and, for several lateral roots up layer in their entirety. A representative profile of each species has been drawn up to 1 m from the trunk (Fig. 1). Because of the limit of the scale on the figure, lateral roots have not been drawn.

Results

Wood and herbaceous root distribution and soil water profiles are presented in Figure 1. It was observed that, on the three stations, communities of annual grasses which constitute the herbaceous strata, have roots only in the upper soil layer (20–25 cm of depth). Differences are shown in the wood root distribution in relation to annual soil water distribution.

The vertisol had available water from June to November in the upper horizons. In August, water content was maximum at 20 cm depth and it was the highest of the three stations. Water was abundantly available for plants up to

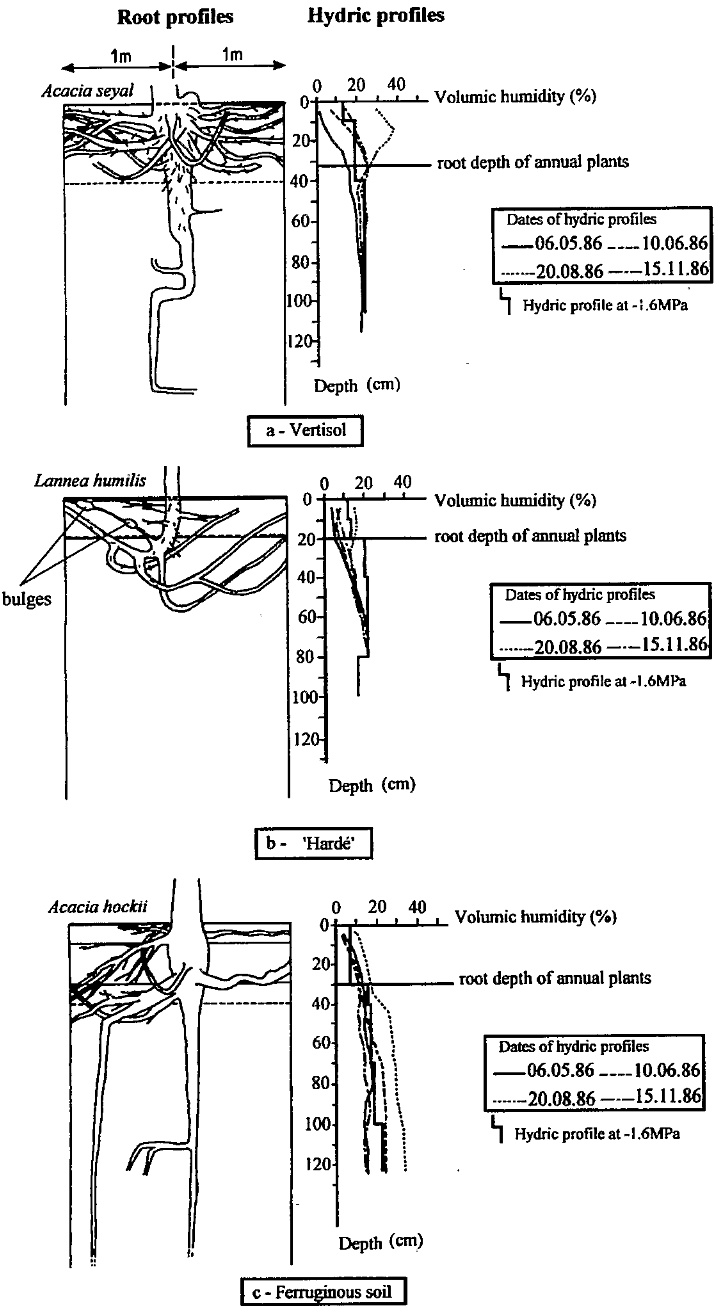

Fig. 1. Root profiles of three woody species in relation to some soil water profiles during the rainy season 1986 in three types of soil in the North-Cameroon; (a) vertisol, (b) 'hardé', (c) ferruginous soil.

40 cm deep during the entire rainy season. 'Hardé' contained very little available water: only in the top 20 cm and only in August. Ferruginous soil also had little available water in the 30 cm depth. Much more water was available for plants in the subsoil than in surface layers during the rainy season, as water did not stay

in the upper sandy layers. As the rains fell, the drainage from the top horizons was fast and important and the infiltrated part was stocked first in the more clayey deep horizons (below 120 cm). Thus, the intense drainage of the soil was favourable to high amounts of available water in deep layers from June to September or October, according to the length of the rainy season.

All trees have plenty of long lateral roots (up to more than 10 m) and most large roots were found in the upper 40 cm of soil, although some differences in root distribution appeared among the three trees. On typical vertisol, *Acacia seyal* had a double underground system: superficial lateral roots and a taproot system. The majority of roots were superficial; it was made up of a lot of small (inferior or equal to 1 cm of diameter) and dense roots which could be compared with herbaceous root systems. This upper system was developed in the principal water storage zone (down to 40 cm depth). Only one big taproot constituted the deep system. Its bent form and the absence of a deep water layer in this soil suggest that this taproot had developed along a shrinkage crack. Free water was available in the cracks at the beginning of the rainy season but gradually the cracks closed with water imbibition up to saturation. On the contrary, no water was available (moisture under $-1{\cdot}6$ MPa) in the first 40 cm depth of the soil before June and never below 40 cm depth (Fig. 1a). On 'hardé', except below the tree trunk, the root system of *Lannea humilis* was not more than 20 cm deep. Just below the tree trunk, it was deeper because the central root had grown strongly enough to reduce soil compaction and allowed water to seep deeper. Secondary roots were smaller and too weak to grow deeply. They went back up to extract small quantities of available surface moisture, the only available soil water (Fig. 1b). *L. humilis* has specialized water storage organs (bulges, Fig. 1b). These being small widenings of the root which soak up water. On ferruginous soil (Fig. 1c), for *Acacia hockii*, surface roots (down to 50 cm depth) were more abundant than deep ones, but there were more deep roots than in the first two situations. In all the stations, shrubs had most of their roots in the top 40 cm of soil. Upper root systems were highly developed and showed very long lateral running roots extending up to more than 10 m from the tree trunk in all the three types of soil. Consequently, trees roots and grasses roots are near to each other on a large area around trees trunks.

Discussion

Depending on the possibilities of water infiltration in the soil, the three woody species studied showed differences in their root patterns, and thus in their strategies of soil exploitation during the humid season.

The densest lateral upper root system of the woody plants studied was in *Acacia seyal*. On typical vertisol, it reached a depth of 40 cm. The reason for the constitution of this dense surface root system could be that no drainage exists in the vertisol, except through open cracks at the beginning of the rainy season. This type of soil can contain much water in the moist front but, because of its high water-holding capacity, for a given amount of water in the soil, less is available to the plants than in a sandy soil. Thus, at the beginning of the rainy season, *Acacia seyal* had access to water through deep roots in open cracks while annuals' roots were not yet sufficiently developed. As soon as moisture becomes available in the soil outside of the cracks, and, subsequently, as the cracks close, grasses could use this resource for growth and fast development of their root system in this fertile (high organic matter and nutrient rates) and humid substrate (Seiny-Boukar, 1990). From this moment, herbaceous plants and woody plants like *Acacia seyal* do exploit the same surface soil layers up to 20–25 cm, the depth of grass roots, after annual vegetation has been installed. Trees were favoured only by their durability at the beginning of the rainy season. Since annual species were installed in dense stands, their development was favoured by their dense and compact roots in this type of soil (cover up to 90%).

Hydrological characteristics of the 'hardé' soil, i.e. low water infiltration leading to a shallow moisture depth in addition to a very short period of water availability to the plants, result in a situation where only surface roots grow, as showed on *Lannea humilis*. No stratification of the underground system exists. Consequently, soil layers exploited by grasses and this shrub could not be complementary, even if the use of extracted water could be deferred for ligneous species, thanks to specialized water storing roots and, perhaps, in stems (Beatley, 1974; Kemp, 1983; Pierce, 1984). Walter's hypothesis is inadequate in this case. The competition must increase to the extent that available water is limited to a thin surface layer. However, in this station the herbaceous cover was so low that soil water extraction by this stratum was apparently not so intense as to limit water availability for woody plants.

In the ferruginous soil, by contrast, *Acacia hockii* must have a double strategy for soil water exploitation. As the first rains fell, durability of root system in the upper horizons should have an advantage compared to the herbaceous plants. In the upper soil of this station, which had a coarse texture, the dense root system of adult grasses should not be as efficient as the diffuse root system of woody plants (Walter, 1971). To be available very quickly during its infiltration (because of a small amount of water at $-1{\cdot}6$ MPa), water was also quickly evaporated or drained because of a low water-holding capacity of those horizons. Exploiting a large soil volume, as woody plants do, is more suited to the soil water properties than intensely exploiting a small soil volume, as grasses do. Moreover, the chemical poorness of the upper soil must limit annual vegetation growth (Seghieri, 1990) while for woody species like *Acacia hockii*, this effect must be restricted to the young states. Indeed, according to their permanency from one year to the next, trees could develop enough deep roots through the cuirass fissures to exploit abundant available moisture in the more clayey horizon which would be rarely exploited by herbaceous plants. Thus, adult trees could take advantage of the fertile deep layer to which grass roots do not have access because of the ferruginous cuirass and the small soil volume that their short roots could exploit. This should explain, at least in part, why there were more trees at this station than the other two in relation to the intermediate herbaceous cover.

The woody plants studied here exploited a large soil volume in the upper layers on the three types of soil. Okali *et al.* (1973) found similar results in the Accra plain in Ghana under an average of 750 mm annual rainfall. Having a root system well developed in the upper layers of the soil seems to be more worthwhile than a deep system in a semi-arid climate.

Consequently, at the beginning of the rainy season and immediately after the rains, woody plants had wide access to surface soil water, in the upper 40 cm depth. Annual communities had to complete their development every rainy season before becoming able to extract available water. Moreover, woody roots access deep layers while annual plants do not. Thus, according to their life form, woody species exploit soil water for a longer period of time during the rainy season than annual species. That should contribute to an increase in their period of photosynthetic activity compared to annual species on non degraded soils (Seghieri, 1990; Seghieri *et al.*, 1995).

The results presented here show that trees and grasses are both abundant in the first surface layers (up to 20–25 cm depth). Lawson *et al.* (1968) showed that thick horizontal laterals roots of woody species from guinea savanna (Ghana) seem to be produced more frequently just under the zone of main concentration of grass roots, i.e. between 20 cm and 30 cm. It is difficult to assess whether root competition or direct environment is responsible for root behaviour. Much more data are required on the variations of rooting systems of the two components of the savanna to understand the laws which determine their equilibrium in relation to the variability of the ecosystems.

Conclusion

Walter's (1971) hypothesis of a two-layer rooting zone for savanna vegetation cannot come into general use in view of the high heterogeneity of savanna soils, nor should it be the base of models explaining the dynamic equilibrium of woody/herbaceous vegetation in all African savanna types. In the savannas of Northern Cameroon, edaphic aridity and fertility, and thereby root development, depends strongly on the soil type and its state of degradation.

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