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Patterns of root growth and water uptake of a maize-cowpea mixture grown under greenhouse conditions

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Abstract

This study investigated the patterns of root growth and water uptake of maize (*Zea mays* L.) and cowpea (*Vigna unguiculata* (L.) Walp) grown in a mixture under greenhouse conditions. The plants were grown in root boxes for 5 weeks under 2 watering regimes; fully irrigated and water stress conditions, followed by a 5-day drying cycle imposed during the 6th week of growth. Water uptake patterns were analysed during the drying cycle. The two-dimensional distribution of the roots of both plants in the boxes was determined immediately at the end of the drying cycle. Under well-irrigated conditions, the roots of the component plants grew profusely into all sections of the root box and intermingled considerably. Water stress resulted in the decline of root growth of maize and cowpea but the root:shoot ratios of maize and cowpea were not affected, suggesting that there was no significant effect of water stress on root:shoot partitioning. However, water stress affected the biomass distribution between fine and coarse roots in cowpea. About 64% by weight of cowpea roots under water stress were coarse whereas as against 48% under well-irrigated conditions. Furthermore, water stress generally restricted the lateral extent of the roots of both maize and cowpea with a tendency of clumping together of the root systems and a reduced degree of intermingling. Thus, the extent of mixing of the root systems was apparently controlled by the availability of soil water. Water uptake from the well-irrigated soil in the root boxes was initially restricted to the sections directly below the base of each plant. Although roots of both plants were present in almost all sections of the root box, all the sections did not contribute simultaneously to water uptake by each plant. Water uptake was delayed from the middle intermingled zones. In effect, uptake patterns did not relate generally to the root distribution. The tendency was for the component plants to initially 'avoid' water uptake from zones of intense intermingling or competition.

Introduction

Knowledge and understanding water uptake is important for the development of crop models, which have become important tools for agronomic research and crop management. Over the past 2 decades, many models, mainly for sole crops have been published and are being used extensively in research and for agricultural decision making. The development and use of simulation models for crop mixtures, however, continue to lag behind, apparently due to the lack of complete understanding of resource partitioning between component plants in a mixture.

In particular, the analysis of the below ground growth and resource use by plants presents tremendous challenges as there are still general methodological difficulties in studying root systems of plant mixtures, despite the advances in techniques and equipment design. For example, roots of the component plants can intermingle (Gregory and Reddy, 1982), making the task of separating the respective root systems very cumbersome. Staining techniques generally fail to distinguish one root system from another. Other possibilities such as the isotopic dis-

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crimination of ^{13}C between C_3 legumes and C_4 cereals are expensive and require special equipment (Wong and Osmond, 1991). In the absence of detailed information on root system behaviour of crop mixtures, the quantitative description of root distribution patterns are often based on very simplistic assumptions. Kiniry et al. (1992) assumed that roots of the component plants are either completely separate whereas others (Adiku et al., 1995; Carberry et al., 1992), assume that root systems are completely mixed. More recent studies, however, indicate that indeed, varying degrees of root intermingling may occur in mixed crop systems (Ozier-Lafontaine et al., 1998) and, therefore, no one single assumption (e.g. completely mixed or completely separate) is adequate to describe the system. Thus, crop models developed based on simplistic assumptions would tend to have limited validity.

A further constraint to the modelling of crop mixtures relates to the difficulties in determining water uptake and use by each component crop in a mixture. Earlier research on water use by crop mixtures or intercrops have, therefore, simply compared total water use of the sole and intercrops (e.g. Morris and Garity, 1993) without seeking to understand how the process of water partitioning proceeds. Water partitioning modules of the few published intercrop models also use somewhat simple assumptions. For example, Kiniry et al., (1992) assumed that all the component plants in a mixture extract water from a 'common pool', which would imply that a direct competition for water would occur in every zone of the soil profile, even if the root systems are clumped into localised zones of the soil profile. Direct measurements of the transpiration of component plants is now possible through the technique of sap flow (Ozier-Lafontaine et al., 1997, 1998) and this should help shed more light on the problem.

It is worth noting that patterns of root growth is guided by a genetic code but the ultimate configuration of the root system is largely determined by environment factors such as water availability (Smucker and Aiken, 1992) and nutrient distribution (Drew et al., 1973). Root growth and activity is enhanced in 'favourable zones' of the soil. It is thus conceivable that when several plants compete for limited resources, each component would reduce growth and activity in regions of intense competition and seek favourable zones. But scientific data on these aspects are lacking although such information is required for the development of more comprehensive intercrop models.

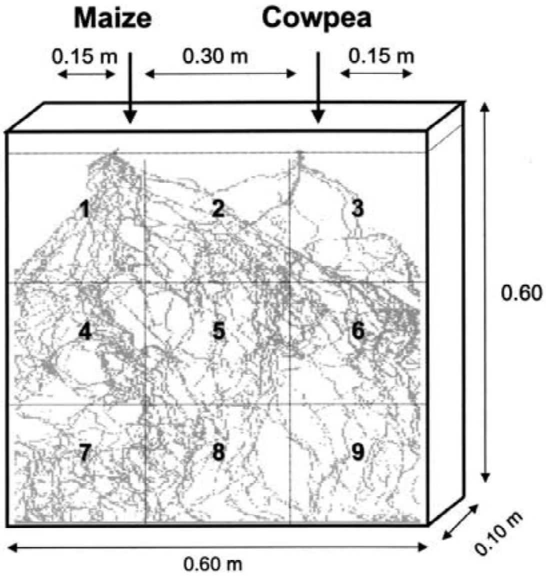


Figure 1. Schematic representation of the wooden box containing the maize-cowpea mixture used in the study. An illustration of the 2-dimensional shape of the root systems of maize and cowpea is presented in filigree.

The aim of this study is to investigate the patterns of root growth and activity of a maize-cowpea mixture grown in root boxes under varying soil water conditions in the greenhouse. The research is designed to focus only on the behaviour of plants in mixtures, hence comparison with the sole plants is not part of the study. Implications for modelling water partitioning between plants are discussed.

Materials and methods

Maize (*Zea mays* L. 'Desirade 103'), a short duration variety and cowpea [*Vigna unguiculata* (L.) Walp 'Fond d'Or 46-2'] were grown as mixtures in wooden boxes (dimensions $0.60 \times 0.10 \times 0.60$ m^3) (Figure 1) under greenhouse conditions between March and May 1999 in Guadeloupe (16° 17′ N, 61° 16′ W). The soil used, which was an Oxisol (34% sand; 33.4% silt; 32.6% clay) with a pH of 4.3, was packed to an average bulk density of 1.10 kg m^{-3} into the boxes. Each box weighed between 42 and 45 kg after filling with soil. There were 12 boxes in all, 6 of which were installed with gypsum blocks (Type 14.22.05, SDEC France) at depths of 0.05, 0.25 and 0.45 m and at 3 horizontal positions (0.15, 0.30 and 0.45 m) at each depth, giving a total of 9 gypsum blocks per box. Data on temperature, humidity and incident photosynthetic active radiation (PAR) were recorded using thermocouples, hygrometers (Vaissala HMP35, Helsinky, Finland) and amorphous silicon cells (Solems, Palaiseau, France), respectively. The temperature of the greenhouse had a cycle of 37.9 °C/19.2 °C and a relative humidity cycle of 25.2%/97.4% at midday and midnight, respectively.

Treatments

Two seeds each of maize and cowpea were planted in all boxes at a distance of 0.15 m from either edge of the box (Figure 1) on March 19, 1999. The emerged seedlings were thinned to 1 seedling per plant type at 11 days after planting (DAP). The initial soil moisture was near field capacity and the plants were liberally watered until thinning. Two water regimes: *Ir* (full irrigation with matric potential, Ψ_m, maintained at about -10 kPa) and *D* (dry treatment with Ψ_m maintained at about -60 kPa) were imposed from 11 DAP. There were 6 replicates for each water treatment, with each treatment having 3 of the boxes installed with gypsum blocks. At 24 DAP, all the boxes were applied with fertiliser at the rate of 5 g box^{-1} using N P K S compound fertiliser with N: 15%, P_2O_5: 11%, K_2O: 22% and $S0_3$: 14%.

Water application followed the two irrigation treatments, *Ir* and *D*, until 34 DAP (Figure 2) when all the plants (including all the *D* treatments) were watered to field capacity after which the surfaces of the soil were covered with plastic sheets to minimise direct soil evaporation. Three days later (38 DAP) a further irrigation was applied to each box, after which a further water treatment was imposed. All boxes of *Ir* and *D* with installed gypsum blocks (3 boxes for each water treatment) underwent a 5-day drying cycle (*DC*) while all the other boxes (3 for each water treatment) continued to be irrigated, *CW* (for continuous watering) during this 5-day period. Water treatments, therefore, increase to 4 namely: *Ir-DC*, *Ir-CW*, *D-DC* and *D-CW*. For the *Ir-CW* and *D-CW* treatments, water application rate was equal to the daily weight loss of the boxes (Figure 2).

Transpiration and soil water content measurements

The sap flow method, which was based on the heat balance of the stem (Ozier-Lafontaine and Tournebize, 1993; Sakuratani, 1981) was used to measure maize transpiration. Sensors constructed in our laboratory were similar to those of Tournebize and Boistard (1998) and were installed between 28 and 34 DAP on maize stems in 10 out of the 12 boxes. The maize stem diameters ranged from 14 to 20 mm. Sapflow readings were taken and stored at 30 min intervals on a multiplexed data logger (Campbell CR21X, Shepshed, Leicestershire, UK). Although the stem heat balance method was successfully applied to small diameter stems (< 10 mm) elsewhere (Senock and Ham, 1993), the cowpea stems (< 7 mm) were difficult to fit with our sensors, apart from the possible over-heating problems which may cause tissue damages. Thus, to estimate cowpea transpiration, each box was weighed 2 times a day (morning and evening) on a digital scale (KB 60 s.2 METLER – TOLEDO: Max = 60 kg; Min = 0.05 kg) during the 5 days of the *DC*. This enabled the determination of the total weight loss due to the combined transpiration of maize and cowpea. The transpiration of the cowpea was obtained as the difference between the total weight loss and the maize transpiration, which was measured with sap flow. The combined transpiration ratio of both plants (i.e. ratio of actual *Ea,* to the maximum *Ep* transpiration) was also determined during the 5-day cycle.

Gypsum block readings were also taken at each time of weighing. The readings were converted to volumetric soil water content via an established calibration curve. The soil moisture characteristic was also obtained from the soil textural data in combination with measured saturated water content and saturated hydraulic conductivity, using algorithms, RETFIT (Hutson and Wagnet, 1992). The moisture characteristic enabled the conversion of moisture content to matric potential. The leaf water potential was determined at midday on leaf samples taken on plants with and without imposed *DC* using a pressure bomb (Model PMS CORVALIS, OR, USA).

Root shoot partitioning

At the end of the *DC* (45 DAP), the above ground parts of the plants were harvested and the leaf area was determined using a leaf area meter (Model LI-3100, LI-COR INC. LINCOLN, USA). The total above ground dry matter was also determined after oven-drying at 70 °C for 2 days.

The roots in the boxes were obtained by washing off the soil after one side of the boxes was removed to expose the soil. A nail-board was constructed using 288 nails (9 nails per 100 cm^2), each of length 5 cm protruding on one side of a wooden board of same dimensions as the removed side of the root box. The nail board was then pressed onto the exposed soil in

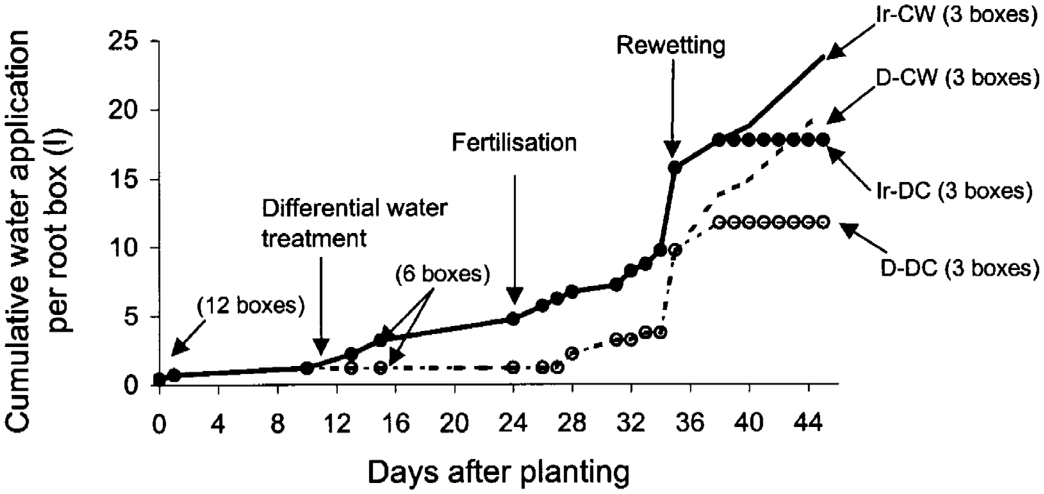


Figure 2. Cumulative water application to the treatments *Ir-CW, Ir-DC, D-CW* and *D-DC.*

Table 1. Regression equations for the various classes of maize and cowpea roots

Plant	Class	Equation	r^2
Maize	coarse	Y = 1243 * X	0.82**
	fine	Y = 2688 * X	0.96**
Cowpea	coarse	Y = 234 * X	0.89*
	fine	Y = 3626 * X	0.96*

the root box and the remaining parts of the root box were dismantled. The soil was carefully washed off the roots on the nail board leaving the roots in their general shape and preserving a 2-dimensional distribution pattern (Figure 1). This procedure is similar to that used by Eghball et al. (1993). After washing, the roots were trisected both horizontally and vertically into 9 sections (Figure 1), each of dimension 0.20 × 0.17 m^2, corresponding approximately to the zone of measurement of a gypsum block. The roots from each section were separated into maize and cowpea using the following criteria: (i) the colour of the roots; maize roots being more white, (ii) the presence of nodules on cowpea roots, and (iii) the distinct scent of the roots characteristic of most legumes (Ozier-Lafontaine et al., 1999).

The roots of maize were separated into 3 qualitative classes: prop roots, coarse roots and fine roots. In the case of cowpea, there were only 2 classes, coarse and fine roots. The lengths of samples of the prop and coarse roots were measured directly with a meter rule. To determine the length of the fine roots, samples of the roots of each plant were spread randomly on transparent sheets and traced out using a sharp pointed blue marker pens, in order to ensure the continuity of lines. The root drawings were then scanned using a desktop scanner at 300 dpi (HP Scanjet). The scanned root images were processed using the software ROOTEDGE (Kaspar and Ewing, 1997) to determine the root length. All the coarse and fine roots of each plant were then dried at 70 °C for 2 days to determine the root dry weight. The regression of root length (Y cm) on root weight (X g) for the various root classes are given in Table 1 and these were used to convert the weights of the roots to lengths. The total root length for each plant was obtained by summing over all the sections.

Results

Plant growth and leaf area development

Table 2 shows the growth parameters of the maize and cowpea under the *Ir-DC* and *D-DC* treatments at the end of the drying cycle period (45 DAP). Maize under the *Ir-DC* conditions attained a leaf area of 0.31 $m^2 plant^{-1}$. Although it was higher than that under the *D-DC* treatment (0.29 m^2 $plant^{-1}$), the difference was not significant. The leaf area of the cowpea under the *Ir-DC* condition (0.20 $m^2 plant^{-1}$) was significantly higher ($P < 0.05$) than that under the *D-DC* conditions (0.15 $m^2 plant^{-1}$).

Table 2. Dry matter distribution of maize and cowpea under irrigated and dry treatments (n = 3; ± refers to standard deviation)

Plant type	Cowpea		Maize	
Water treatment	*Ir-DC*	*D-DC*	*Ir-DC*	*D-DC*
Growth attribute				
Leaf area (m^2 $plant^{-1}$)	0.21±0.01	0.15±0.01	0.31±0.02	0.29±0.01
Shoot weight (g $plant^{-1}$)	15.00±1.00	11.00±2.00	41.10±3.00	33.00±2.00
Root weight (g $plant^{-1}$)	1.30±3.00	1.00±1.00	8.50±2.00	7.30±3.00
Root:shoot ratio	0.087	0.091	0.207	0.221
Fine roots (%)	52.0	36.0	52.5	51.5
Coarse roots (%)	48.0	64.0	47.5	48.5

The shoot weight of maize and cowpea varied with water treatment. Maize accumulated a total of 41.10 and 33.00 g $plant^{-1}$ under *Ir-DC* and *D-DC* conditions, respectively. Cowpea under *Ir-DC* conditions accumulated a total of 15.00 g $plant^{-1}$ and this was significantly ($P < 0.05$) higher than that of the *D-DC* treatment (11.00 g $plant^{-1}$).

The root growth of the plants was also affected by the water treatment. Maize produced a total of 8.50 and 7.30 g $plant^{-1}$ under the *Ir-DC* and *D-DC* conditions, respectively, resulting in a root:shoot ratio of 0.207 and 0.221, respectively. There was no apparent effect of water treatment on the ratio of fine to coarse roots of maize. Cowpea produced 1.30 and 1.00 g $plant^{-1}$ under *Ir-DC* and *D-DC* conditions, respectively, giving a root:shoot ratio of 0.087 and 0.091, respectively. Unlike maize, a high percentage (64%) of the cowpea roots in the *D-DC* treatment were coarse while only 48% of the roots were coarse under the *Ir-DC* treatment, even though the root:shoot ratios were similar (Table 2). Thus, water stress affected the relative distribution of mass between the coarse and fine roots in cowpea but not in maize. Whether this shift in distribution of mass is an adaptive response of cowpea to water stress is not immediately clear.

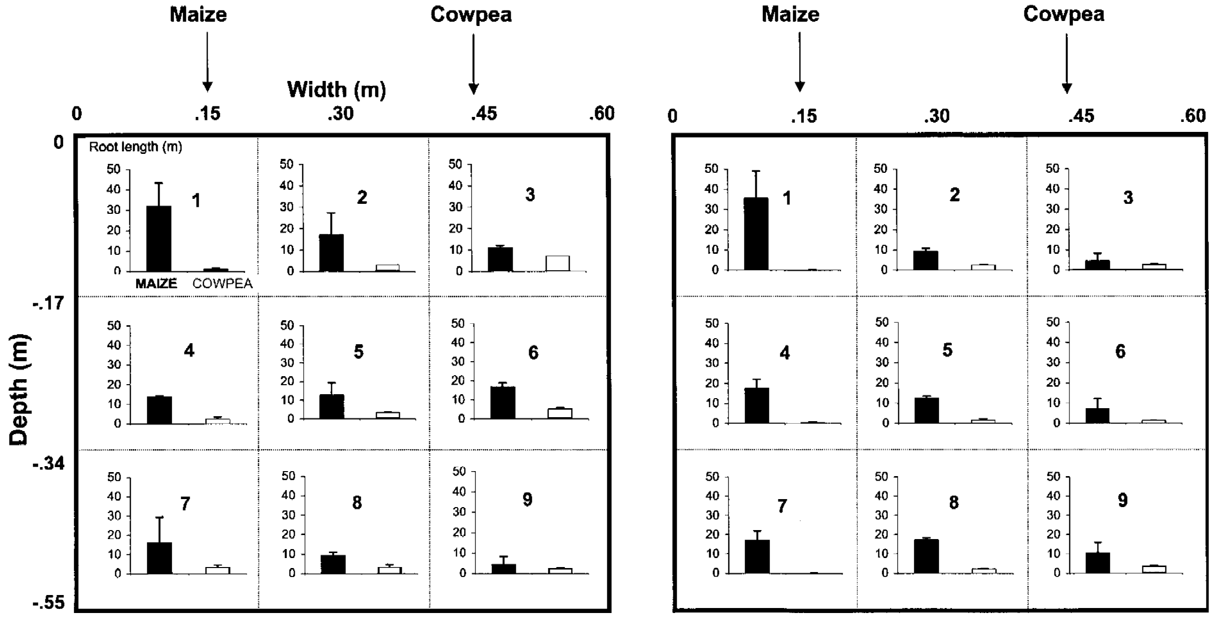
Root distribution patterns

Figure 3a presents the horizontal and vertical distribution of root length of maize and cowpea for the *Ir-DC* conditions. The data are presented according to the sections shown in Figure 1. For ease of reference, we will describe sections 1, 4 and 7 as 'maize zones' and 3, 6 and 9 as 'cowpea zones'. The zone between the maize and cowpea (2, 5 and 8) will be referred to as 'inter-row' position.

Maize roots were present in all sections of the root box and the total root length was 143.95 m. The highest root length (22%) was located in section 1 just below the crown. Although the root length decreased both laterally and vertically away from the crown, the growth pattern was irregular. The lowest root length of 8.89 m was located in section 9 but root length in section 7 (17.34 m) was higher than that of section 4 (13.38 m). Maize roots were not restricted to the maize zone but traversed into the cowpea zone and proliferated there. About 31% of the total root length were in the cowpea zone and about 27% of the root length were in the inter-row position.

As for maize, cowpea roots were also present in all sections under the *Ir-DC* conditions. However, the length of cowpea roots was far less than that of maize. The total root length was 27.82 m and 25% of this was located in zone 3, and 19.6% in the maize zone. There is a general intermingling of the maize and cowpea root systems suggesting that any allelopathic effects of one plant root system on the other was minimal.

Figure 3b presents the root distribution of the maize-cowpea mixture under the *D-DC* water treatment. Maize root length (total length = 129.43 m) was slightly lower than that of the *Ir-DC* conditions, but roots were also present in all sections. As for *Ir-DC* conditions, the highest root length (35.43 m) was in section 1. However, only 16% of the total root length was found in the cowpea zone, whereas as much as 54% of the total root length remained in the maize zone. For cowpea, the total root length was considerably reduced (12.17 m) although the total root mass was not significantly different from that of the fully irrigated treatment (Table 2). As indicated above, a high percentage of the roots was coarse, making a high contribution to the total mass but not to the total length. The lateral spread of the root length was also



(a) ***IR-DC*** **(b)** ***D-DC***

Figure 3. Distribution of root length under *Ir-DC* and *D-DC*.

restricted, so that cowpea roots were generally absent from the maize zone but concentrated in the cowpea zone (55%).

Transpiration

Figure 4b shows the daily transpiration rates of maize and cowpea (kg d^{-1} box^{-1}). The variations of the actual transpiration (*Ea*) follow the PAR variations (Figure 4a) during the first 3 days of the drying cycle but decline sharply thereafter. Maize transpiration in treatment *Ir-DC* (Figure 4b) dominated that of cowpea until the latter times of the drying cycle (day 5). Maize transpiration in *D-DC* (Figure 4c) was at par with that of cowpea for the first 3 days. By the 5th day of the *DC*, cowpea transpiration exceeded that of maize, suggesting that cowpea has a better capacity to continue water uptake under limiting water conditions.

Measurements of leaf water potential indicated that by the 4th day of the *DC* maize leaf water potential was about −13 000 kPa at midday in the *Ir-DC* treatment and showed obvious signs of wilting. On the contrary, the leaf water potential of cowpea in both *Ir-DC* and *D-DC* treatments on the 4th day of the *DC* was about −9000 kPa with no signs of wilting.

Figure 4d shows that the variation of the transpiration ratio for *Ir-DC* conditions. It is observed that the ratio began to fall below unity after about 50 h whereas in the *D-DC* conditions, this decline became evident after about 60 h from the commencement of the drying cycle. Furthermore, the transpiration ratio for *Ir-DC* declined to 0.25 after about 95 hours at which time the ratio for *D-DC* conditions was still fairly high (0.45).

Variation of soil water content and patterns of water uptake

Figure 5 shows the water content patterns during the *DC* under the *Ir-DC* conditions. Water content changed very little during the first 2 days of the *DC*. Substantial changes in the soil water content became evident from the third day of the *DC*. At the commencement of the third day of the *DC*, (t = 45 h), the water content in section 1 of maize declined from an initial value of 0.49 to 0.42 m^3 m^{-3} (Figure 5a). However, the bottom of the maize zone did not show any appreciable change in water content. By the end of day 3 of the *DC* (t = 54 h), there was a rapid decrease in the soil water content with the water content at the top section reaching 0.34 m^3 m^{-3} which was close to the lowest water content recorded during this experiment. By day 4 (t = 68 h) of the *DC*, the water content declined to 0.33 m^3 m^{-3} at all depths within the maize zone.

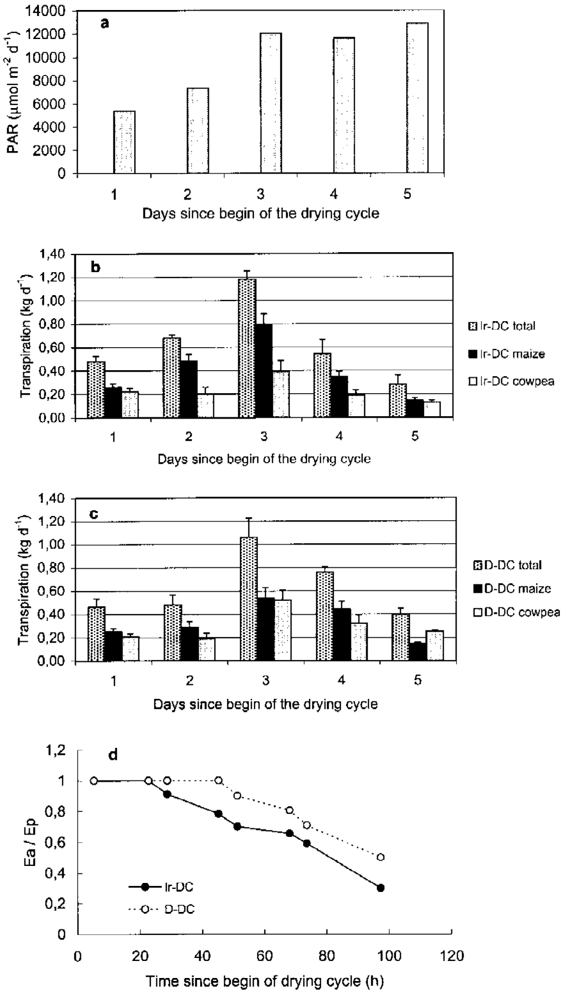


Figure 4. Daily patterns of (a) PAR variation during the *DC*, (b) transpiration of maize and cowpea under treatment *Ir-DC*, (c) transpiration of maize and cowpea under treatment *D-DC* and (d) hourly variation of the transpiration ratio (Ea/Ep).

Figure 5b shows the changes of water content in the inter-row position. It was observed that there was hardly any change in water content in this zone even at time $t = 54$ h, at which time the top section of the adjacent maize zone was already fairly dry.

Contrary to the observations made for maize zone (Figure 5a), the rate of decline in the soil water in the cowpea zone (Figure 5c) was much slower. Even at the end of day 3 ($t = 54$ h), the water content in the cowpea zone hardly fell below 0.45 m^3 m^{-3}. Only the bottom section of the cowpea zone, which had an appreciable quantity of maize roots (Figure 3) indicated an appreciable decline in water content. At time $t = 48$ h, when the water in the maize zone was almost depleted, the driest part of the cowpea zone (which was the top section) had water content of about 0.40 m^3 m^{-3}.

Figure 6a shows that water depletion rates were much slower in the *D-DC* treatments than in the corresponding *Ir-DC* (Figure 5a). At time 54 h, when the top section of the maize zone in the *Ir-DC* treatment was almost at the lowest measured water content of 0.33 m^3 m^{-3}, the corresponding water content in the *Ir-DC* treatment was still very high (about 0.40 m^3 m^{-3}). Furthermore, in the *D-DC* treatment, the lowest water content was only attained after about 100 h of drying cycle.

Figure 6b shows water content changes in the interrow position of the *D-DC* treatments. As for *Ir-DC* (Figure 5b), a marked decline in water content became evident only about 54 h, even though the maize zone (especially the top sections) were already fairly dry by this time. In the case of the cowpea zone (Figure 6c), a marked decline in the water content only after about 68 h of drying cycle.

The observations indicate that even in such a relatively small rhizotrons as those used in this work, water content distribution was very patchy, with very dry regions falling adjacent to fairly wet sites. Despite the large water content gradients, lateral flow did not seem to be substantial enough to equilibrate water contents. This may be a peculiar feature of the soil used.

Discussion

Root distribution

The observed patterns of root distribution indicate that under well-watered conditions, roots of the component plants in a mixture would grow to occupy large volumes of soil. Also, root branching and intermingling was considerable. This pattern of profuse proliferation has also been observed in maize in response to high nitrogen application rates (Eghball et al., 1993). The effect of water stress, apparently, was not only to reduce the mass or total root length, as shown by Huang and Fry (1998) for tall fescue, but also to change the pattern of distribution, even for the same planting distance. In cowpea, water stress also led to the production of more coarse roots.

Under water stress conditions, a tendency for the root systems to cluster within their 'own' zones may be observed – i.e. cowpea in the *D-DC* treatment. Hence, in very severe water stress conditions, the root

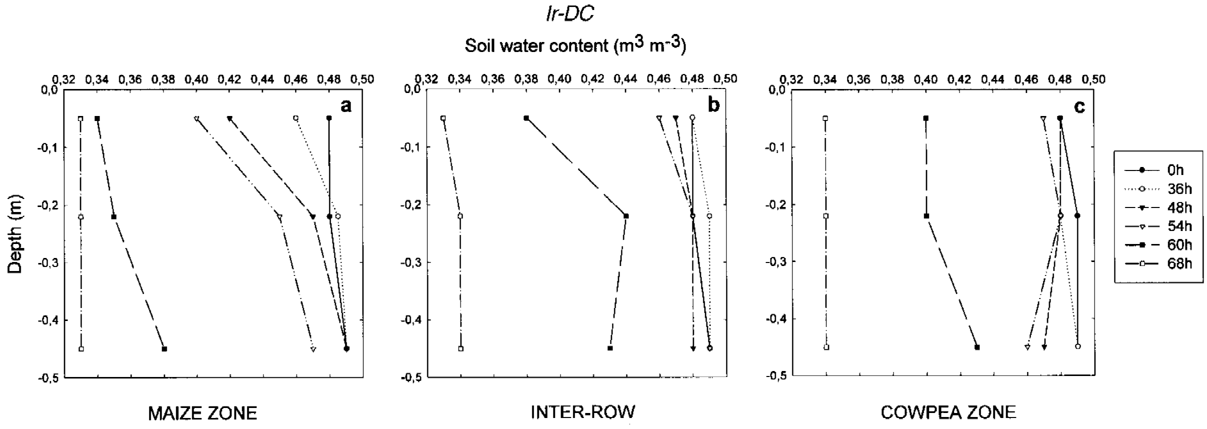


Figure 5. Variations in the soil water content in various sections of the root box during the *Ir-DC* (0 h indicates the beginning of the *Ir-DC* cycle).

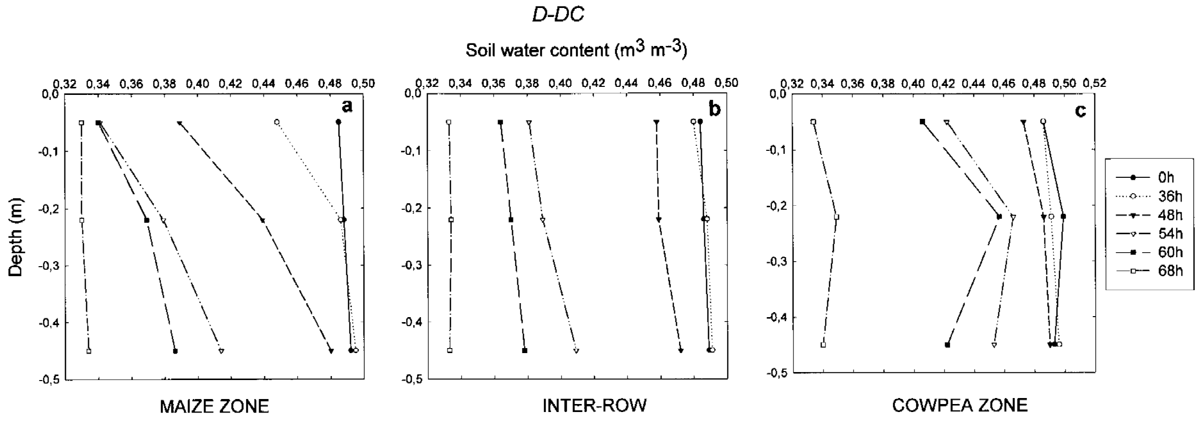


Figure 6. Variations in the soil water content in various sections of the root box during the *D-DC* (0 h indicates the beginning of the *D-DC* cycle).

systems of component plants may not intermingle at all. Thus, unless there is a substantial vertical and lateral water transport from wetter to drier regions of the soil, there may be no real inter-species competition for water. This is an important point to be considered in root growth and water competition modelling. The heterogeneity in root distribution also indicates that at least a 2-dimensional consideration is necessary for an adequate description of root distribution.

Transpiration and water uptake

The rates of transpiration by the plants from the initially wet soils correlated well with light interception and with leaf area. Under these conditions, the maize component, which had the higher leaf area dominated cowpea in water use. When soil water declined, the cowpea component contributed more than maize to the total transpiration, particularly in the case of the *D-DC* treatment. These results suggested that when soil water becomes limiting, the ability of a plant to continue water extraction would depend on inherent attributes such as drought tolerance, maintenance of turgor, and stomatal opening. Maize with a higher leaf area would have had a higher water demand, which the soil was unable to supply, and hence showed stress symptoms earlier than cowpea.

The faster decline of the water content in section 1 (maize zone) (Figures 5a and 6a) suggests an initial concentration of water withdrawal immediately below the root crown, where the root density was also highest (Figure 3). Noteworthy, however, is the delay in water extraction by the plants from the inter-row position. In the case of the *D-DC* treatments (Figure 6b), the delay in extracting from this zone may be attributed to the lower root lengths (Figure 3). But root length alone cannot offer an explanation for the observations in the *Ir-DC* treatment because the root length in section 2 was not only higher than those of sections 4 and 7 but also this section was closer to the crown. It would be expected that a faster water depletion would take place from section 2 than for sections 4 and 7. Even in the case of the *D-DC* treatments, the root length of maize in section 8 was comparably high but the apparent rate of change of water content at this position was somewhat slower than the top sections. As pointed out by Gardner (1983), water uptake from deeper soil zones are often delayed so long as the surface soils are wet, even if root lengths are high in the deeper zones.

These observations have important implications for modelling water competition. First, root distribution patterns change with resource availability so that there can be varying degrees of root intermingling. These dynamic variations in root distribution need to be considered in root growth models. Second, even if the roots of the component plants penetrate the soil and proliferate profusely, water extraction may not occur in all the sections at the same time. There seems to be preference zones of water extraction by each root system and a delay in water extraction from the strongly intermingled (inter-row positions) zones. Third, the water uptake patterns may not relate to root distribution alone. Hence, sharing water between component root systems on the basis of root length alone may not be entirely correct. The challenge for developing water partitioning models seems to lie in the identification of the 'preferred' zones of water uptake by each plant component in the mixture, rather than to develop models that seek to 'force' the component plants to compete, even if they do not have to do so.

Conclusions

This work may be considered as a methodological contribution to the understanding of water partitioning in plant mixtures. Original approaches were combined to investigate the effects of water stress on root growth distribution and activity, transpiration partitioning and soil water depletion in the case of a maize-cowpea mixture.

Root distribution was generally irregular in space under both well-irrigated and water stress conditions. Under well-irrigated conditions, the roots of the component plants grew profusely into all sections of the root box and intermingled in each soil section. Under water stress conditions, not only was the total root mass (or total root length) lower than the well watered situation, but the lateral extent of the roots were also restricted. There was a reduced degree of intermingling.

Water uptake from uniformly wetted soils was initially restricted to the sections directly below the base of each plant and there was a delay in water extraction from the inter-row positions. Large gradients in water content developed in various sections of the root box but the rate of lateral flow of water was apparently slow to equilibrate the soil water in the box. Even though the roots were present in every section of the root box, all sections did not contribute simultaneously to water uptake, so that uptake patterns did not relate generally to the root distribution. The challenge remains to develop water competition models that are able to mimic these realities.

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