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Productivity of yams (Dioscorea *spp.*) as affected by soil fertility

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1 SUMMARY

Field experiments were conducted in central Côte d'Ivoire during the growing seasons of 2001, 2002 and 2003 to investigate the effect of natural soil fertility and inorganic fertilizer on productivity of yams. *Dioscorea alata* cv. TDa 95/00010 and *Dioscorea rotundata* cv. TDr 98/02461 were grown with and without fertilizer application in a savannah site with a low fertility soil and in a forest site with a more naturally fertile soil. The fresh tuber yield (FTY), the area under the curve (AUC) of shoot and tuber and the AUC of nitrogen and potassium contents all significantly increased in the forest site than in the savannah site. This was due to the greater soil organic matter and exchangeable K, Ca and Mg contents observed at the forest site. The inorganic fertilizer applied had no effect on the FTY, while it significantly increased the AUC of shoot and tuber of *D. rotundata* in the savannah site. The shoot AUC of *D. alata* was increased with fertilizer application in the forest site in 2001, but this was not reflected in increased tuber dry matter (DM), suggesting a side effect of the fertilizer on DM balance between above and underground organs. The increase in the canopy establishment and tuber initiation growth phase in *D. alata* in the savannah site suggests a better adaptation of this species to low fertility soil and might explain its better overall productivity in the experiments. In contrast, the development of *D. rotundata* was rather fixed allowing a weak adaptation to low fertile soils. The results showed clear importance of soil organic matter in productivity of yams, which is not compensated in soils with low organic matter content by the use of inorganic fertilizers. It is recommended that management practices that favour maintenance or build up of soil organic matter content be evaluated and applied in yam production systems.

2 INTRODUCTION

Yams (*Dioscorea* spp) are a staple tuber crop for many of the poorest in West Africa, South East Asia, the Caribbean and Oceania. In many of these areas yams are also culturally important. Up to 95% of the world's yams are produced in West Africa (FAO, 2009). The increased demand for yams in West Africa has been met by an increase in cultivated area, e.g. in Côte d'Ivoire the area under yams increased from 150,000 ha in 1960 to 692,000 ha in 2007. However, yam average yields has increased little over time, e.g. in Côte d'Ivoire average tuber yield increased from 8 t fresh tuber ha^{-1} in 1960 to 8.5 t ha^{-1} in 2007 (FAO, 2009). Since the demand for yams keeps increasing due to the continued population growth and on the other side reserves of arable land are diminishing and fallow duration is decreasing, it is becoming necessary to sustainably increase yam productivity and to include yams in sedentary cropping systems (O'Sullivan & Ernest, 2008).

In most production systems, yams are grown almost without external inputs following long term fallow (Degras, 1993). This is because yam yields are reported to decline sharply when grown after short fallow of about 1-3 years duration (Watson & Goldsworthy, 1964). Similarly, strong yield declines were observed under continuous yam cultivation (Kowal & Kassam, 1978). These yield declines have been related to pests (mainly nematodes) , weed pressure and to soil fertility depletion (Asiedu, 2003). Recent progress in yams research can help to cope with the increased pests and weed pressure. The adoption of new yam cultivars that are tolerant to diseases, and the development of low cost methods to combat yam nematodes (Coyne *et al.*, 2006) can help smallholders farmers to cope with the increased pest pressure. The adoption of vigorous creeping cultivars that are able to totally cover the soil surface within a few weeks after sprout emergence can help to limit weed infestation.

The decline of yam yields under continuous cultivation has led to the largely accepted conclusion that yams require a high level of natural soil fertility (O'Sulllivan *et al.*, 2008). The better yields observed on naturally fertile fallow soils can probably be explained by the relatively high organic matter content of these soils that allows for a high rate of nutrient release to the plant, and optimum water retention capacity. Yam tubers are indeed known to export large quantities of nitrogen (N) and potassium (K) (O'Sullivan & Ernest, 2008). The presence of beneficial soil micro organisms such as arbuscular mycorrhizal populations can also explain better yam growth in naturally fertile fallow soils (Tchabi *et al.*, 2009).

Solutions to restore soil fertility and increase yam yields might include the introduction of legumes in the cropping system and the use of organic or mineral fertilizers. Yam-legumes association or rotation of legumes with yams were shown to maintain or increase tuber yields in low fertility soils (Budelman, 1990a; Budelman, 1990b; Carsky *et al.*, 2001; O'Sullivan and Ernest, 2008). The addition of organic fertilizers has also been shown to often slightly increase tuber yields (Kowal & Kassam, 1978). The use of mineral fertilizers (mostly NPK) to improve fresh tuber yield, however, showed variable results (O'Sullivan & Ernest, 2008), but the reasons explaining these variable effects have not been fully investigated. As most of the pevious studies were conducted under field conditions, many other factors might have influenced (in a complex manner) the effect of mineral fertilizers on tuber yield. More specifically, there is no study relating plant productivity and nutrient uptake kinetics to soil fertility, mineral fertilizer input, and climatic conditions.

The objective of this study was to assess the relationship between soil fertility and yam tuber production.

3 MATERIALS AND METHODS

3.1 Site description and land preparation: Experiments were conducted from 2001 to 2003 between May and December at the field station of the Swiss Centre for Scientific Research in Côte d'Ivoire (CSRS) in the village of Bringakro, about 180 km north-west of Abidjan. The village is located in a transitional equatorial climate at the interface between a largely degraded moist semi-deciduous dense forest and a shrub savannah on the West side of the so-called "V Baoulé" which is located between the forest vegetation in the south and a pre-forestry savannah in the central part of Côte d'Ivoire. Soil characteristics are different under both vegetations but climate conditions are similar.

One experimental site was located in the forest part of the "V Baoulé" ("forest site") (6°40'N, 5°09'W, altitude 165 m above sea level), while the other was in the pre-forestry savannah part ("savannah site") (6°40'N, 5°08'W, altitude 150 m). At each site, one hectare (100 m x 100 m) of land was cleared of vegetation and plant debris were removed without burning. Soil samples were taken in the 0-20 cm layer before planting. The soil samples were air-dried, and ground to pass through a 2 mm sieve after hand removal of plant residues. The samples were analyzed for soil texture, pH, total N and C, Olsen P, exchangeable K, Ca and Mg and cation exchange capacity using routine analysis methods. The rainfall and the air temperature were monitored using a meteorological station (Delta-T Devices Ltd www.delta-t.co.uk).

3.2 Planting materials: As yams species respond differently to soil fertility decline (Kowal and Kassam, 1978), a cultivar of *Dioscorea rotundata* Poir (TDr 89/02461) and a cultivar of *D. alata* L. (TDa 95/00010), both from the International Institute of Tropical Agriculture (IITA) were used for the experiments. Setts weighing 100 g were prepared by cutting whole tubers that had broken dormancy. The setts were soaked in a liquid mixture of 31.2 g oxamyl L^{-1}, 1 g imazalil sulphate L^{-1} and 0.34 g deltamethrine L^{-1} and air-dried for 24 hours in order to protect the setts against nematodes, fungi and insects, respectively.

3.3 Fertilizer application: Two fertilizer treatments were applied in 2001 and 2002: (i) no fertilization, as control and (ii) application of 240-11-269-8.5-11-66 kg ha^{-1} of N-P-K-Ca-Mg-S, aimed at optimum growth. The rate of fertilizer application was calculated so as to reach a yield potential of 60 t fresh tuber ha^{-1} (Kowal & Kassam, 1978) based on nutrients export by yam tubers per hectare per year given by (Degras, 1993). Fertilizers were applied as a combination of urea, potassium sulphate, triple super phosphate and magnesium sulphate. Half of the nutrients were added at 60 days after planting (DAP), and the other half at 100 DAP. Each plant was fertilized using the sideband method as described by (Nwinyi & Enwezor, 1985). The fertilizer was mixed with soil and applied manually in 3-4 cm deep grooves on the four sides of each mound. Care was taken to avoid damaging roots during fertilizer application. In 2003, the effect of fertilizer was not studied, but 240-11-269-8.5-11-66 kg ha^{-1} of N-P-K-Ca-Mg-S was applied in all plots as in 2001 and 2002.

3.4 Experimental design and cultural practices*:* In each site (forest or savannah), the trial was arranged in a randomized complete block design with two factors (yam species and fertilizer application) in 2001 and 2002 and with one factor in 2003 (yam species). In all cases, four replicated blocks were established. The soil surface was manually ploughed at an approximate depth of 20 cm and top soil was heaped into mounds of ca. 50 cm high. The mounds were made at a density of 2 m^{-2}, and one sett was planted per mound. After planting, the mounds were mulched with dry vegetation to preserve soil moisture and prevent sett desiccation. The setts were planted in May and harvested in December of each year.

In each plot in 2001, four plants were destructively sampled at random at 53 days after planting (DAP) (90% shoot emergence), at 120 DAP (the maximum growth of the above-ground organs, i.e. when the soil was fully covered by the green foliage), at 170 DAP (the maximum growth of the tubers), and at 200 DAP (final harvest). In 2002, the destructive sampling was performed on three adjacent plants per plot when the following growth stages occurred: shoot emergence of more than 95% of the plants (57 DAP), tuber initiation (78 DAP), maximum growth of the above-ground organs (107 DAP), rapid growth of the tubers (136 DAP for *D. alata* and 107 DAP for *D. rotundata*), tuber maturity (160 DAP), and harvest (195 DAP for *D. rotundata* and 220 DAP for *D. alata*). As in 2002, three adjacent plants per plot were collected at each sampling date. In 2003 at shoot emergence of more than 95% of the plants (51 DAP), tuber initiation (76 DAP), maximum growth of the above-ground organs (103 DAP), rapid growth of the tubers (140 DAP for *D. alata* and 103 DAP for *D. rotundata*), tuber maturity (163 DAP), and harvest (194 DAP for *D. rotundata* and 220 DAP for *D. alata*).

3.5 Crop growth measurements

3.5.1 Fresh tuber yield and dry biomass production: Final fresh tuber yield was estimated based on fresh weight of tuber harvested during the last sampling in 2001, 2002 and 2003. At each sampling date, plants were separated into leaves, vines and tubers and the fresh weight of each was recorded. A sub-sample from each plant part was selected, cut into small pieces and oven-dried at 70°C to constant weight for dry matter estimation. The dry matter (DM) production in shoot was calculated as the sum of leaf and vine dry matter, while the total DM was calculated as the sum of tuber, leaf and vine dry matter. In 2002, the N and K concentrations were measured in a sub-sample of leaves, vines and tubers. The N or K contents of a given organ were calculated as follows:

N or K contents (kg ha^{-1}) of an organ = N or K concentrations (%) in the organ X Dry matter produced by the organ (kg ha^{-1})

Nitrogen concentration in leaves, vines or tubers was measured with a carbon nitrogen analyzer, while K concentration was measured with an ICP-OES after incinerating the leaves at 550°C for 6 hours and solubilizing the ashes in concentrated HNO_3.

3.5.2 Area under the curve (AUC): The dry matter accumulation in the shoot and the tuber during the overall growing season was modelled using the AUC. The graphs of the dry matter accumulated in shoot or tuber over the growing seasons were plotted and the AUC for each graph was calculated according to Daellenbach *et al.* (2005).

3.6 Statistical analysis: The statistical analyses were conducted separately for each yam species. The area under the curve (AUC) allowed comparison between growth seasons in spite of the differences in experimental designs between years. For each of the dry matter graphs mentioned above, repeated measurement data recorded over the growing season were transformed into a single number representing the AUC (Daellenbach *et al.*, 2005). The fresh tuber yield, the AUC of shoot and tuber dry matter production, and the AUC of N and K contents in shoot and tuber were subjected to analysis of variance using *SAS v8.02*. Treatment differences were identified using the standard error of the difference between means at $p \leq 0.05$.

4 RESULTS

4.1 Soils and climate*:* The forest soil was two-fold richer in clay compared to the savannah soil (Table 1). Soil texture in the forest and the savannah sites was sandy loam. Soil organic C and total N contents were about twice higher in the forest than in the savannah. Similarly, exchangeable bases (K, Ca and Mg) and the CEC was about 2 to 3-fold higher in the forest soil compared to the savannah soil. The Olsen P was also higher in the forest soil.

Table 1: Mean values ± standard errors of selected soil parameters at two sampling depths (0-10 cm and 10-20 cm) of the forest and savannah sites in 2001 after clearing the natural vegetation.

Soil properties	**Forest site**		**Savannah site**	
	0-10 cm	**10-20 cm**	**0-10 cm**	**10-20 cm**
Coarse sand (g kg^{-1} soil)	388 ± 13.7	371 ± 3.2	463 ± 10.3	480 ± 2.5
Fine sand (g kg^{-1} soil)	294 ± 2.4	271 ± 9.8	303 ± 7.1	291 ± 12.4
Coarse silt (g kg^{-1} soil)	74.3 ± 3.1	78.8 ± 2.0	80.5 ± 3.0	74.7 ± 5.7
Fine silt (g kg^{-1} soil)	43.5 ± 5.4	48.5 ± 3.5	36.3 ± 2.1	30.4 ± 2.6
Clay (g kg^{-1} soil)	188 ± 16.1	221 ± 10.8	102 ± 3.4	114 ± 11.1
pH water	6.5 ± 0.11	6.2 ± 0.13	6.2 ± 0.13	5.8 ± 0.13

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Total N content (g kg^{-1} soil)	1.23 ± 0.09	0.87 ± 0.06	0.50 ± 0.04	0.42 ± 0.03
Soil organic C content (g kg^{-1} soil)	14.4 ± 1.05	9.75 ± 0.78	7.49 ± 0.63	5.43 ± 0.37
P content (Olsen) (mg kg^{-1} soil)	12.4 ± 2.27	11.2 ± 2.08	9.5 ± 3.22	7.8 ± 2.19
Exchangeable K (cmol+ kg^{-1} soil)	0.20 ± 0.03	0.14 ± 0.02	0.13 ± 0.02	0.09 ± 0.01
Exchangeable Ca (cmol+ kg^{-1} soil)	4.82 ± 0.40	3.88 ± 0.36	1.63 ± 0.21	1.29 ± 0.20
Exchangeable Mg (cmol+ kg^{-1} soil)	1.27 ± 0.09	0.95 ± 0.08	0.82 ± 0.10	0.65 ± 0.10
Cation exchange capacity (cmol+ kg^{-1})	6.37 ± 0.48	5.03 ± 0.42	2.66 ± 0.32	2.14 ± 0.30

Total rainfall and distribution was similar at both sites in the 2001, 2002 and 2003 growing seasons (Figure 1). Season 2001 was relatively more humid with a mean total rainfall in both sites of 808 mm compared to 750 and 728 mm in 2002 and 2003, respectively. Rainfall was particularly low in the drier months of August and September in 2002. Temperature was similar at both sites at monthly mean air temperature during the growing seasons of 26°C in 2002 and 24°C in 2003 (data not shown).

4.2 Yam biomass production: No major pest attack was observed at either site during the 3 growing seasons. In *D. alata*, the fresh tuber yield (FTY) of the non-fertilized treatment was significantly higher ($p < 0.05$) in 2001 than in 2002 in the forest site (figure 2). No significant difference was found between the growing seasons in the savannah site and in the fertilized forest. The fresh tuber yield was significantly higher in the forest than in the savannah at each season and for each fertilization treatment except in 2002. No fertilizer effect was observed in all treatments. The fresh tuber yield obtained in the fertilized savannah site in 2002 was similar to that obtained in the same year in the forest site without fertilizer application.

In *D. rotundata*, a significant difference was observed between growing seasons in the forest site. Fresh tuber yield was higher in 2001 with or without fertilizer compared to the other seasons. No significant difference was observed between 2001 and 2002 in the savannah site with fertilizer application or not, while the FTY was significantly higher in 2001 than in 2003 in the fertilized treatment. Fresh tuber yield was significantly higher at the forest site than at the savannah site at each growing season and for each fertilization treatment except in 2002. No fertilizer effect was observed in all treatments.

The area under the curve (AUC) of the shoot in *D. alata* was significantly higher in 2002 than in 2001 at both sites in non-fertilized treatments, while no difference was observed in the fertilized forest at both sites. A significant difference was observed between 2002 and 2003 in the fertilized savannah. The AUC of the shoot was significantly higher in the forest than in the savannah in the three growing seasons. Fertilizer application significantly increased the shoot AUC in both sites in 2001 (Table 2). The AUC of the tuber was significantly reduced in 2002 compared to 2001 in the forest site, but not in the savannah site. No difference was observed between the fertilized treatments of 2002 and 2003 at both sites. The AUC of tuber was significantly higher in the forest compared to the savannah in 2001 and 2002, but not in 2003. Fertilizer application did not increase the tuber AUC both in 2001 and 2002 (Table 2)

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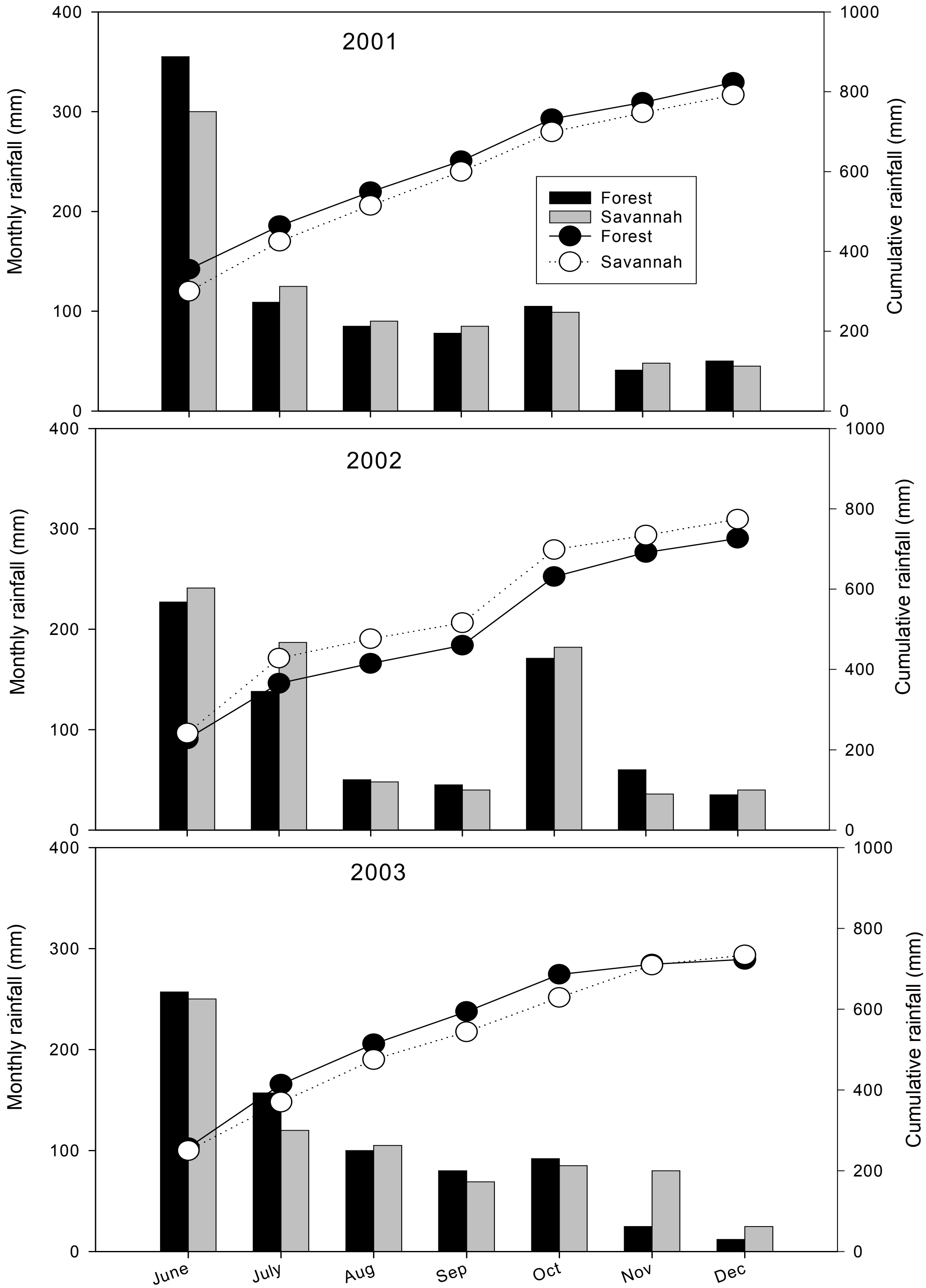

Figure 1: Monthly (columns) and cumulative (lines) rainfall in the experimental forest and savannah sites in central Cote d'Ivoire in the growing seasons of 2001, 2002 and 2003.

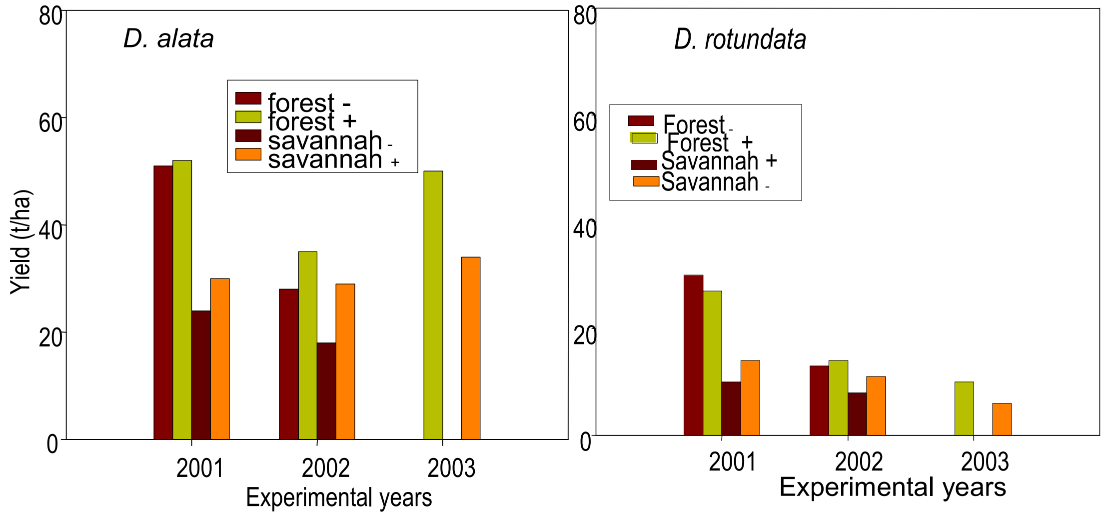

Figure 2: Fresh tuber yield at harvest of *Dioscorea alata* and *Dioscorea rotundata* grown without (-) and with (+) fertilizer application at a forest and a savannah site in 2001, 2002 and 2003 in central Côte d'Ivoire.

In *D. rotundata*, the AUC of the shoot was significantly higher in 2001 than in 2002 in the fertilized forest and the non-fertilized savannah (Table 3). No difference was observed between 2003 and 2002 at both sites. The AUC of the shoot was significantly increased in the forest than in the savannah in 2001 and 2002, but not in 2003. The fertilizer application significantly increased the shoot and tuber AUC in the savannah in 2001 and 2002. The AUC of the tuber was significantly higher in 2001 compared to 2002 in the forest site (Table 3). The tuber AUC of *D. rotundata* was significantly higher at the forest site compared to the savannah sites in all treatments and seasons.

Table 2: Area under the curve values of shoot and tuber dry matter of *Dioscorea alata* as affected by fertilizer application in the forest and the savannah sites.

Site	Fertilizer	Yam shoot [(t ha^{-1}) days]					Yam tuber [(t ha^{-1}) days]				
		2001	**2002**	**2003**	**Mean**	**s.e.d.**	**2001**	**2002**	**2003**	**Mean**	**s.e.d.**
Forest	-	296	360	n/a	328	26	566	374	n/a	470	60
	+	370	392	416	393	30	524	323	394	414	44
Savannah	-	139	168	n/a	154	30	250	233	n/a	242	54
	+	236	218	302	252	32	365	276	280	307	57
Mean		260	285	359			426	302	337		
s.e.d.		24	31	37			61	43	55		

n/a: not applicable (all plots were fertilized in 2003); - Non-fertilized treatments; + Fertilized treatments
s.e.d.: standard error of the difference between means

Table 3: Area under the curve values of shoot and tuber dry matter of *Dioscorea rotundata* as affected by fertilizer application in the forest and the savannah sites.

Site	Fertilizer	Yam shoot [(t ha^{-1}) days]					Yam tuber [(t ha^{-1}) days]				
		2001	**2002**	**2003**	**Mean**	**s.e.d.**	**2001**	**2002**	**2003**	**Mean**	**s.e.d.**
Forest	-	205	163	n/a	184	29	465	245	n/a	355	46
	+	230	170	153	184	19	500	248	269	339	51
Savannah	-	114	91	n/a	103	7	141	104	n/a	123	17
	+	196	165	130	164	25	291	170	172	211	59

Mean		186	147	141			349	192	221		
s.e.d.		23	23	15			66	29	35		

n/a: not applicable (all plots were fertilized in 2003); - Non-fertilized treatments; + Fertilized treatments
s.e.d.: standard error of the difference between means

4.3 Phases of yam growth: In *D. alata*, the duration of the different phases of plant growth changed from year to year, except phase I (tuber germination and sprout emergence) (Figure 3). The phase II (canopy establishment and tuber initiation) which started at about 50-57 days after planting (DAP) lasted 50 days (d) in the forest in 2002 and 79 days in the savannah, while in 2003 the duration of phase II was similar in both sites (Figure 2). Phase III (maximum canopy development and maximum tuber growth rate) started at 107 DAP in 2002 and lasted 47 d in the forest site, and 24 d in the savannah. In 2003, the duration of phase III was 23 d in the forest and 45 d in the savannah. The application of fertilizer slightly delayed the end of phase III by 9 d in the forest and by 12 d in the savannah. The duration of phase IV (canopy senescence and tuber maturity) depended on the end of phase III since all plots were harvested at the same time.

In *D. rotundata*, the duration of phase I was similar to that of *D. alata* (Figure 4). In the forest site, the durations of growth phases were similar between 2002 and 2003. Phase II lasted 50 and 52 d in 2002 and 2003, respectively. Phase III started at 107 DAP in 2002 and 103 DAP in 2003 and lasted 16 and 17 d, respectively, while phase IV was observed between 123 and 195 DAP in 2002 and between 120 and 194 DAP in 2003. In the savannah site in 2002, tuber and shoot development occurred at the same time in contrast to the forest where they occurred sequentially, thus phases II and III could not be distinguished separately at the savannah site. Both phases together started at 57 DAP and lasted 65 d while phase IV lasted 73 d. In the savannah site in 2003, the transition between growth phases III and IV (when the dry matter weight of the developing tuber exceeded that of the shoot) was observed before the transition between phase II and III (at the peak of the above-ground biomass), these two growth phases were thus confounded as in the same site in 2002. Fertilizer application had no effect on the duration of the growth phases.

4.4 Nitrogen (N) and potassium (K) contents in shoot and tuber: In *D alata*, the average amount of N exported by tuber at harvest was 64 and 50 kg ha^{-1} in the forest and the savannah sites, respectively. The addition of fertilizer increased these values to 117 and 88 kg ha^{-1}, respectively. The amount of K exported in the meantime was 81 and 52 kg ha^{-1} in the forest and the savannah site, respectively, and it increased to 106 and 79 kg ha^{-1}, respectively, with fertilizer application. The AUC of shoot N and K contents were significantly increased at the forest than at the savannah site in both fertilized and non fertilized treatments, while significant difference was observed in the AUC of tuber N and K between both sites, but only in the non fertilized treatments (Table 4). The fertilizer applied increased only the AUC of tuber N content in the savannah site. In contrast to the forest site, the AUC of tuber N and K contents in the savannah site were interestingly higher than the N and K content of plant shoot (except for the N content in the fertilized savannah site). This might be linked to the direct uptake of N and K by tuber roots which develop in large numbers in this cultivar at this site (Hgaza, CSRS, *personal information*).

Table 4: Area under the curve values of shoot and tuber nitrogen (N) and potassium (K) contents in yam in 2002 expressed in [(kg ha^{-1})*days].

Site	Fertilizer	*D. alata*				*D. rotundata*			
		N		K		N		K	
		Shoot	Tuber	Shoot	Tuber	Shoot	Tuber	Shoot	Tuber
Forest	-	1 327	962	1 417	991	820	536	690	644
	+	1 737	1 069	1 598	992	1 019	744	688	730
Savannah	-	509	540	418	487	441	263	247	219

	+	1 040	885	493	605	1 196	818	554	426
Mean		*1 153*	*839*	*982*	*769*	*869*	*590*	*545*	*505*
s.e.d.		*305*	*113*	*293*	*198*	*215*	*129*	*148*	*205*

- Non-fertilized treatments; + Fertilized treatments; *s.e.d.*: standard error of the difference between means

In *D. rotundata*, the amount of N exported by tuber at harvest was 41 and 23 kg ha^{-1} in the forest and the savannah sites, respectively. Fertilizer application increased N exported by tuber to 56 and 55 kg ha^{-1}, respectively. The amount of K exported in the meantime was 40 and 20 kg ha^{-1} in the forest and the savannah, respectively, and it increased to 56 and 33 kg ha^{-1}, respectively, with fertilizer application. The AUC of N and K contents in the shoot and the tuber were significantly higher in the forest than in the savannah in the non fertilized treatments, while no difference was observed between both sites in the fertilized treatments (Table 5). The inorganic fertilization significantly increased the AUC of shoot N and K contents in the savannah site, but not in the forest site. The AUC of tuber N and K content were not affected by the application of inorganic fertilization in both sites.

5 DISCUSSION

5.1 Effects of natural soil fertility and rainfall on yams productivity: There were no major differences between the climates of the forest and the savannah sites in each season in terms of rainfall, temperature and solar radiation regimes. However, differences were observed between soil properties. Differences in the soil properties between the forest and the savannah reported in this study confirmed those already observed in the "V Baoulé" region (Koné *et al.*, 2008)

The lower soil organic matter, clay and exchangeable bases content of the savannah soil explained the poorer growth of yams in this site compared to the forest site. Indeed, the forest soil released significantly higher amounts of N and K during plant growth than the savannah soil, which might have boosted yam productivity. Given the relatively high available P content, typical of long term fallow soils of this region (Mordelet *et al.*, 1993), and the low levels of P needed by yams (O'Sullivan & Jenner, 2006; O'Sullivan & Ernest, 2008), we can state that P did not limit yam growth at either of the sites in this study.

In addition to N and K availability, rainfall amount and distribution affected yam productivity. The fresh tuber yield and the area under the curve (AUC) of tuber dry matter in both yam species studied were indeed greatest in the most humid growing season (2001). Moreover, the limited rainfall experienced during the growth phases II and III in 2002 probably explained the lower fresh tuber yield and shoot and tuber dry matter AUC in this growing season, supporting the report by Craufurd *et al.* (2001) that these phases are highly sensitive to water stress. This water limitation was more marked in *D. rotundata* compared to *D. alata*, suggesting greater sensitivity of the former species to water stress.

5.2 Effects of inorganic fertilizer on yam productivity: We applied large amounts of N and K in the fertilizer since these are the nutrients most limiting yam productivity (Degras, 1993; O'Sullivan & Jenner, 2006; O'Sullivan & Ernest, 2007; O'Sullivan & Ernest, 2008). In contrast, phosphorus was applied in low amounts as P demand by yams is low (Vander Zaag *et al.*, 1980). This was confirmed by the amount of P found in the shoot and tuber observed in our study (< 5 kg ha^{-1}) (data not shown).

The limited response of yam fresh tuber yield to inorganic fertilizer confirmed earlier observations in different yam producing areas (Gooding, 1971; Koli, 1973; Azih, 1976; Lugo *et al.*, 1993; Sotomayor-Ramirez *et al.*, 2003; O'Sullivan & Ernest, 2008). In contrast to the fresh tuber yield, the shoot dry matter (DM) increased following the application of inorganic fertilizer.. This was the case in *D. alata* in 2001 in both sites and in *D. rotundata* in the savannah site in 2001 and 2002. In *D. alata* however, this increase in shoot DM was not reflected in tuber DM increase, suggesting possible physiological disorders associated with the inorganic fertilizer. These disorders could be due to an imbalance in N and K content in the added fertilizer, possibly providing too much N in comparison to K. In potatoes, for example, a high level of nitrogen fertilization results in stronger development of shoots and a reduction of tuber yield due to a delay in tuber bulking and a smaller harvest index (Biemond & Vos, 1992), while on the other hand, K application improves the transfer of assimilates to the tubers (Marschner, 1995). For yams, Enyi (1972) observed that K application increased *D. esculenta* yield by increasing tuber bulking rate as well as bulking duration phase through induction of earlier tuber initiation.

The amounts of N found in the shoot and tuber of both yam species observed in our study were in the range of those observed by (Obigbesan & Agboola, 1978), whereas the K contents were rather low compared to those reported by these authors. Since the inorganic fertilizer increased N contents more strongly in shoot and tuber compared to the K contents, we conclude that K was probably more limiting to growth than N.

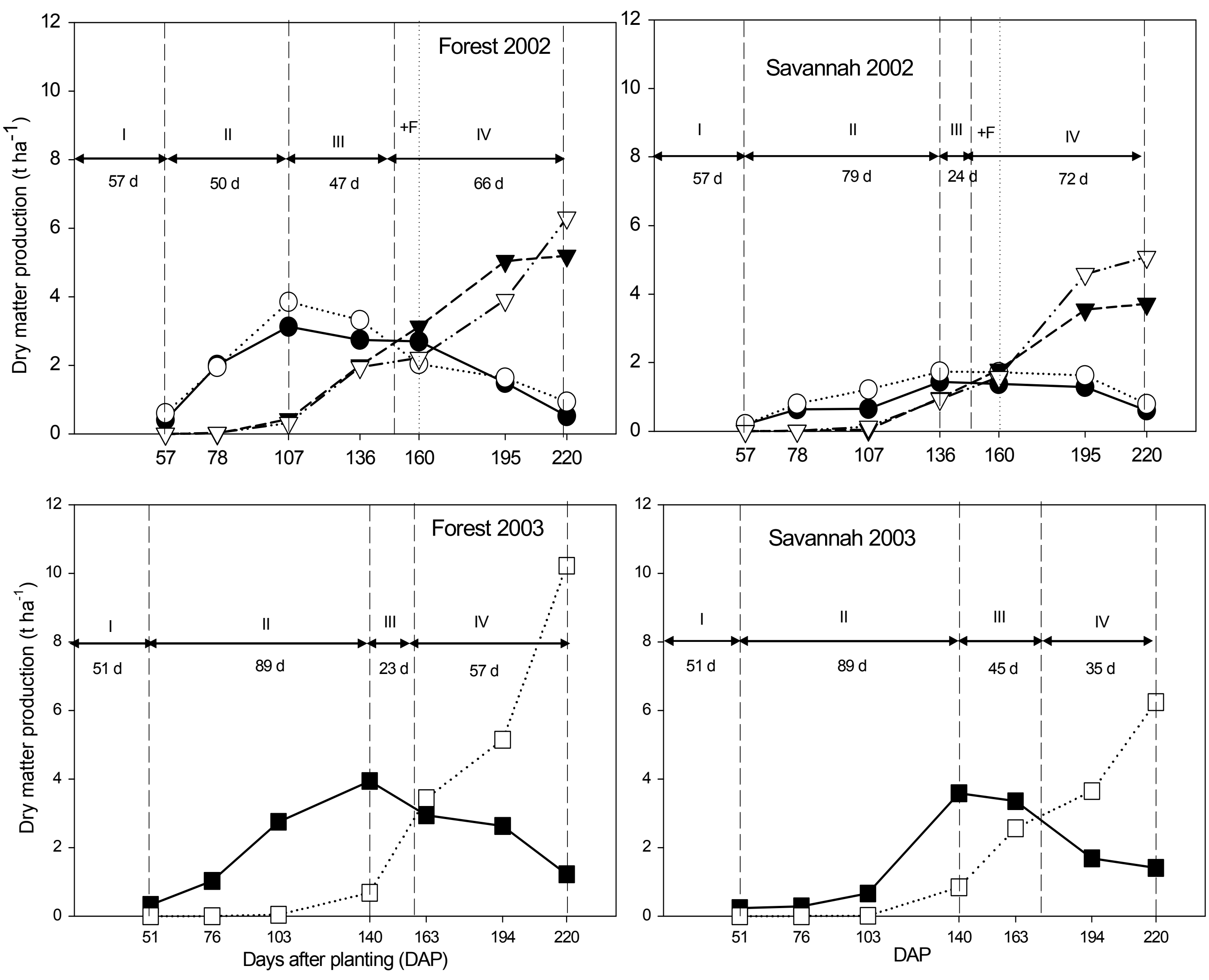

Figure 3: Growth phases of *Dioscorea alata* distinguished as a function of shoot and tuber biomass production. In 2002, (○) and (●) represent shoot dry matter production for fertilized and non fertilized treatments respectively, ( ) and (▼) represent tuber dry matter for fertilized and non fertilized treatments respectively. In 2003, (■) and (□) represent the dry matter in the shoot and the tuber respectively. I, II, III and IV indicate the different growth phases while the numbers indicate the duration of the different phases in

days. + F indicates the delay in the end of the growth phase III following fertilizer application

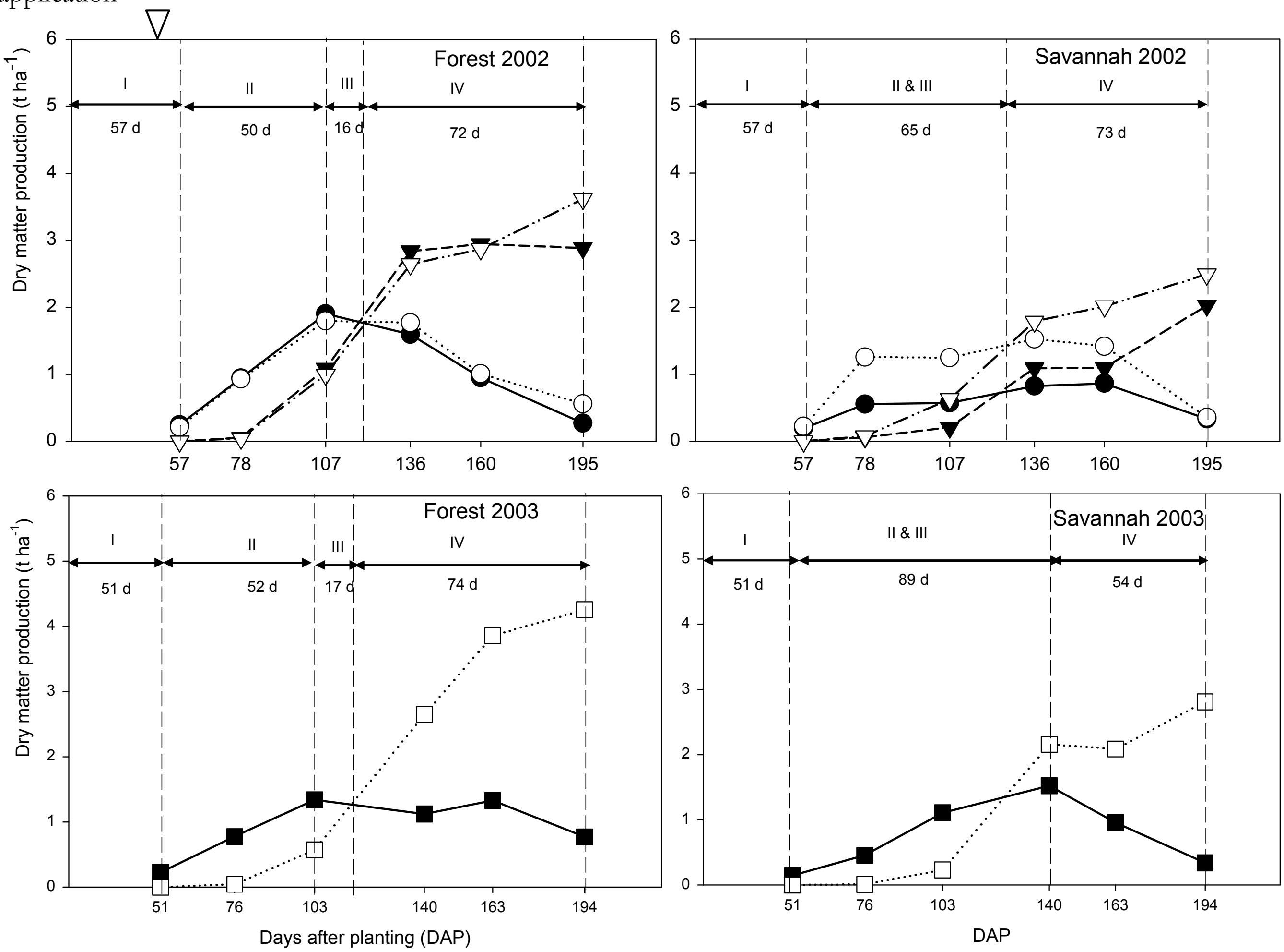

Figure 4: Growth Phases of *D. rotundata* distinguished as a function of shoot and tuber biomass production. In 2002, (○) and (●) represent shoot dry matter production for fertilized and non fertilized treatments respectively, ( ) and (▼) represent tuber dry matter for fertilized and non fertilized treatments respectively. In 2003, (■) and (□) represent the dry matter in the shoot and the tuber respectively. I, II, III and IV indicate the different growth phases while the numbers indicate the duration of the different phases in days.

5.3 Response of yam speciesD. alata and D. rotundata to low soil fertility: *D. alata* had higher fresh tuber yield, shoot and tuber AUC than *D. rotundata*, both in the fertile and in the non-fertile soils. This confirms the better adaptation of *D. alata* to low fertility soils as already reported by Kowal and Kassam (1978). This better adaptation might be explained by a higher growth plasticity of *D. alata* when placed in a stressful environment. This hypothesis is supported by the changes in the onset of the different growth phases of *D. alata* when grown in the savannah soil (increase in phase II length) resulting in low shoot and tuber AUC. On the contrary, the input of nutrients resulted in an increase in the duration of phase III and the shoot AUC. The better adaptation of *D. alata* can also be explained by the important development of tuber roots (Hgaza, CSRS, *personal information*) which probably contributed to nutrient uptake late in the season in the savannah site. On the contrary the growth phases of *D. rotundata* did not change from the forest to the savannah sites and from year to year. This suggests that the development of *D. rotundata* is less variable, allowing less adaptation to stressful conditions.

5.4 Management of soil fertility in yam production systems: Our results, together with earlier studies, allow us to suggest some management practices for maintaining and improving soil fertility in yam production systems. Since soil organic matter plays a fundamental role in yam productivity, which is not compensated in a soil with low organic content by the addition of inorganic fertilizers, all management practices that will favour the maintenance or build up of soil organic content must be evaluated in yam production systems. These are manure application (Kowal & Kassam, 1978; Budelman, 1989), yam planting after a green manure legume (Carsky *et al.*, 2001), and intercropping of yams and legumes (Budelman, 1990a; O'Sullivan, 2008). Since preparing mounds at planting probably results in a flush of N mineralization that can not be used by the plant, and in disturbance of the arbuscular myccorhizal fungal hyphae (Jansa *et al.*, 2006), which would limit their later beneficial effects on plant nutrition, we suggest to minimize soil preparation at the time of planting. Systems as those practiced in Oceania where yam tubers are planted in small holes and covered with soil (O'Sullivan & Ernest, 2008) might allow better nutrient use efficiency, and could also be tested in West Africa. Finally, in very low fertility sites, where organic matter inputs are not possible, the best option is to grow adapted germplasm such as the *D. alata* cultivar that was used in this study.

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