International Journal of Botany

ISSN: 1811-9700

science alert

ANSInet
an open access publisher
http://ansinet.com

OPEN ACCESS International Journal of Botany

ISSN 1811-9700
DOI: 10.3923/ijb.2017.115.125

Research Article

Dry Matter Production, Biomass Partitioning and Seed Setting Efficiencies in Early- and Late-rainy Season Cowpea in the Rainforest Agroecology of South-West Nigeria

S.O. Agele, I.K. Oyewusi, O.P. Aiyelari and I.B. Famuwagun

Department of Crop, Soil and Pest Management, Federal University of Technology, Akure, Nigeria

Abstract

Background and Objective: The prevailing environmental factors of the early- and late-rainy seasons are critical factors in the processes of yield determination in cowpea. It is hypothesized that crop growth rate (B), dry matter partitioning to pods/seeds (P) and seed setting efficiency of cowpea are affected by the prevailing weather of the growing seasons. These were quantitatively described among cowpea varieties sown as early- and late-rainy season crops using a simple physiological model. **Materials and Methods:** Field experiments were conducted to evaluate the responses of growth and yield of cowpea varieties to the prevailing soil and weather conditions of the early- and late-rainy seasons between 2014 and 2015 at in a rainforest zone of South West Nigeria. The parameters of the physiological model were evaluated using data obtained from field evaluation of cowpea varieties. Regression coefficient (R^2) were worked out among cowpea growth and yield components and accumulated seasonal rainfall, minimum temperatures, growing degree days (GDD) and vapour pressure deficits (VPD). **Results:** Significant differences were obtained among cowpea varieties for crop growth rates (CGR), dry matter partitioning coefficient (P), minimum assimilate required per seed (MAR), seed setting efficiency (Ef) and harvest index (HI). Dry matter partitioning coefficient was best for IT98K-573-2-1 compared with other varieties. Although, the duration of the reproductive growth phase (ReGRc) was shorter in the late season, dry matter partitioning, seed set efficiency (EF), pod and seed yields were significantly better for late season cowpea. The regression equations showed that about 40% of yield components in late season cowpea can be explained by cumulative seasonal rainfall, growing degree days, minimum temperatures and atmospheric dryness (VPD). **Conclusion:** Findings can find use to fine tune crop growth models for the prediction of crop productivity and weather dependent production risks of the sowing seasons in the humid tropics. It is concluded that the weather conditions of the early- and late-rainy seasons are critical factors in the processes of determination of growth and yield characters of cowpea.

Key words: Physiological model, biomass, partitioning, seed set, efficiency, reproductive structures

Citation: S.O. Agele, I.K. Oyewusi, O.P. Aiyelari and I.B. Famuwagun, 2017. Dry matter production, biomass partitioning and seed setting efficiencies in early- and late-rainy season cowpea in the rainforest agroecology of South-West Nigeria. Int. J. Bot., 13: 115-125.

Corresponding Author: S.O. Agele, Department of Crop, Soil and Pest Management, Federal University of Technology, Akure, Nigeria Tel: + 234 803 5784 761

Copyright: © 2017 S.O. Agele *et al.* This is an open access article distributed under the terms of the creative commons attribution License, which permits unrestricted use, distribution and reproduction in any medium, provided the original author and source are credited.

Competing Interest: The authors have declared that no competing interest exists.

Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Cowpea (*Vigna unguiculata* L. Walp), is an important food legume of the tropics, plays a major role in human and livestock nutrition. Its edible seeds provide cheap alternative source of protein compared to animal protein. Cowpea is a major grain legume crop in tropical and subtropical regions characterized by large seasonal variations in soil moisture regimes, soil and air temperatures[1,2]. The humid rainforest zone of Nigeria is characterized by bimodal pattern of rainfall distribution with more variability of the average date of onset of the rains than its cessation[2,3,4]. The average daily temperatures during the growing seasons varies by only a few degrees from 27-29°C and day length on 21, June varies from 13.37-13.68 h/day at 8 and 13°N[5-7]. Cropping opportunities are provided by the earlier and later parts of the rainy season. The optimal sowing date of cowpea in the rainforest zone of Nigeria is at the beginning of the rains and not when rainfall has fully established while the crop's reproductive growth phase particularly seed maturity falls into the short dry spell which marks the end of the first modal rainfall[8,9]. The dry spell is characterized by abundant sunshine and negligible cloud overcast sky. The late sowing season falls within the second mode of rainfall distribution (terminal drought situation) between August/September and December, is occasioned by limiting soil moisture status, extreme high soil temperatures, high irradiance and atmospheric vapour deficits[10,11]. There is therefore great need to examine traits associated with adaptation in cowpea varieties to environmental conditions of the sowing seasons.

Crop simulation models calculate or predict crop yield as a function of weather and soil conditions, crop management scenarios, crop genetic coefficients and potential production determined by solar radiation and temperature as input, simulate growth and development and plant carbon balance (photosynthesis, respiration, partitioning)[11-13]. More sophisticated models may also consider yield reductions due to, limited water, limited nitrogen and other nutrients ,insects, diseases and weeds. The prevailing environmental factors of a sowing season may impose limitations on growth and processes of yield determination in crops. The effects of environmental alterations due to changing temperature, light intensity, water availability and vapour pressure deficit on plant growth rates, dry matter production and tissue water relations has been reported[12,14]. Gillett *et al.*[15] and Vega *et al.*[13] reported the effects of temperature on dry matter partitioning while Duncan *et al.*[16] and Sato *et al.*[17] noted strong cultivar by environment interactions on plant growth rate. Although, the partitioning of biomass to fruits is important to yield in crops, its physiological regulation is poorly understood[18,13]. A simple physiological model developed by Duncan *et al.*[16] can be adapted to overcome the constraints imposed by the prevailing environmental factors of the growing seasons on crop growth and yield. This model states that:

$$Y = RD * P * CGR \quad (1)$$

where, Y is pod or fruit yields, RD is reproductive duration, P is the ratio of photosynthetic assimilates partitioned to reproductive sinks compared with the sources, referred to as partitioning coefficient, CRG is crop growth rate, PGR is pod growth rate.

Other sets of functions are used to relate dry matter partitioning, yield, crop growth or development rate of in crops to environmental factors[15,19-21]. Heuvelink[20] and Agele and Olabomi[11] reported that information on the dynamics of dry matter production and distribution extended with detailed climatic data are still very scarce for tropical crops.

Charles-Edwards[22], Egli and Zhen-Wen[23] and Ball *et al.*[24] proposed that each reproductive structure requires a minimum rate of assimilate supply during its initial development to sustain growth:

$$SNP = PGRc\ P_R\ \lambda^{-1} \quad (2)$$

This proposition emphasizes the role of carbon as an energy source and its adequacy to integrate effects of other resources[11,13].

Pod yields of cowpea are attributed to a number of factors[25,26,9]. In crops, the prevailing environmental factors of a sowing season may impose limitations on growth and processes of yield determination. It is hypothesize that crop growth (B), dry matter partitioning to seed (P) and yield of cowpea may differ between sowing seasons. Studies should be conducted to evaluate this hypothesis with the aim of generating information on seasonal weather conditions of crop growth and yield.

The concept of thermal times describes crop development[27]. The response of crop development to temperature regimes is important to the description of the rate of progression towards key events, for example, onset of flowering and harvest index[28]. Accumulated heat units (thermal time) is calculated from temperature coefficients for individual crops. The general cowpea breeding scheme includes evaluating a number of genotypes at various stages and testing selected ones at several locations and seasons across the years. Yield is a complex quantitative character and

is generally influenced by environment, climate and soil fluctuations, hence, the selection for superior genotypes is based on yield at a single location may not be very effective[29]. Thus, evaluation of cowpea genotypes for stability of performance under varying agro-ecologies of soil and climatic conditions is an essential part of crop breeding program[9].

This study appraised the effects of soil and weather factors especially at the pre- and post-flowering growth phases on functional traits and yield adaptation of selected cowpea varieties planted in the early- and late-seasons in South West Nigeria. The study provided information on the values of fitness of the humid rainforest agro ecological zones for screening cowpea cultivars for adaptation to environmental conditions of the sowing seasons and the potentials for expansion of production for increased yield of cowpea.

It is hypothesized that crop growth rate (B), dry matter partitioning to fruits (P) and yields of cowpea are affected by weather conditions of the sowing seasons. Experiments were conducted to quantitatively describe the effects of prevailing environmental factors of the early- and late-rainy seasons on the processes of yield determination in cowpea in terms of biomass production and dry matter partitioning to seed using simple physiological models.

MATERIALS AND METHODS

Field experiments were conducted to evaluate the responses of growth and yield of cowpea varieties to the prevailing soil and weather conditions of the early- and late-rainy seasons between 2014 and 2015 at in a rainforest zone of South West Nigeria. The early- and late-rainy season crops were sown in April and September of 2014 and 2015 at the Teaching and Research Farm of the Federal University of Technology, Akure, Nigeria.

The parameters of the physiological model were evaluated using the data obtained from field evaluation of cowpea varieties on growth, seed yield and yield components of the crop were deployed to evaluate parameters of the physiological model. Therefore, the limitations imposed by the prevailing environmental factors of the sowing seasons on the processes of yield determination in cowpea in terms of biomass production and dry matter partitioning to seed (P) was quantitatively described using a simple physiological model. It is hypothesized that crop growth rate (B), dry matter partitioning to pods/seeds (P) of cowpea are affected by the prevailing weather conditions of the growing seasons. The parameters of the physiological model were evaluated using data obtained from field evaluation of cowpea varieties. The number of days from sowing to flowering (DFF) and pod maturity (DH) were noted. At pod maturity between 60-80 days after sowing, the cowpea plants on each plot were harvested.

Based on Duncan *et al.*[16] model which approximate crop growth to be linear, as it is stated as Eq. 1.

The model parameters were evaluated. where Y is pod or fruit yields, RD is reproductive duration, P is the ratio of photosynthetic assimilates partitioned to reproductive sinks compared with the sources, referred to as partitioning coefficient, CRG is crop growth rate (CGR = T/DH), PGR is pod growth rate (PGR = Y/RD). The harvest index was calculated as the ratio of seed weight to total shoot biomass. Some other codes used are defined as follows: DFF: Number of days to 50% flowering, DH is number of days to maturity, RD is reproductive duration (RD = DH-DFF), Y is pod weight (kg ha^{-1}), H is crop residue or haulm weight which includes leaves and stem, T is total biomass (T =Y+H), HI is harvest index, Ef is seed set efficiency, P_R is dry matter partitioning efficiency, P is partitioning coefficient is (P is the ratio of pod growth rate to crop growth rate, P = PGR/CGR).

Charles-Edwards[22], Egli and Zhen-Wen[23] and Ball *et al.*[24] proposed that each reproductive structure requires a minimum rate of assimilate supply during its initial development to sustain growth:

$$PNP = PGRc\ P_R\ \lambda^{-1} \quad (3)$$

$$ReGRc = Prc^{*}P_R \quad (4)$$

$$Ef = \frac{SNP}{ReGRc} \quad (5)$$

$$\lambda = \frac{1}{Ef} \quad (6)$$

$$PRc = \frac{ReGRc}{PRc} \quad (7)$$

where, PRc is plant growth rate (vegetative growth phase), PR is the proportion of growth partitioned to reproductive organs PNP is number of pod per plant, ReGRc is plant growth rate during the critical period for pod/seed set, λ is the minimum assimilate requirement per seed.

Plant growth rate (vegetative growth phase) PGRc, the proportion of growth partitioned to reproductive organs (P_R) and the minimum assimilate requirement per fruit (λ) were

computed. Crop growth rates (CGRc) were calculated over the entire crop growth duration. The growth rate during the critical period for fruit set (ReGRc) was estimated as the ratio between accumulated biomass in shoots or reproductive structures and the duration of the period, assuming reproductive biomass is negligible at the beginning of the critical period. Seed set efficiency (Ef) was computed from the ratio of PNP and ReGRc while the minimum assimilate requirement per seed, (l: mg/fruit/day) was estimated as the inverse of the predicted maximum efficiency in seed set[11,13]. The growth, seed yield and yield components of cowpea varieties were taken. Growth indices measured were vine length, number of leaves, number of branches, number of peduncles, root length, root weight, number of nodules, size of nodules and weight of nodules. At the reproductive stage, parameters taken were, days to 50% flowering, number and weight of pod , number of seeds per plant. The duration (days) of vegetative growth, onset of podding to physiological maturity were observed and recorded in addition to the duration of reproductive growth phase. At maturity, parameters taken were, total shoot biomass, 100 seed weight, chlorophyll concentration, crude protein content of the leaves. Total dry weight of shoot, dry matter partitioning (leaf, stem and root dry weight) was recorded. The samples were separated into shoot and root biomass, weighed and oven dried to constant weight at 105 degrees for determination of dry matter content. Collection of data started 3 weeks after planting. Ten plants on which the growth parameters were taken were randomly chosen and tagged on each plot from 2 m^2 at the centre of each plot. At physiological maturity, data were collected on plot basis for agronomic characters.

The response of crop development to temperature regimes is important to the description of the rate of progression towards key events, for example, onset of flowering and harvest index[26,27]. The concept of thermal time describes crop development according to McMaster and Wilhelm[27] and Bell and Wright[28], proposed that the response of crop development to temperature regimes is important to the description of the rate of progression towards key events, for example, onset of flowering. Accumulated heat units (thermal time) is calculated from temperature coefficient for individual crops. Thermal times (degree days: °C d) for the phenological phases were calculated from the daily maximum (T_{max}) and minimum (T_{min}) temperatures measured at the Meteorological station.

Cardinal temperatures of Tb 8°C, T_{opt} 32°C, T_{max} 42°C were assumed in the calculation of heat unit accumulation measured as growing degree days (GDD)[30] using equation of McMaster and Wilhelm[27].

The calculation of the GDD considers a linear function between the base and optimum temperatures and between optimum and maximum temperatures. The degree days calculated and summed over duration of the experiment in each sowing season gave thermal time accumulated during maize growth.

Growing degree days (GDD) value was computed during the growth of maize using the following algorithm:

$$GDD = \sum\left(\frac{[T_{max}+T_{opt}] * day_{1-x}}{2}\right)-Tb \quad (8)$$

where, T_{max} represents maximum air temperature, T_{opt} represents optimum temperature and T_b represents base (minimum) temperature for maize and 1-x represents time intervals during which measurements were made (day one to the day last).

Data on meteorological variables such as rainfall amount, minimum and maximum temperatures and vapour pressure deficit (VPD) were obtained from the Meteorological Station of the Department of Meteorology, Federal University of Technology, Akure, Nigeria. These weather factors were regressed against plant attributes such as shoot biomass, number of seed, reproductive duration, days to 50% flowering and seed yield per plant.

RESULTS

Biomass production and partitioning, seed set and seed yield among cowpea varieties in the early- and late-season: The growth and yield characters of cowpea varieties differed between the early (April-July) and late (September-December) rainy season crops (Table 1). Crop growth rate (CGR) especially the growth rate during reproductive phase ($ReGR_C$), a critical period for seed set was significantly faster for early-rainy season cowpea in addition to the longer time for the respective vegetative and reproductive growth phases. The fraction of biomass allocated to seed was higher in late season crop despite the insufficient soil moisture during the reproductive growth phase. Dry matter partitioning coefficient (P) was best for IT98K-573-2-1, this variety also produced significantly higher pod yields and harvest index (HI) compared with other varieties. Cowpea varieties IT98K-573-2-1 and Oloyin Brown, had significantly higher values of shoot biomass, pod weight, numbers of pods and seeds per plant, seed yield and seed weight were produced. The effects of biomass and ReGRc on the number of pods and seeds

Table 1: Biomass production and partitioning, seed set and seed yield in cowpea varieties as early- and late-rainy season crops

Parameters	Dtm	RD	Shoot biomass	CGR	PGR	(P_R)	ReGRC (mg g^{-1}/day)	Ef	MAR (λ)	Number of seeds/plant	Number of pods/plant	Pod yield (kg ha^{-1})	HI
Varieties													
IT98K-205-8	62.30	8.40	87.47	9.77	10.55	1.011	9.42	0.96	0.90	9.75	33.91	892.70	6.98
Ife brown	57.20	8.10	99.12	9.65	10.56	1.024	9.32	0.96	0.87	9.73	33.66	879.90	7.00
IT96D-610	62.30	8.10	94.66	9.30	10.67	1.063	8.96	0.99	0.91	9.69	33.41	882.20	7.16
IT98K-573-2-1	64.20	7.70	90.66	9.24	11.73	1.085	8.87	1.04	0.94	10.00	33.39	976.50	7.37
Oloyin brown	66.20	7.80	103.90	8.92	10.74	1.099	8.52	1.03	0.93	9.78	32.91	923.40	7.48
IT97K-568-18	69.50	8.00	82.61	8.89	10.88	1.173	8.47	0.85	0.85	9.73	33.16	902.70	8.07
LSD (0.05)	1.22	0.32	1.58	0.35	0.23	0.120	0.43	0.11	0.10	0.11	0.39	13.80	0.29
Seasons													
Early-rainy season	94.80	11.60	142.80	12.90	13.05	1.020	12.71	0.99	1.02	12.64	37.00	1239.80	8.46
Late-rainy season	75.20	9.20	103.70	11.63	15.71	1.330	11.60	1.16	0.86	13.48	38.00	1154.90	10.70
LSD (0.05)	1.58	0.50	2.14	0.41	0.55	0.190	0.41	0.20	0.15	0.32	0.61	3.27	0.52

Dtm: Days to maturity, RD: Reproductive duration, CGR: Crop growth rate, PGR: Pod growth rate, P_R: Dry matter partitioning coefficient, $ReGR_C$: Plant growth rate during critical period for seed set, Ef: Seed set efficiency, MAR: Minimum assimilate required per seed, HI: Harvest index

produced per plant seemed to be exerted through current assimilate partitioning during the critical period. The varieties which exhibited high Ef were also characterized by higher partitioning efficiency and assimilate demand from the larger number of simultaneously developing sinks. This trend was obtained for varieties having high number of pods and seeds per pod. Reproductive characters such as reproductive partitioning (P_R) and seed set efficiency (Ef) in terms of number of pods and seeds per unit of reproductive growth were best for late season cowpea despite the insufficient soil moisture status shorter duration of reproductive growth phase (Table 2). The inherent potentials of the six tested cowpea varieties appeared to be remarkably expressed in the late-rainy season (September-December). The reproductive characters such as reproductive partitioning (P_R) and seed set efficiency (Ef), the number of pods and seeds per unit of reproductive growth were significantly higher for late season compared with the early-rainy season cowpea. The duration of the reproductive growth phase (ReGRc) is particularly critical period for pod and seed number determination. Early-rainy season cowpea took more time to flower and complete reproductive process while the time to first flowering was delayed from early to late season while reproductive duration on average was shorter in the late-season than the early season crop. Pod yield was higher in the rainy season, however, seed yield and harvest index were lower compared with the late season crop (Table 2). Significant interactions were obtained for variety and season of sowing for most biomass production and partitioning and seed yield characters evaluated for cowpea (Table 3). These interactions were reflected in 8 and 15% decline in yield between the early- and late-rainy season cowpea.

Association of growing degree days (GDD), cumulative seasonal rainfall, minimum temperature and vapour pressure deficits (VPD) with biomass production, partitioning and seed yield production in the early- and late-season cowpea: Regression equations were worked out between cowpea growth and seed yield characteristics and prevailing weather conditions in terms of cumulative seasonal rainfall, minimum temperature, vapour pressure deficit (VPD) and thermal time requirements/growing degree days (GDD) for the respective early- and late-rainy season cowpea (Table 4 and 5). These relationships were characterized by variable regression coefficients (R^2). The regression coefficients (R^2) show that on the average, about 40% of seed yield components in early- and late-season cowpea can be explained by cumulative growing degree days (thermal time

Table 2: Effects of season on the biomass production and partitioning, seed set efficiency and seed yield of cowpea varieties

Varieties	Dtm	RD	Shoot biomass	CGR	PGR	(P_R)	ReGRC (mg g^{-1}/day)	Ef	MAR (λ)	Number of seeds/plant	Number of pods/plant	Pod yield (kg ha^{-1})	HI
Early season													
IT98K-205-8	83.00	12.00	135.0	13.55	12.21	0.90	13.55	0.86	1.16	11.70	34.00	1013.8	7.48
Ife brown	95.00	11.00	143.2	12.93	13.04	1.09	11.78	0.98	1.02	10.80	31.00	981.4	7.85
IT96D-610	87.00	11.00	142.4	12.95	12.58	0.97	12.95	0.97	1.04	12.50	37.00	1094.3	7.68
IT98K-573-2-1	109.00	12.00	162.3	13.53	16.52	1.22	13.52	1.07	0.93	14.50	43.00	1801.2	11.10
Oloyin brown	92.00	11.00	149.6	14.96	14.22	0.95	14.96	0.92	1.09	13.70	40.00	1308.4	8.75
IT97K-568-18	103.00	13.00	123.7	9.52	9.53	1.00	9.52	1.14	0.88	12.60	37.00	1242.0	7.93
LSD (0.05)	1.98	3.30	10.5	2.14	0.41	0.55	0.52	0.20	0.15	0.14	0.32	77.7	0.19
Late season													
IT98K-205-8	70.00	10.00	100.4	10.40	10.64	10.60	10.04	1.23	0.82	12.30	32.00	872.5	8.69
Ife brown	66.00	8.00	98.4	12.30	14.92	1.21	12.30	1.04	0.96	123.00	35.00	984.6	10.00
IT96D-610	73.00	9.00	109.6	12.18	16.66	1.37	12.18	1.16	0.86	14.20	33.00	1155.8	11.10
IT98K-573-2-1	76.00	9.00	112.4	11.87	17.33	1.41	11.67	1.15	0.88	12.80	41.00	1216.2	12.10
Oloyin brown	84.00	10.00	122.5	12.25	19.29	1.57	12.25	1.19	0.83	14.70	46.00	1620.3	13.20
IT97K-568-18	82.00	9.00	100.6	11.18	15.44	1.38	11.18	1.19	0.83	13.40	38.00	1081.1	10.70
LSD (0.05)	1.85	0.61	9.2	0.66	1.19	0.29	0.66	0.18	0.16	0.66	2.24	61.3	0.86

DTM: Days to maturity, RD: Reproductive duration, CGR: Crop growth rate, PGR: Pod growth rate, P_R: Partitioning coefficient, $ReGR_C$: Plant growth rate during the critical period for seed set, Ef: Seed set efficiency, MAR: Minimum assimilate required per seed, HI: Harvest index

Table 3: Variety and season interaction on biomass production and partitioning, seed set efficiency and seed yield in cowpea

Varieties	Dtm	RD	Shoot biomass	CGR	PGR	(P_R)	ReGRC (mg g^{-1}/day)	Ef	MAR (λ)	Number of seeds/plant	Number of pods/plant	Pod yield (kg ha^{-1})	HI
IT98K-205-8	76.5	11.0	118.0	12.0	11.0	1.2	11.8	1.05	0.99	12.0	33.00	943.2	8.09
Ife brown	80.5	10.0	121.0	13.0	14.0	1.2	12.0	1.01	0.99	12.0	33.00	983.8	8.92
IT96D-610	80.0	10.0	126.0	13.0	15.0	1.2	12.6	1.07	0.95	13.0	35.00	1125.0	9.39
IT98K-573-2-1	92.5	11.0	137.0	13.0	17.0	1.3	12.6	1.11	0.91	14.0	42.00	1509.0	11.60
Oloyin brown	88.0	11.0	136.0	14.0	17.0	1.3	13.6	1.06	0.96	14.0	43.00	1464.0	11.00
IT97K-568-18	69.5	10.0	96.3	12.0	14.0	1.1	11.6	0.92	0.87	12.0	32.00	953.6	8.50
Variety (Var)	2.0	1.9	9.8	1.4	0.8	0.4	0.4	0.90	0.16	0.4	1.28	9.5	0.53
Season (Sn)	1.6	0.5	2.1	0.4	0.6	0.2	0.4	0.20	0.15	0.3	0.61	3.3	0.51
Var×Sn	*	Ns	*	ns	ns	*	ns	*	ns	*	*	*	*

^{ns}Not significant at $p<0.05$, *Significant at $p<0.05$, DTM: Days to maturity, RD: Reproductive duration, CGR4: Crop growth rate, PGR: Pod growth rate, P_R: Partitioning coefficient, $ReGR_C$: Plant growth rate during the critical period for seed set, Ef: Seed set efficiency, MAR: Minimum assimilate required per seed, HI: Harvest index,

Table 4: Relationship between some weather variables and cowpea growth and seed yield characters (Early season crop)

Parameters	Regression equation	R^2	Parameters	Regression equation	R^2	Parameters	Regression equation	R^2
C/rain and HI	Y = 3450x+119.7	0.88	M/T and HI	Y = 3450x+119.7	0.88	VPD and HI	Y = -14.37x+5.28	0.62
C/rain and NOS	Y = 48.55x+122.0	0.61	M/T and NOS	Y = 48.55x+122.0	0.61	VPD and NOS	Y = 0.283x-0.557	0.92
C/rain and S/WT	Y = 9.108x+474.4	0.56	M/T and S/WT	Y = 9.108x+474.4	0.56	VPD and S/WT	Y = -0.002x+4.261	0.79
C/rain and 100 S/WT	Y = 29.77x+283.1	0.69	M/T and 100 S/WT	Y = 29.77x+283.1	0.69	VPD and 100 S/WT	Y = -0.067x+4.421	0.75
C/rain and RD	Y = 35.89x+239.2	0.62	M/T and RD	Y = 35.89x+239.2	0.62	VPD and RD	Y = 0.168x+0.970	0.41
C/rain and 50% Flo	Y = 49.38x-2479	0.65	M/T and 50% Flo	Y = 49.38x-2479	0.65	VPD and 50% Flo	Y = 0.027x+4.659	0.02
C/rain and (Ef)	Y = 399.0x+340.1	0.52	M//T and Ef	Y = 399.0x+340.1	0.52	VPD and Ef	Y = -0.472x+3.318	0.02
C/rain and (λ)	Y = 712.3x+13.74	0.68	M//T and (λ)	Y = 712.3x+13.74	0.68	VPD and (λ)	Y = 0.343x+2.499	0.01
C/rain and (P_R)	Y = 445.6x+273.1	0.36	M//T and (P_R)	Y = 445.6x+273.1	0.36	VPD and (P_R)	Y = 0.995x+1.845	0.13

C/rain: Cumulative rainfall, M/T: Minimum temperature, VPD: Vapour pressure deficit. P_R: Dry matter partitioning, HI: Harvest index, NOS: Number of seed, S/WT: Seed weight, 100 S/WT: 100 seed weight, RD: Reproductive duration, 50% FLO: Days to 50% flowering, Ef: Seed set efficiency, λ: Minimum assimilate required per seed

Table 5: Relationship between some weather variables and cowpea growth and seed yield characters (late season crop)

Parameters	Regression equation	R^2	Parameters	Regression equation	R^2	Parameters	Regression equation	R^2	Parameters	Regression equation	R^2
GDD and (P_R)	Y = 2693.9x+2928.4	0.88	C/rain and HI	Y = 1159.5x126.29	0.84	M/T and HI	Y = -11.874x+25.224	0.76	VPD and HI	Y = 7.12x +1.08	0.65
GDD and HI	Y = -1515+11798	0.52	C/rain and NOS	Y = -47.529x+1017	0.90	M/T and NOS	Y = -0.4138x+27.272	0.73	VPD and NOS	Y = -0.2752x+6.1289	0.72
GDD and NOS	Y = -3.619x+5459	0.47	C/rain and S/WT	Y = 1.2858x-211.35	0.82	M/T and S/WT	Y = -00098x+26.271	0.72	VPD and S/WT	Y = -0.00063x+5.3494	0.76
GDD and S/WT	Y = -123.9x+4700	0.39	C/rain and 100 S/WT	Y = 17x+23.231	072	M/T and 100 S/WT	Y = -0.1657x+26.181	0.72	VPD and 100 S/WT	Y = -0.1305x+5.8984	0.53
GDD and 100 S/WT	Y = -272.1x+8866	0.65	C/rain and RD	Y = 50.388x-15.892	0.42	M/T and RD	Y = -3.44+29.803	0.43	VPD and RD	Y = -0.2418x+4.923	0.79
GDD and RD	Y = -118.0x+8866	0.65	C/rain and 50% Flo	Y = -9.2205x-24.573	0.85	M/T and 50% Flo	Y = -0.062x+25.084	0.83	VPD and 50% Flo	Y = -0.0575x+5.4731	0.75
GDD and 50% FLO	Y = -6730.9x+10158	0.65	C/rain and (Ef)	Y = 730.22x-407.89	0.30	M//T and Ef	Y = -2.6189x+26.67	0.47	VPD and Ef	Y = -0.787x+3.8798	0.54
GDD and (Ef)	Y = 2006x+4026	0.49	C/rain and (λ)	Y = 547.91x-46.779	0.51	M//T and (λ)	Y = 4.0954x+18.46	0.42	VPD and (λ)	Y = -2.7004x+5.0675	0.74
GDD and ((λ)	Y = -1143.2x+3794.1	0.74	Curain and (P_R)	Y = 234.7x+103.22	0.74	M//T and (P_R)	Y = -3.3672x+25.548	0.57	VPD and (P_R)	Y = -1.4228x+4.5223	0.74

GDD: Growing degree days, C/rain: Cumulative rainfall, M/T: Minimum temperature, VPD: Vapour pressure deficit, P_R: Dry matter partitioning, HI: Harvest index, NOS: Number of seed, S/WT: Seed weight, 100 S/WT: 100 seed weight, RD: Reproductive duration, 50% FLO: Days to 50% flowering, Ef: Seed set efficiency, λ: Minimum assimilate required per seed

requirements), cumulative seasonal rainfall, minimum temperatures and atmospheric dryness (vapour pressure deficit). There was strong positive correlation between cumulative rainfall and harvest index and a moderately strong positive correlation with number of seed yield characters. In contrast, in the late rainy season, there was a strong positive correlation between cumulative rainfall and harvest index, seed weight and dry matter partitioning (P_R) and while moderate correlation were found for minimum assimilate required per seed (λ). Specifically, GDD was strongly positively correlated with dry matter partitioning and moderately with seed set efficiency ($R^2 = 0.49$). The correlation between GDD and all other parameters were negative for the late season crop. In the late season crop, all the measured parameters were negatively correlated with minimum temperatures except minimum assimilate required per seed. The relationship between vapour pressure deficits (VPD) and yield characters in the early-rainy season showed weak negative correlation between VPD and reproductive duration (RD), seed set efficiency (Ef), minimum assimilate required per seed (λ) and dry matter partitioning (P_R). In contrast, in the late rainy season, there was a strong negative correlation between VPD and reproductive duration (RD), seed set efficiency (Ef), minimum assimilate required per seed (λ) and dry matter partitioning (P_R). The association of reproductive growth phases and thermal time differed between seasons, the relationship yielded higher R^2 in the late season cowpea. Significant interactions were obtained for variety and season for most of the biomass production and partitioning and seed yield characters evaluated for cowpea.

DISCUSSION

The parameters of a physiological model that describes process of crop yield determination from dry matter production and partitioning to reproductive structures were evaluated for cowpea varieties sown as early- and late-rainy season crops. The findings from the evaluation supported the hypothesis that the yield of cowpea sown in the early- and late-season cropping periods is due to differences in biomass production and partitioning to seed. Significant variations were found between seasons and among cowpea varieties with respect to crop a growth rates, dry matter partitioning and seed set efficiency and harvest index. The cowpea varieties differed in their efficiency for dry matter partitioning to reproductive sinks indicating variations in the efficiency of assimilate utilization for seed production. For example, dry matter partitioning and seed set efficiencies and seed yields were highest for IT98K-573-2-1. Saini and Westgate[31] and Agele and Agbi[9] attributed high crop yields under the low soil moisture and high temperatures of the late season to high assimilate partitioning. High assimilate partitioning therefore appeared as a desirable attribute for cowpea varietal adaptation to the environment of the study area.

Dry matter partitioning (P) may be a major cause of yield differences for cowpea between seasons of sowing. Despite lower biomass yields in the late season cowpea crop, assimilate partitioning was optimized. Poorer biomass partitioning observed in early-rainy season cowpea may contribute to its low yield despite the huge biomass produced. Dry matter partitioned into harvestable organs contribute to yield of crops, this underscore the importance promoting dry matter partitioning in crops[11,32]. In plants, the reproductive sinks compete for assimilate with the shoot thereby decreasing dry matter allocation to vegetative phase during seed development[9,33]. However, this phenomenon may be supplanted by translocation of stored assimilates produced prior to pod/seed production. Cowpea planted in the late-rainy season had significantly lower biomass but higher seed yields in addition to high harvest indices. The days to 50% flowering and the duration of reproductive growth were shorter for late season crops. In the late-rainy season, cowpea varieties were characterized by improved harvest index in addition to signified efficient biomass partitioning from the lower shoot biomass accumulated.

Earliness in maturity and shortened reproductive growth phase was obtained of the late rainy season which on average was shortened by about 2 days compared with the early-rainy season crop. Increasing intensities of soil moisture deficits and supra-optimal soil temperatures characterized late sowing season in the tropical rainforest environment and would have hastened crop growth rates and hence earliness to the attainment of reproductive phase. Earliness in plants is a possible mechanism for dehydration avoidance, characterized by shortened growth duration in addition to higher growth attributes and biomass accumulation across varieties and groups under stress and profound dry season conditions[9,31]. These assertions can explain the high biomass accumulation and seed yield production in the IT98K-573-2-1 and Oloyin Brown varieties as the best performing lines. The number of pods produced by plant depends on the ability of the plant to reduce abscission of potential and fertilize florets, an ability that is strongly related to the amount of dry matter accumulated before anthesis[34]. Low seed yield in field grown cowpea had been attributed to pests and diseases infestation, high fruit abortion and excessive vegetative growth at the expense of fruiting. Besides genotype and development stage of the plant, many growth conditions and internal regulation by the plant may affect seed yields[27].

Variations in soil moisture content and evaporative demand can be sources of differences in the efficiency of P and dry matter production and partitioning. The lower biomass accumulated and the faster crop growth rate in the late season cowpea suggests that canopy development is sensitive to high temperatures and soil moisture deficits, but this low value of crop growth rate was compensated for by the higher dry matter partitioning (p) to seeds. The temperature regimes during the pod production appeared to have enhanced dry matter in partitioning in cowpea[26,34]. The late season cowpea produced higher number of seeds and significantly higher seed yields compared with the rainy season crop. Number of seeds per pod increases with average solar radiation received. The high seed set of the late season crop may be attributed to efficiency of pollination and low pest and disease pressures and high solar radiation intensity. Higher number of seeds per pod might have resulted from the increases in the fraction of dry matter partitioned to the seed[11,20].

Significant differences were found for measured growth and yield traits among the cowpea varieties, this may imply differences in varietal adaptation to the weather conditions of the sowing seasons. The measured traits in the tested cowpea varieties are presumably the underlying indicators of varietal adaptation. However, the contributions of these traits to seed yield production appear to vary depending on growth phase when unfavourable environmental conditions were experienced[9]. The maintenance or improvement of HI is of critical importance for grain yield under terminal drought stress[35]. The increase in HI under drought condition was most probably associated with a higher remobilization of assimilates to fill the grains. Previous studies showed that the contribution of dry matter partitioning from stems and leaves to grain filling increased with the severity of drought stress[36]. In crops unfavorable growing environment condition such as drought imposes assimilate limitation, restricts pollination and decreases kernel set. In particular, prevailing environmental conditions after the initiation of reproductive growth can change floral development, alter pollination, or prevent seed filling and ultimately seed yield in crops[37]. In addition to the prevention of pollination presumably by low water potentials during grain filling can arrest ovary growth and cause embryo abortion[36]. Plants possess traits which are important to the survival and productivity parameters, these traits are also involved in setting tolerance limit to and confer increased productivity under variable weather conditions[37]. The identification and understanding of the values of these traits is important in the strategies to improve genotypic adaptation of crops in areas and seasons when varying degrees of soil moisture deficits and temperature extremes are encountered at some stages of crop growth cycle.

Regression equations were worked out between cowpea growth and seed yield characteristics and prevailing weather conditions in terms of cumulative rainfall, minimum temperature, VPD (evaporative demand) and growing degree days (GDD) (Table 4-5). These relationships were characterized by variable regression coefficients (R^2). The regression coefficients (R^2) show that on the average, about 40% of seed yield components in early- and late-season cowpea can be explained by cumulative growing degree days (thermal time requirements), cumulative seasonal rainfall, minimum temperatures and atmospheric dryness (vapour pressure deficit). Specifically, GDD was strongly positively correlated with dry matter partitioning ($R^2 = 0.88$) and moderately with seed set efficiency ($R^2 = 0.49$). Negative correlations were most times obtained between cumulative thermal requirements (accumulated growing degree days, GDD) vapour pressure deficits (VPD) and cumulative seasonal rainfall during the growing season and cowpea dry matter production and partitioning to seeds. In the late season, the cowpea cultivars exhibited more sensitivity to thermal time (growing degree days) in terms of growth duration and seed yield. Negative correlation between the amounts of rainfall received and seed yield characters of cowpea during the late season. Seed yield production is determined by the amount and spread of rainfall and hence soil moisture availability to a crop[2]. In the late season, declining status of soil water from rainfall and increasing intensities of stressful situations had profound effect on cowpea biomass and seed yield. High availability of soil moisture during the vegetative growth-prior to reproductive phase while low rainfall-enhanced status of soil moisture at pod setting and filling and seed maturity coincided with critical growth stages in cowpea. The varying degree of association between cowpea growth and seed yield attributes and the prevailing weather conditions obtained in this study can explain cowpea growth and productivity under variable weather conditions of the early- and late-rainy seasons. Also, the results of the regression relationships between cowpea performance and weather factors can serve as inputs in the development and fine-tuning crop growth models for the prediction of varietal adaptation and yield potentials and weather-dependent production risks associated with crop performance under the variable weather or environmental conditions of the sowing seasons in the humid rain forest zone of South West Nigeria.

CONCLUSION

The limitations imposed by the prevailing environmental factors of the sowing seasons on the processes of yield determination in cowpea in terms of biomass production and dry matter partitioning to seed (P) was quantitatively described using a simple physiological model. Date set generated from field study were deployed to establish functional relationships between some weather factors and seed yield characters of cowpea varieties. The results showed that the weather conditions of the early- and late-rainy seasons are critical factors in the processes of determination of growth and yield characters of cowpea.

SIGNIFICANCE STATEMENT

The study quantitatively described the limitations imposed by the prevailing environmental conditions of the sowing seasons on the processes of yield determination in cowpea using a simple physiological model. Findings showed that crop growth rate (B) and dry matter partitioning for pod and seed setting (P) of cowpea are affected by the prevailing weather conditions of the early- and late-rainy seasons. This information will be useful to fine tune crop growth models for the prediction of crop productivity potentials and weather dependent production risks in the respective early- and late-sowing seasons in the humid tropics.

REFERENCES

1. IPCC., 2007. Major assessment of climate change science. Intergovernmental Panel on Climate Change. https://www.ipcc.ch/pdf/assessment-report/ar4/wg2/ar4_wg2_full_report.pdf
2. Agele, S.O., G.O. Iremiren and S.O. Ojeniyi, 2011. Evapotranspiration, water use efficiency and yield of rainfed and irrigated tomato. Int. J. Agric. Biol., 13: 469-476.
3. Akinseye, F.M., S.O. Agele, P.C.S. Traore, M. Adam and A.M. Whitbread, 2016. Evaluation of the onset and length of growing season to define planting date-a case study for Mali (West Africa). Theor. Applied Climatol., 124: 973-983.
4. Omotosho, J.B., S.O. Agele, I.A. Balogun and E.A. Adefisan, 2013. Climate variability, crop-climate modeling and water ecophysiology research: Implications for plant's capacities for stress acclimation, yield production and food security. Global J. Plant Ecophysiol., 3: 56-69.
5. Agele, S.O., 2005. Biomass production and partitioning in early and late season tomato, in the humid South of Nigeria. AMSE: Model. Meas. Control, 66: 5-6.
6. Agele, S.O., G.O. Iremiren and S.O. Ojenigi, 1999. Effects of plant density and mulching on the performance of late-season tomato (*Lycopersicon esculentum*) in Southern Nigeria. J. Agric. Sci., 133: 397-402.
7. Wardlaw, I.F., 2002. Interaction between drought and chronic high temperature during kernel filling in wheat in a controlled environment. Ann. Bot., 90: 469-476.
8. IAR and T., 2000. 20th Package recommendation for food crops production in Western Nigeria. Institute of Agricultural Research and Training, Ibadan, Nigeria, pp: 60.
9. Agele, S.O. and M.A. Agbi, 2012. Growth and yield responses of selected cowpea (*Vigna unguiculata* L. Walp) cultivars to weather and soil factors of the sowing seasons. Res. Rev. BioSci., 7: 265-276.
10. Agele, S.O., A. Olufayo and G.O. Iremiren, 2002. Effects of season of sowing on water use and yield of tomato in the humid South of Nigeria. Afr. Crop Soc. J., 10: 231-237.
11. Agele, S.O. and A. Olabomi, 2010. Growth, fruit set efficiency and incidence of Blossom End Rot (BER) in *Capsicum* species grown in the rainy and dry seasons in a humid zone of Nigeria. Applied Trop. Agric., 15: 112-124.
12. Monteith, J.L., 1981. Does Light Limit Crop Production? In: Physiological Processes Limiting Plant Productivity, Johnson, C.B. (Ed.). Chapter 2, Butterworths, London, UK., ISBN-13: 9780408106498, pp: 23-38.
13. Vega, C.R.C., V.O. Sadras, F.H. Andrade and S.A. Uhart, 2000. Reproductive allometry in soybean, maize and sunflower. Ann. Bot., 85: 461-468.
14. Thompson, D.S., P.W. Smith, W.J. Davies and L.C. Ho, 1999. Interactions between environment, fruit water relations and fruit growth. Acta Hortic., 487: 65-70.
15. Gillett, A.G., N.M.J. Crout, D.T. Stokes, R. Sylvester-Bradley and R.K. Scott, 2001. An approach to modelling the effect of environmental and physiological factors upon biomass accumulation in winter wheat. J. Agric. Sci., 136: 369-381.
16. Duncan, W.G., D.E. McCloud, R.L. McGraw and K.J. Boote, 1978. Physiological aspects of peanut yield improvement. Crop Sci., 18: 1015-1020.
17. Sato, S., M.M. Peet and J.F. Thomas, 2002. Determining critical pre and post anthesis periods and physiological processes in *Lycopersicon esculentum* Mill. exposed to moderately elevated temperatures. J. Exp. Bot., 53: 1187-1195.
18. Hadley, P., E.H. Roberts, R.J. Summerfield and F.R. Minchin, 1983. A quantitative model of reproductive development in cowpea [*Vigna unguiculata* (L) Walp.] in relation to photoperiod and temperature and implications for screening germplasm. Ann. Bot., 51: 531-543.
19. De Koning, A.N.M., 1994. Development and dry matter distribution in glasshouse tomato: A quantitative approach. Ph.D. Thesis, Agricultural University, Wageningen, The Netherlands.

20. Heuvelink, E., 1995. Growth, development and yield of a tomato crop: Periodic destructive measurements in a greenhouse. Scient. Hortic., 61: 77-99.
21. Sakata, T. and A. Higashitani, 2008. Male sterility accompanied with abnormal anther development in plants-genes and environmental stresses with special reference to high temperature injury. Int. J. Plant Dev. Biol., 2: 42-51.
22. Charles-Edwards, D.A., 1984. On the ordered development of plants 1. An hypothesis. Ann. Bot., 53: 699-707.
23. Egli, D.B. and Y. Zhen-Wen, 1991. Crop growth rate and seeds per unit area in soybean. Crop Sci., 31: 439-442.
24. Ball, R.A., L.C. Purcell and E.D. Vories, 2000. Short-season soybean yield compensation in response to population and water regime. Crop Sci., 40: 1070-1078.
25. Ntare, B.R., J.H. Williams and B.J. Ndunguru, 1998. Effects of seasonal variation in temperature and cultivar on yield and yield determination of irrigated groundnut (*Arachis hypogaea*) during the dry season in the Sahel of West Africa. J. Agric. Sci., 131: 439-448.
26. Purseglove, J.W., 1988. Tropical crops: Dicotyledons. Longman, London, pp: 232.
27. McMaster, G.S. and W.W. Wilhelm, 1997. Growing degree-days: One equation, two interpretations. Agric. For. Meteorol., 87: 291-300.
28. Bell, M.J. and G.C. Wright, 1998. Groundnut growth and development in contrasting environments. 1. Growth and plant density responses. Exp. Agric., 34: 99-112.
29. Shrestha, S., F. Asch, J. Dusserre, A. Ramanantsoanirina and H. Brueck, 2012. Climate effects on yield components as affected by genotypic responses to variable environmental conditions in upland rice systems at different altitudes. Field Crops Res., 134: 216-228.
30. Boràas, L., G.A. Maddonni and M.E. Otegui, 2003. Leaf senescence in maize hybrids: Plant population, row spacing and kernel set effects. Field Crops Res., 82: 13-26.
31. Saini, H.S. and M.E. Westgate, 1999. Reproductive development in grain crops during drought. Adv. Agron., 68: 59-96.
32. Marcelis, L.F.M., H. Heuvelink and J. Goudriaan, 1998. Modelling biomass production and yield of horticultural crops: A review. Scient. Hortic., 74: 83-111.
33. Lafarge, T.A. and G.L. Hammer, 2002. Predicting plant leaf area production: Shoot assimilate accumulation and partitioning and leaf area ratio, are stable for a wide range of sorghum population densities. Field Crops Res., 77: 137-151.
34. Zinselmeier, C., B.R. Jeong and J.S. Boyer, 1999. Starch and the control of kernel number in maize at low water potentials. Plant Physiol., 121: 25-36.
35. Fukai, S., J. Basnayake and O. Makara, 2009. Drought Resistance Characters and Variety Development for Rainfed Lowland Rice in Southeast Asia. In: Drought Frontiers in Rice: Crop Improvement for Increased Rainfed Production, Serraj, R., J. Bennett and B. Hardy (Eds.)., Chapter 5. World Scientific, Manila, Philippines, pp: 75-89.
36. Rang, Z.W., S.V. Jagadish, Q.M. Zhou, P.Q. Craufurd and S. Heuer, 2011. Effect of high temperature and water stress on pollen germination and spikelet fertility in rice. Environ. Exp. Bot., 70: 58-65.
37. Pressman, E., M.M. Peet and D.M. Pharr, 2002. The effect of heat stress on tomato pollen characteristics is associated with changes in carbohydrate concentration in the developing anthers. Ann. Bot., 90: 631-636.