American Journal of Potato Research (2019) 96:457–471
https://doi.org/10.1007/s12230-019-09737-4

Intercropping Optimizes Soil Temperature and Increases Crop Water Productivity and Radiation Use Efficiency of Rainfed Potato

Shadrack O. Nyawade[1,2] · Nancy N. Karanja[2] · Charles K. K. Gachene[2] · Harun I. Gitari[3] · Elmar Schulte-Geldermann[4,5] · Monica L. Parker[1,4]

Published online: 3 September 2019

Abstract

Integrating crop species with different photosynthetic pathways has great potential to increase efficiency in the use of scarce resources. In order to tap the resource complementarity emanating from this mix, this study intercropped potato (*Solanum tuberosum* L.) with lima bean (*Phaseolus lunatas* L.) and dolichos (*Lablab purpureous* L.), and related soil temperature with radiation use efficiency and crop water productivity of rainfed potato in the upper midland (1552 m above sea level (masl), lower-highland (1854 masl) and upper-highland (2553 masl)) agro-ecological zones of Kenya. Leaf area index (LAI), light interception, soil temperature and soil water contents (SWC) were quantified at different stages of potato growth and related with the radiation use efficiency (RUE) and crop water productivity (CWP) of potato. Intercropping increased crop LAI by 26–57% relative to sole potato stands and significantly lowered the soil temperatures in the 0–30 cm depth by up to 7.3 °C. This caused an increase in SWC by up to 38%, thus increasing RUE by 56–78% and CWP by 45–67%. Intercropping potato with legumes is coupled with optimum root-zone soil temperature and soil water content, thus potentially exerting additive relations in radiation interception and subsequent conversion into crop biomass.

Resumen

La integración de especies de cultivos con diferentes rutas fotosintéticas tiene un gran potencial para aumentar la eficiencia en el uso de escasos recursos. A fin de aprovechar la complementariedad de la fuente surgida de esta mezcla, en este estudio se intercaló la papa (*Solanum tuberosum* L.) con el frijol lima (*Phaseolus lunatus* L.) y frijol de Egipto (*Lablab purpureous* L.), y se relacionó con temperatura del suelo, con el uso de la eficiencia radioactiva y la productividad del agua del cultivo de la papa de secano en área de altura media (1552 metros sobre el nivel del mar, masl), tierra elevada baja (1854 masl) y tierra elevada alta (2553 masl) en la zona agroecológica de Kenia. Se cuantificó el índice de área foliar (LAI), la intercepción de la luz, la temperatura del suelo y su contenido de agua (SWC), a diferentes etapas del crecimiento de la papa y se relacionó con el uso eficiente de la radiación (RUE) y la productividad del agua del cultivo de la papa (CWP). Los cultivos mezclados aumentaron el LAI en 26–27% en relación al cultivo de la papa sola y bajó significativamente las temperaturas del suelo en los 0–30 cm de profundidad hasta 7.3 °C. Esto causó un incremento en SWC por hasta 38%, incrementando, por ende, la RUE en 56–78% y la CWP en 45–67%. Intercalando papas con leguminosas se acopla con la temperatura óptima de la zona radical del suelo y el contenido de agua, ejerciendo, en consecuencia, potencialidad en las relaciones aditivas en la intercepción de la radiación y la subsecuente conversión hacia la biomasa del cultivo.

Keywords Intercropping · Radiation interception · Radiation use efficiency · Soil water content · Soil temperature

Introduction

Sustainable potato production requires careful optimization of the use of resources to improve soil fertility and crop productivity. This does not preclude the use of solar radiation and soil moisture resources. Biomass productivity of potato crops grown under optimum growth conditions has accordingly been described by the amount of soil water utilized per unit biomass production and the efficiency by which solar radiation is converted into plant biomass (Monteith 1977; Monteith 1965). These processes are partly determined by the leaf area index (LAI), and an index of radiation interception referred to as the extinction coefficient

✉ Shadrack O. Nyawade
shadnyawade@gmail.com

Extended author information available on the last page of the article

(Lizaso et al. 2003). As LAI increases, more radiation is intercepted per unit ground area resulting in higher assimilation rates (Ewert 2004).

The efficiency by which the intercepted radiation is converted into dry matter by potato crop has great relation with the soil temperature and soil moisture contents. Under water deficit conditions, potatoes curl their leaves so as to lower transpiration rates (Struike et al. 1989). This mechanism reduces the radiation interception and in turn negatively impacts plant water uptake. Optimal foliage growth and therefore light interception of potato occurs at soil temperature range of 15–20 °C (Rykaczewska 2015; Thornton et al. 1996). Elevated soil temperatures within the potato rhizosphere induce moisture stress that increases total dry matter allocation to roots and stems at expense of tubers thus reducing crop water productivity (Thornton et al. 1996). Raising night temperatures over the range of 0–20 °C increases potato root length while temperature increase to above 25 °C induces sharp reduction in the number and weight of tubers (Wilkinson and Davies 2002; Nyawade et al. 2018b).

The adverse effects of elevated soil temperatures on potato growth can be optimized by cropping systems capable of enhancing persistence of leaf area coverage. Intercropping is one of such systems well recommended due to its multiple benefits (Muthoni et al. 2013; Gitari et al. 2018a, 2018b, 2019; Nyawade et al. 2018a). Intercropping achieves greater complementarity of light use per unit area of land through the use of crop mixtures having different rooting ability, canopy structure, height, and nutrient requirements (Nyawade et al. 2019a, 2019b). This complementarity in the use of resources depends on microclimate modification created by the two crops grown in companion.

Nevertheless, little information is available on crop water productivity and radiation use efficiency of potato in relation to soil thermal regimes generated by legume intercrops. This information is needed for identification of management practices that may optimize the high soil temperature conditions prevalent in the tropical and sub-tropical potato growing areas. Therefore, the present work was designed to test the hypothesis that potato yield, crop water productivity and radiation use efficiency of potato grown in intercropping systems have no relation to soil temperature and soil moisture contents in three contrasting agro-ecological zones of Kenya (upper midland, lower highland and upper highland).

Materials and Methods

Site Description

The trials were carried out during the rainy seasons of 2017-2018 in three agro-ecological zones of Kenya; upper-midland-Kirinyaga (1552 m above sea level (masl)), lower-highland-Kabete (1854 masl) and upper-highland-Nyanadarua (2553 masl) (Fig. 1). Nyandarua lies along latitude 0°14′39.08″S and longitude 36°17′18.99″E, Kirinyaga, 0°29′35.71″S and 37°20′55.29″E and Kabete 0°14′45.00″S and 36°44′19.51″ E. These areas exhibit bimodal distribution of rainfall, with the long rains occurring from early March to late May and the short rains from mid-October to late December (Jaetzold et al. 2012). Nyandarua receives mean annual temperature of 18.2 °C with an annual rainfall amount of 1500 mm Kabete receives average temperature of 21.2 °C and annual rainfall of 1100 mm. Kirinyaga exhibits relatively lower annual rainfall amount ranging between 600 and 1000 mm and mean annual temperature of 24.4 °C.

The soils in Kabete are dark red friable clay, with clear, smooth boundaries classified as Humic Nitosol, while the Kirinyaga soils are well drained, shallow to very deep, dark reddish brown silty loam classified as Rhodic Ferralsol (FAO 2012). The soils in Nyandarua are dark brown to very dark red brown firm clay to silt loam clay classified as Ferric Luvisol. Soil physico-chemical properties of the 0–120 cm depth is given in Table 1.

Experimental Design and Crop Husbandry

The trials were laid out in a randomized complete block design with four replications. The plots measured 6.5 m long by 4.25 m wide, and were separated by 1 m path. A heat and water stress tolerant potato (*Solanum tuberosum* L.) cultivar, Unica (CIP 392797.22) (CIP 2008), was used for this study. The potato was grown in sole stands and in intercropping with either lima bean (*Phaseolus lunatus)* or dolichos (*Lablab purpureous*). Intercropping arrangement constituted 2 rows of potato alternating with 2 rows of legumes. Pre-sprouted tubers were planted at a uniform depth of 10 cm on pre-hilled ridges spaced at 75 cm with an inter-seed spacing of 30 cm. Two legume bean seeds were planted per hole at within row space of 20 cm and inter-row space of 75 cm between potato and legume strips and 50 cm between two legume strips.

Fertilization was based on soil analysis and was adjusted seasonally taking into account the amount of total N in the soil prior to planting and the crop N requirements. On average, this activity consisted of basal application of 180 kg ha^{-1} of NPK (14-26-10) and single topdressing with 20 kg urea (46-0-0). Topdressing was done 15–25 days after potato emergence depending on the general soil moisture conditions. Legumes received only basal phosphorus applications (triple super phosphate, 0-46-0) at rates averaging to 20 kg P ha^{-1}.

Weeding was performed at 14–21 days after crop emergence by hand hoeing and entailed earthing up the soil around potato vines' base to about 20 cm high and slight tamping of soil around legumes' stem base. The legumes were sprayed

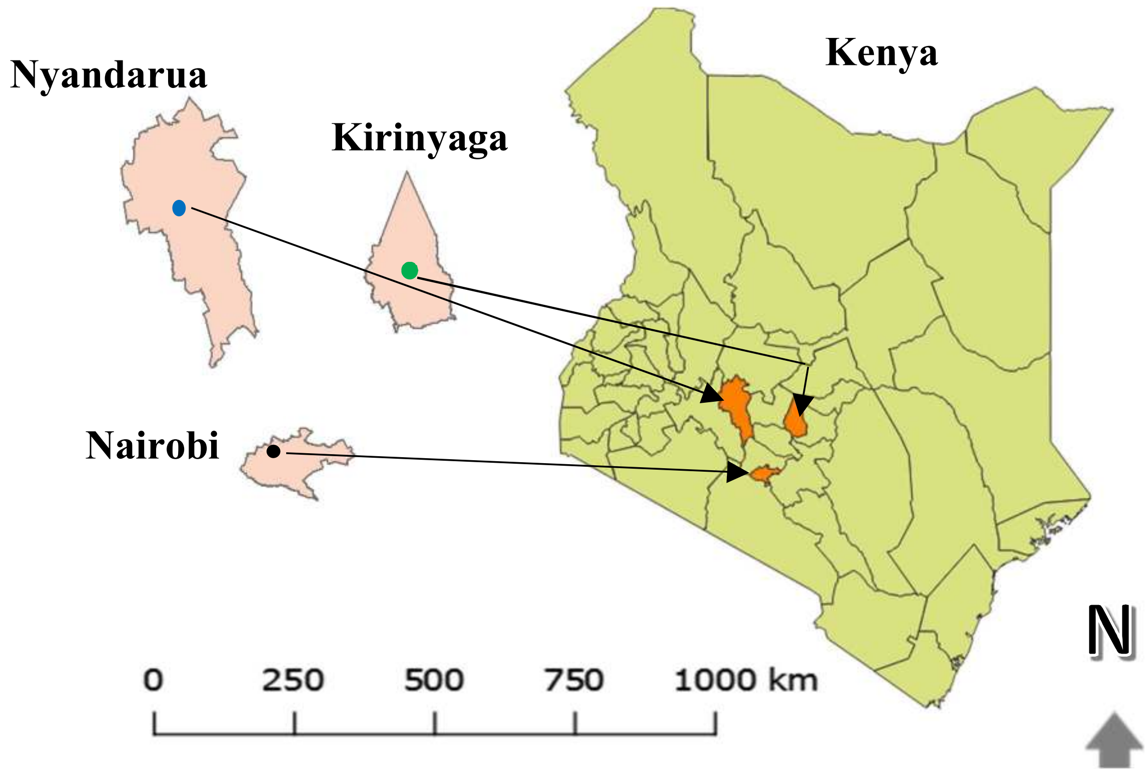

Fig. 1 Map of sites selected for establishment of the trials

with Duduthrin 1.7 EC (Lambda-cyhalothrin 17.5 g L^{-1}) alternating with Bestox 100 EC (Alpha-cypermethrin 50 g L^{-1}) to control aphids while potato crops were sprayed alternately with Ridomil Gold MZ 68WG (Mefenoxam 40 g kg^{-1} + Mancozeb 640 g kg^{-1}) and Dithane-M (Mancozeb) to control potato blight disease.

Potatoes were harvested at maturity (90–112 days after planting) by digging out the tubers using hand hoes while legumes were left growing in the field (a period of 45 days after potato harvest) till they attained physiological maturity. The biomass from each plot was weighed, chopped and together with the potato residues, incorporated back into the soil within one week to potato planting.

Climatic Data

Rainfall amount was recorded immediately after every rainfall event using an onsite rain gauge. Daily global radiation was estimated from the daily sunny hours recorded from the meteorology station located at about 200 m from the experimental sites. Air temperature was obtained from HOBO temperature sensors installed in the experimental sites. Micro-lysimeters installed to a depth of 30 cm below the soil surface were used to estimate the soil surface evaporation.

Soil Characterization

Sampling of soils was done at start of the experiment using soil piston augers for every 10 cm interval along soil profile of 0–120 cm. The samples for each treatment were composited for each depth and frozen until analysis for soil pH (by water), soil texture (hydrometric) (Gee and Bauder 1986), total N (Keeney and Nelson 1982) and total organic carbon (Nelson and Sommers 1996). Extraction of soil samples for analysis of available P and extractable K was done using Mehlich 1 procedures (Mylavarapu et al. 2002) and determined using UV–vis spectrophotometer and flame photometry methods, respectively (Murphy and Riley 1962).

Determination of Soil Water Content

Soil water content (SWC) of each plot was measured at 0–30 cm, 30–60, 60–90 and 90–120 cm depth intervals using tensiometers (0–100 kPa) installed in the interrow of potato and legumes (presentation in this study is presented with SWC at 0–30 cm interval (potato root depth). The tensiometers were inserted in holes drilled using soil auger with a diameter slightly narrower than the tensiometer shaft. The required soil depth was marked on the auger to ensure the correct depth of installation. Little water was poured down the hole to lubricate the sides and help the ceramic tip to make good contact with the

Table 1 Initial soil properties: soil bulk density (ρb); soil water content at permanent wilting point (θwp), field capacity (θfc) and saturation (θs); saturated hydraulic conductivity (Ks); pH; soil organic carbon (SOC); total nitrogen (N); available phosphorus (P) and exchangeable potassium (K)

	Soil depth (cm)	Clay	Silt %	Sand	Textural class[b]	ρb gcm^{-3}	θwp $cm\ cm^{-3}$	θfc	θs	Ks $mm\ h^{-1}$	pH	SOC %	N %	P ppm	K cmol/kg
Upper midland	0–30	24.5	33.3	42.2	CL	1.19	0.07	0.21	0.51	55.13	4.99	1.82‡	0.13‡	33.30	1.23#
	30–60	24.2	36.9	38.9	CL	1.24	0.04	0.19	0.52	49.21	4.99	1.04	0.23	23.40	1.33
	60–90	28.9	29.8	41.3	CL	1.34	0.03	0.25	0.58	40.33	4.93	0.88	0.11	24.40	1.19
	90–120	23.8	32.4	43.8	CL	1.35	0.03	0.28	0.55	32.22	4.92	0.33	0.09	20.20	1.09
Lower highland	0–30	49.7	22.5	27.8	C	0.99	0.09	0.38	0.41	33.33	5.11	2.06#	0.19†	24.40	1.13#
	30–60	49.2	24.2	28.9	C	1.04	0.06	0.37	0.41	27.56	5.14	1.56	0.11	18.20	1.16
	60–90	50.1	24.2	25.7	C	1.14	0.04	0.36	0.49	23.28	5.16	0.98	0.06	17.70	1.11
	90–120	51.3	24.8	23.9	C	1.19	0.05	0.38	0.48	14.98	5.20	0.42	0.02	16.60	1.00
Upper highland	0–30	38.3	56.1	5.6	SC	0.97	0.09	0.37	0.43	29.89	5.21	3.09‡	0.22†	16.60	1.16#
	30–60	36.9	58.4	4.7	SC	1.00	0.08	0.39	0.42	26.87	5.22	2.34	0.24	17.90	1.15
	60–90	34.6	59.5	5.9	SCL	1.08	0.03	0.35	0.45	18.32	5.26	1.92	0.11	15.50	1.03
	90–120	33.9	57.9	8.2	SCL	1.11	0.04	0.36	0.41	9.04	5.28	0.98	0.09	14.90	1.02

[b] C, CL, SC, SCL denote clay, clay loam, silt clay and silt clay loam respectively, ‡ and # denote potato root-zone (0–120 cm) nutrient contents below and within the recommended levels respectively. Critical levels for potato production: SOC, 2.5%, N, 0.2%, K, 1.0 cmol/kg, and P, 30 ppm (Gough and Wolf 1996)

soil. Firmly but gently, the tensiometers were pushed down to the base of the hole. Each of the tensiometers was installed on a different vertical line to avoid mutual interference. Matric potential readings were made at weekly interval and immediately after rainfall events. The matric potential values measured using tensiometer installed at different depth intervals and the respective gravimetric soil water content was used to plot soil moisture characteristic curve from which a relationship used to compute the volumetric soil water content was derived.

Calibration of the Tensiometers

Prior to their installation, the tensiometers used in this study were calibrated using gravimetric soil moisture measurements taken at soil depth intervals similar to that of tensiometers. The values obtained from the gravimetric measurements were plotted against the tensiometer readings in a scatter plot and a regression equation between the two methods was established. A highly significant positive correlation between the two methods was found ($r = 0.81$; $p < 0.001$) making it reliable to use the tensiometers to measure the soil moisture.

Estimation of Soil Temperature

The soil temperature was measured using temperature sensor probes (Onset HOBO USeries, UX120–006 M). The probes were installed at the depth of 0–30 cm in each experimental plot. The installation was done in the middle rows of potatoes and legumes. The soil around the probes was tamped at the surface to prevent surface water from running down around the sensors. Soil temperature measurements were taken between sowing and harvesting and recorded by automatic data-logging equipment at every 1 h common step. The soil temperature probes were calibrated with mercury thermometer data taken at different periods of the day. The averaged data for the four replicates were used for the computations.

Determination of Leaf Area Index, Light Interception, Crop Yield, Light Extinction and Radiation Use Efficiency

Radiation interception of photosynthetically active radiation (PAR) and leaf area index (LAI) were measured from 14 days after potato emergence and progressively at 14 days interval until physiological maturity using a Sunfleck Ceptometer-LP-80 (Decagon Devices, Pullman, WA, USA). Measurements were taken only under sky-blue conditions with no or minimum clouds between 1130 and 0130 h (local time), and during a period of constant incident solar radiation. This was meant to eliminate the effect of solar elevation on light interception. Data collection interval thus deviated by about 1–3 days depending on the sky conditions. Dead and brown plant materials were removed from the experimental plots before each radiation measurement. For each measurement, nine above and below canopy readings were taken perpendicularly to the crop rows to ensure that more leaf area was exposed to the light sensors. Corresponding LAI values were directly read upon averaging the above and below canopy readings. Plot values were computed from the average of four successive middle row readings. The PAR intercepted was calculated using Eq. (1–3) (Koocheki et al. 2016).

$$\mathrm{PAR}_{intercrop} = PAR_o\left[1-\exp\left(\left(-\lambda_{potato}*LAI_{potato}\right)+\left(-\lambda_{legume}*LAI_{legume}\right)\right)\right] \quad (1)$$

$$\mathrm{PAR}_{potato} = \frac{\lambda_{potato}*LAI_{potato}}{\left(\lambda_{potato}*LAI_{potato}\right)+\left(\lambda_{legume}*LAI_{legume}\right)} \quad (2)$$

$$\mathrm{PAR}_{legume} = \mathrm{PAR}_{intercrop}-\mathrm{PAR}_{potato} \quad (3)$$

Where PAR = photosynthetically active radiation (400–700 nm); LAI = leaf area index, λ = light extinction coefficient; PAR_o = PAR incident equal to half the daily global radiation (Monteith and Unsworth 1990). Daily global radiation was estimated from the daily sunny hours recorded from the adjacent meteorological station.

The light extinction coefficient (λ) was determined from the slope of the linear regression between the natural logarithm of radiation transmission and leaf area index (Monteith 1965).

The tuber and legume yields were estimated from the central 1.2 m^2 area of each plot. Tubers were dug out using fork hoe at 85–95 days after planting when the stems were completely dry, brushed and fresh weight taken. About 500 g of the samples from each plot were sliced and dried in an oven at 65 °C for 72 h and reweighed to determine tuber dry weight (DW). Harvesting for lima bean and dolichos was done at 110 and 120 days respectively. The shoot biomass estimations was done by cutting the plants at the soil surface using machetes. The dry mass was determined by oven-drying about 500 g samples at 65 °C to a constant mass. The yields (tubers and legumes) were converted into potato equivalents (PEY) using Eq. (4). For dolichos, the estimations considered grain and shoot biomass separately for this legume is used both as pulse and forage.

$$PEY\ \left(t\ ha^{-1}\right) = PY\left(kg\ ha^{-1}\right) + LY\ \left(kg\ ha^{-1}\right)*LP\left(US\frac{kg^{-1})}{PP\ \left(US\ kg^{-1}\right)}\right) \quad (4)$$

Where PEY = potato equivalent yield, PY = potato yield, LY = legume yield, PP = market price of potato (0.38 US\$ kg^{-1}) and LP = market price of legumes (0.21, 0.05 and 1.15 US\$ kg^{-1} for lima bean grain, dolichos forage and dolichos grain respectively).

Radiation use efficiency (RUE) (g MJ^{-1}) of each cropping system was estimated by fitting a linear regression (least square) to the cumulative amount of radiation absorption (MJ m^{-2}) and dry matter accumulation from successive harvests (g m^{-2}) (Monteith 1994). The slope of each regression was taken as the RUE for each treatment. Data taken at crop physiological maturity were excluded from RUE calculations due to its negligible role in biomass accumulation (Black and Ong 2000).

Estimation of Crop Water Productivity

Crop water productivity (CWP) was computed from the soil water balance equation and potato equivalent yield (Allen et al. 1998, Eq. (5)), as:

$$CWP = \frac{PEY}{P + CR + \Delta SW + I - RO} \quad (5)$$

Where PEY = potato equivalent yield obtained; P = precipitation; CR = capillary rise of water; ΔSW = change in soil water storage in root zone between planting and harvesting period (ΔSW) and I = irrigation (I); R = runoff. Capillary rise was assumed to be negligible because the groundwater table was more than 25 m below the soil surface (Karuku et al. 2014). The irrigation water depth was measured using flow meters installed at the plots' inlets while the total amount of surface runoff was quantified by flow meters installed within the plots. Micro-lysimeters installed in each plot to a depth of 30 cm below the soil surface were used to estimate the soil surface evaporation. Deep percolation was estimated by tensiometers installed to 180 cm soil depth.

Statistical Analyses

The data was analyzed using R software, version 3.5.2. The treatment effects on soil water content, soil temperature, crop water productivity and radiation use efficiency were tested using a mixed model analysis of variance (ANOVA) with cropping system, season and agro-ecological zone considered as fixed factors and block as random factor. Whenever the interaction of cropping system and season was found significant, data were analyzed in separate seasons. The homogeneity of variances was tested by Bartlett test and where the variances were not homogeneous, data were transformed by the function y = X1/2 or y = log(x). Tukey's honest significant difference test was applied for multiple mean comparisons between treatments and tests with $p < 0.05$ were considered statistically significant. Mean standard error was used to validate the equations used for parameter tests.

Results

Climatic Variables Measured during the Study Period

Averaged across the seasons, the mean rainfall amounts received during the study period were higher in the 2017 long rains followed by 2018 long rains, 2018 short rains and were lowest in the 2017 long rains (Table 2). These rains were 30–60% lower than the long term averages and occurred mainly at tuber emergence and vegetative growth regardless of the site. The diurnal and night temperatures were highest in the upper-midland zone and lowest in the upper-highland zones. Mean global solar radiation indicated were numerically greater in the upper-midland zone compared to the lower-highland and upper-highland zones. Soil evaporation ranged between 4.48 mm day^{-1} in the upper-highland zone and 11.23 mm day^{-1} in the upper-midland, and saturation water deficit ranging between 5.23 and 7.99 mbars across the sites.

Leaf Area Index Development

The development of leaf area index (LAI) differed significantly between the treatments and was greatest in legume intercropping (1.24–3.78 m^2 m^{-2}) relative to sole potato cropping (Fig. 2). Intercrop of potato and dolichos recorded the maximum LAI in the upper-midland (1.25–2.68 m^2 m^{-2}) and in the lower-highland (1.45–3.13 m^2 m^{-2}) irrespective of the season. This was reversed in the upper-highland zone where intercrop of potato and lima bean recorded the greatest significant LAI (1.78–3.78 m^2 m^{-2}). Leaf area index was significantly greater in the long rains (0.45–3.78 m^2 m^{-2}) than in the short rains (0.06–2.29 m^2 m^{-2}) irrespective of the agro-ecological zone and peaked one week earlier in the upper midland zone compared to the upper highland zone.

Soil Water Content and Soil Temperature

There were significant differences ($p < 0.05$) in the mean volumetric soil water contents (SWCs) measured between the different cropping systems and growing seasons (Table 3). Compared to sole potato stands, the highest significant SWC in the surface soil layer was measured under potato-dolichos in the upper-midland (0.07–0.19 cm cm^{-3}) and in the lower highland zones (0.18–0.31 cm cm^{-3}), but under potato-lima bean in the upper-highland zone (0.24–0.36 cm cm^{-3}). Generally, the SWC was consistently highest in the upper-highland agro-ecology (0.17–0.36 cm cm^{-3}) and lowest in the upper-midland agro-ecology (0.02–0.26 cm cm^{-3}) regardless of the sampling stage.

Mean soil temperature was significantly higher in sole potato plots (22.6–28.1 °C) than in legume intercropping plots (18.1–23.7 °C) irrespective of agro-ecology and seasons. Intercropping with dolichos was effective in lowering the soil temperatures in the upper-midland and lower highland zones, the effect of which diminished in the upper highland zone. Seasons, agro-ecological zones, and cropping systems had significant effect both on soil temperature and soil water content.

Light Interception and Leaf Extinction Coefficient

Fractions of light intercepted were consistently greatest in intercropping of potato and dolichos (0.54–0.59) in the upper-midland and in the lower-highland zones (0.61–0.85), but in potato-lima bean (0.76–0.82) in the upper-highland zone (Table 4). These values were consistently lowest in the sole potato stands and decreased as crop growth advanced to tuber bulking. Intercropping significantly lowered the leaf extinction coefficient of both legumes and potato with the values ranging between 0.35 and 0.65 across the sites. Cropping systems, seasons and agro-ecological zone had significant effect on fractions of light intercepted.

Table 2 Mean rainfall amount, irrigation depth, diurnal and night temperatures, solar radiation, saturation vapor deficit and evaporation for the period between potato planting and harvesting

	2017 LR			2017 SR			2018 LR			2018 SR		
	UM	LH	UH	UM	LH	UH	UM	LH	UH	UM	LH	UH
Cumulative rainfall amount (mm)	290	308	388	184	221	299	243	298	379	190	237	321
Mean diurnal temperature (°C)	28.5	25.4	22.2	29.8	25.4	21	27.3	24.9	21.4	27.9	25.3	22.5
Mean night temperature (°C)	20.3	17.8	14.5	21.3	18.5	16	20.8	18.1	16.5	17.3	16.5	17.3
Mean solar radiation (MJ m^{-2})	21.2	19.8	18.8	21.5	19.3	19.8	20.6	20.4	18.1	21.8	19.1	19.3
Mean saturation vapor deficit (mbar)	7.99	6.12	5.23	7.91	6.45	5.85	7.99	6.1	5.23	7.09	6.09	5.03
Mean soil evaporation (mm day^{-1})	11.2	9.66	4.48	12.5	9.57	4.83	10.87	9.21	4.11	13.6	9.98	4.82

LR, long rains, SR, short rains, UM, LH, UH, upper-midland, lower-highland, upper-highland agro ecological zones respectively

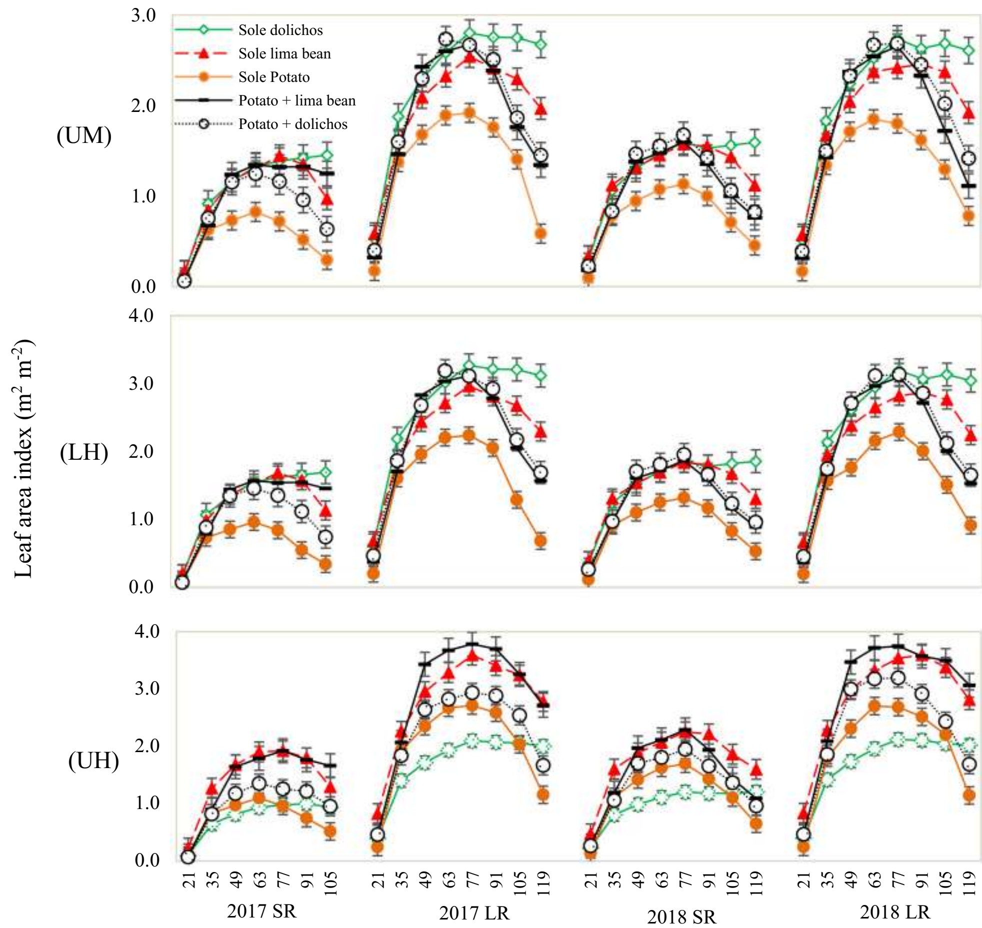

Fig. 2 Development of leaf area index by different treatments in upper midland (UM), lower highland (LH) and upper highland (UH) agro-ecological zones. Vertical bars indicate standard error of means

Intercropping Effect on Potato Yield

Highest potato equivalent yield were recorded by intercropping (7.2–38.2 t ha^{-1}) relative to sole potato (1.3–16.3 t ha^{-1}) and were significantly greater in the long rains (5.4–38.2 t ha^{-1}) than in the short rains season (1.3–27.5 t ha^{-1}) (Table 5). Potato-dolichos intercropping system recorded significantly lower potato equivalent yield (12.8–21.7 t ha^{-1}) compared to that of potato-lima bean (19.4–33.8 t ha^{-1}) in the upper-highland zone. Potato equivalent yield responded significantly to cropping system, seasons and agro-ecological zones.

Intercropping Effect on Crop Water Productivity and Radiation Use Efficiency of Potato

Intercropping potato with legumes showed significantly higher crop water productivity ranging between 4.04 to 9.67 kg ha^{-1} m^{-3} relative to sole potato (1.02–3.23 kg ha^{-1} m^{-3}) (Table 6). Crop water productivity was significantly greater in potato-dolichos intercropping than in potato-lima bean intercropping in the upper midland and lower highland agro-ecology (4.04–9.67 kg ha^{-1} m^{-3}). This was reversed in the upper-highland agro-ecology where potato-lima bean exhibited the highest CWP (3.21–5.98 kg ha^{-1} m^{-3}). Radiation use efficiency (RUE) of potato varied significantly among the treatment and ranged between 0.18 and 0.98 g MJ PAR $^{-1}$ in sole potato and 1.23–2.89 MJ PAR $^{-1}$ in potato-legume intercropping across the agro-ecologies. Agro-ecology had significant effect on the RUE and was highest in the upper-highland zones, intermediate in the lower-highland zone and lowest in the upper-midland zone.

Response of Potato Yield, Crop Water Productivity and Radiation Use Efficiency to Temperature and Soil Moisture

Potato equivalent yield, crop water productivity and radiation use efficiency responded significantly to soil water content, soil temperature, night temperatures and to the interaction of soil water content and soil temperature (Table 7). The interaction of soil temperature and soil water content had the highest significant positive effect on both the potato equivalent yield, crop water productivity and radiation use efficiency. Soil water content showed stronger effect on all the three parameters (potato equivalent yield, crop water productivity and radiation use efficiency) compared to soil temperature and night temperatures.

Table 3 Intercropping effect on soil moisture content and soil temperature across the four seasons of study

		2017 LR	2017 SR	2018 LR	2018 SR	2017 LR	2017 SR	2018 LR	2018 SR
		Volumetric water content[1]				Soil temperature[1]			
Agro-ecology	Cropping system	$cm^3\ cm^{-3}$				°C			
Upper-midland	Sole Potato	0.13a	0.02a	0.10a	0.08a	27.1c	28.1d	26.2.1d	27.5c
	Sole Dolichos	0.26d	0.10c	0.24e	0.22d	20.6a	20.9a	20.3a	21.4a
	Sole Lima bean	0.21c	0.06b	0.21de	0.18c	22.9b	21.5b	21.8ab	21.6ab
	Potato + Dolichos	0.19bc	0.07b	0.18 cd	22.5b	22.4bc	22.2bc	21.9ab	21.9ab
	Potato + Lima bean	0.17b	0.09bc	0.14b	0.15b	23.1b	23.6c	23.7c	22.3b
Lower-highland	Sole Potato	0.22a	0.14a	0.20a	0.15a	24.7c	25.8d	24.8d	25.4c
	Sole Dolichos	0.37e	0.22d	0.32c	0.31d	17.1a	20.4a	17.3a	21.4a
	Sole Lima bean	0.32d	0.16b	0.31c	0.28c	19.5b	21.2b	19.6b	21.3a
	Potato + Dolichos	0.28c	0.18bc	0.31c	0.24b	19.5b	21.1b	20.4bc	21.8ab
	Potato + Lima bean	0.25bc	0.19c	0.25b	0.26bc	20.7b	23.9c	21.8c	22.4b
Upper-highland	Sole Potato	0.26a	0.17a	0.19a	0.18a	22.6d	23.5d	21.7d	22.3e
	Sole Dolichos	0.30b	0.27c	0.34d	0.24bc	15.3a	20.6c	19.3c	18.7bd
	Sole Lima bean	0.38c	0.24b	0.27c	0.25c	17.8b	17.4a	17.8a	15.4a
	Potato + Dolichos	0.31b	0.27c	0.27c	0.22b	17.9bc	19.8bc	17.9a	19.1 cd
	Potato + Lima bean	0.36c	0.24b	0.23b	0.26d	18.1c	18.3ab	18.9bc	17.5b

Letters indicate comparisons for means between the cropping systems at $p \leq 0.05$ by Tukey's HSD test. SR, short rains season, LR, long rains season.
[1] Significant interaction between cropping system, agro-ecology and season was found for volumetric soil moisture content and soil temperature at the 0.05 probability level

Discussions

Spatiotemporal Variability of Crop Leaf Area Index

The greater leaf area index (LAI) due to intercropping could be explained by the differences that existed in the vertical foliage arrangement and canopy architecture of the different crop varieties. As indicated by the significantly lower leaf extinction coefficient, the larger and nearly vertical leaves exhibited by dolichos provided complementarity to the slender and more bent leaves of potato. Ma et al. (2015) observed that potato canopy is characterized by leaf bending, creating bare surfaces between the crop rows which greatly hamper the crop leaf area index. Dolichos provided low dense canopy which closed these bare spaces while the effective canopy overlap by lima bean bridged the inter-row spacing thus enhancing the LAI development (Fig. 3). The canopy closure of potato was effective only after 40 to 45 days followed by rapid decline after physiological maturity. The legume intercrops conferred a complimentary canopy that kept LAI relatively high during these periods.

The variability in leaf area index (LAI) among the cropping systems and between the agro-ecological zones could be related

Table 4 Intercropping effect on light interception and leaf orientation (leaf extinction coefficient)

		2017 LR	2017 SR	2018 LR	2018 SR	2017 LR	2017 SR	2018 LR	2018 SR
Agro-ecology	Cropping system	Fraction of light intercepted[1]				Leaf extinction coefficient			
Upper-midland	Pure potato	0.29a	0.22a	0.27a	0.25a	0.61c	0.65c	0.62d	0.63d
	Pure lima bean	0.44b	0.47b	0.48b	0.48b	0.38b	0.39b	0.41bc	0.37bc
	Pure dolichos	0.58c	0.56c	0.59c	0.54c	0.39b	0.36a	0.42c	0.34a
	Potato + lima bean	0.59c	0.61c	0.65d	0.53c	0.37a	0.38ab	0.41bc	0.36a
	Potato + dolichos	0.73d	0.71d	0.75e	0.69d	0.36a	0.37ab	0.38a	0.38c
Lower-highland	Pure potato	0.35a	0.42a	0.44a	0.30a	0.54c	0.5c	0.57c	0.57c
	Pure lima bean	0.65b	0.71b	0.76b	0.61b	0.42b	0.46b	0.41b	0.44b
	Pure dolichos	0.70c	0.79bc	0.74b	0.64b	0.35a	0.37a	0.42b	0.37a
	Potato + lima bean	0.71c	0.82c	0.85c	0.61b	0.38ab	0.38a	0.42b	0.38a
	Potato + dolichos	0.82d	0.87d	0.88c	0.78c	0.36a	0.37a	0.37a	0.38a
Upper-highland	Pure potato	0.43a	0.45a	0.54c	0.38a	0.51c	0.54c	0.53c	0.54d
	Pure lima bean	0.72c	0.71c	0.79d	0.68c	0.36a	0.37ab	0.38a	0.39bc
	Pure dolichos	0.45a	0.41a	0.46b	0.41a	0.37a	0.36a	0.37a	0.38a
	Potato + lima bean	0.81d	0.82d	0.76d	0.79d	0.39a	0.35a	0.38a	0.37a
	Potato + dolichos	0.54b	0.52b	0.50b	0.50b	0.45b	0.40b	0.44b	0.41c

Letters indicate comparisons for means between the cropping systems at $p \leq 0.05$ by Tukey's HSD test. SR, short rains season, LR, long rains season.
[1] Significant interaction between cropping system, agro-ecology and season was found for fraction of light intercepted at the 0.05 probability level

Table 5 Potato yield as affected by intercropping across the four study seasons

Agro-ecology	Cropping system	2017 LR	2017 SR	2018 LR	2018 SR
		Potato equivalent yield (t ha^{-1})			
Upper-midland	Pure potato	8.9a	1.3a	5.4a	3.2a
	Pure lima bean	12.3b	4.7b	9.9b	6.8b
	Pure dolichos	19.7c	7.3c	12.7bc	9.9c
	Potato + dolichos	25.1d	9.5d	16.9d	18.9d
	Potato + lima bean	17.3c	7.2c	13.2cd	9.8c
Lower-highland	Pure potato	13.9a	2.9a	7.4a	6.5a
	Pure lima bean	18.9b	5.8b	17.1b	9.8b
	Pure dolichos	25.2c	9.6c	22.6c	13.8c
	Potato + dolichos	38.2d	14.5d	34.6d	24.7d
	Potato + lima bean	24.9c	9.4c	23.8c	13.5c
Upper-highland	Pure potato	16.3b	7.9a	9.4a	6.5a
	Pure lima bean	22.2c	19.6c	22.6cd	19.8c
	Pure dolichos	13.1ab	15.8b	11.1a	14.8b
	Potato + lima bean	33.8d	19.4c	26.8d	27.5d
	Potato + dolichos	12.8a	14.5b	19.6b	21.7c

Letters indicate comparisons for means between the cropping systems at $p \leq 0.05$ by Tukey's HSD test. SR, short rains season, LR, long rains season. [1] Significant interaction between cropping system, agro-ecology and season was found for the potato equivalent yield at the 0.05 probability level

to the soil temperature effect of different treatments. Even though the higher soil temperature conditions early in the season favored tuber sprout and early canopy development in the upper-midland and lower-highland zones relative to the upper-highland zone, the restricted peak leaf area index and limited persistence led to no advantage. While evaluating the effect of three temperature regimes (16, 22 and 27 °C) on potato leaf formation, Shah et al. (2004) recorded leaf number values of

Table 6 Crop water productivity and radiation use efficiency in response to intercropping

Agro-ecology	Cropping system	2017 LR	2017 SR	2018 LR	2018 SR	2017 LR	2017 SR	2018 LR	2018 SR
		Crop water productivity[1]				Radiation use efficiency[1]			
		kg ha^{-1} m^{-3}				MJ PAR $^{-1}$			
Upper-midland	Sole Potato	1.13a	1.02a	1.57a	1.32a	0.77a	0.18a	0.28a	0.30a
	Sole Dolichos	4.58b	3.21c	3.04b	4.23c	1.89b	1.09b	1.72b	1.34c
	Sole Lima bean	4.34b	2.02b	3.11b	2.13b	1.78bc	1.21b	1.56b	1.05b
	Potato + Dolichos	6.23c	4.04d	6.96d	5.88d	2.09d	1.38c	2.12c	2.01d
	Potato + Lima bean	5.99d	4.02d	4.02bc	4.01c	1.98cd	1.23b	2.08c	1.32c
Lower-highland	Sole Potato	2.43a	2.12a	2.45a	2.25a	0.87a	0.98a	0.59a	0.65a
	Sole Dolichos	4.63b	4.34c	4.25b	5.33c	1.99b	1.28b	1.84b	1.67c
	Sole Lima bean	5.31c	3.21b	5.19c	3.23b	1.89b	1.27b	1.87b	1.35b
	Potato + Dolichos	5.84c	5.53c	9.67d	6.81d	2.89d	1.43d	2.87d	2.31d
	Potato + Lima bean	4.53b	5.22c	5.16c	5.12c	2.04c	1.33c	2.13c	1.56bc
Upper-highland	Sole Potato	3.23a	2.21a	3.02a	2.87a	0.98a	0.36a	0.54a	0.53a
	Sole Dolichos	3.78a	4.21b	3.23a	5.98c	2.03b	1.76 cd	1.98c	1.98c
	Sole Lima bean	5.98b	3.21b	5.12b	4.56bc	1.94b	1.64c	1.84c	1.97c
	Potato + Dolichos	9.09d	6.54c	8.00d	4.55b	0.97a	1.96d	0.89b	0.98b
	Potato + Lima bean	7.38c	9.20d	7.02c	9.02d	2.56c	1.48b	2.49d	2.36d

Letters indicate comparisons for means between the cropping systems at $p \leq 0.05$ by Tukey's HSD test. SR, short rains season, LR, long rains season. [1] Significant interaction between cropping system, agro-ecology and season was found for crop water productivity and radiation use efficiency at the 0.05 probability level

Table 7 Response of potato yield, crop water productivity and radiation use efficiency to soil moisture and temperature

Dependent variable	Independent variables	Coefficient	Standard error	t Stat	p
Potato equivalent yield	Soil water content (SWC)	2.340	0.936	2.500	0.002***
	Soil temperature	−6.710	3.010	−2.230	0.000**
	Night temperature	−0.642	0.274	−2.346	0.031*
	SWC*Soil temperature	2.100	2.170	0.970	0.043***
	SWC*night temperature	0.420	0.190	2.180	0.019*
	Soil temperature*night temperature	−2.360	0.440	−5.310	0.760
Crop water productivity	Soil water content (SWC)	1.360	7.570	0.180	0.000***
	Soil temperature	−0.137	0.039	−3.513	0.009**
	Night temperature	−0.080	0.044	−1.818	0.023*
	SWC*Soil temperature	7.500	0.560	13.330	0.000 ***
	SWC*night temperature	0.160	0.060	2.820	0.065
	Soil temperature*night temperature	−0.110	9.300	−0.010	0.078
Radiation use efficiency	Soil water content (SWC)	4.130	2.360	1.750	0.006**
	Soil temperature	−0.137	0.039	−3.513	0.009**
	Night temperature	−1.710	0.300	−5.690	0.042*
	SWC*Soil temperature	−7.580	2.810	−2.690	0.007**
	SWC*night temperature	2.750	5.210	0.530	0.069
	Soil temperature*night temperature	−0.140	0.080	−1.630	0.010

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 "1; Adjusted R square-Potato equivalent yield = 0.83; Crop water productivity = 0.78; radiation use efficiency = 0.82

32, 20 and 14, respectively per mainstem indicating depressing effect of high soil temperatures. Potatoes grown under high soil temperature conditions often grow taller with longer internodes, reduced leaf numbers, and are characterized with leaves which are shorter and narrow (Struik et al. 1989). Elevated soil temperatures have further been shown to decrease the number of potato leaves emerging from lateral branches (Nyawade et al. 2018a). All these affect the potential of LAI development and subsequently, radiation interception and use efficiency.

Attainment of peak LAI at different times in different sites suggests that the spatial distribution of LAI was affected by agro-ecological zones. This variability could be explained by changes in the timing of leaf senescence in response to water availability and ambient temperatures. Low nutrient availability under low soil moisture levels in the upper-midland zone may have accelerated leaf senescence to satisfy the nutrient demand of sink organs leading to earlier attainment of peak LAI. Consistent results were found by Sinclair (2000) who argued that water deficit considerably reduces the stomatal conductance leading to an interruption of biomass accumulation. Under such conditions, the water reserves of the plants may be consumed which can lead to termination of LAI development. Zahoor et al. (2010) demonstrated that high ambient temperatures may cause loss of cell wall plastid integrity. This coupled with stomata closure in response to heat stress generally lowers the photosynthetic rates. Stomatal closure occurs due to decreased leaf turgor under low


(a) (b) (c)

Fig. 3 Canopy overlap by potato grown alone (**a**) and intercropped with lima bean (**b**) and dolichos (**c**). Photos taken in the upper midland agro-ecology at vegetative growth of potato atmospheric vapor pressure along with root-generated chemical signals (Chaves et al. 2002). These processes might have shortened the crop leaf longevity leading to decrease in LAI. A better LAI development in the upper-highland zone than in the lower-highland zone could be as a result of the higher and well distributed rainfall amount which led to better nutrient assimilation.

The observed values of leaf extinction coefficient are in agreement with those reported by other authors for potato in tropical Africa (Allen and Scott 1980; Nyawade 2015). The higher leaf extinction coefficient (above 0.5) observed in pure potato stand was an indication of few vertical leaves in these treatments (Sinclair and Muchow 1999). It thus implies that monocropped potato had more bent leaves with increased its propensity to converge solar radiation.

Soil Temperature and Soil Water Content

The high soil moisture content in the 0–30 cm in intercropping was related to the shading conferred by the greater canopy that minimized the soil evaporation losses. In sole potato, heat from the topsoil was more easily lost to evaporation through the intervening bare soil surfaces. Gitari et al. (2018b) found that intercropping potato with *Dolichos lablab* in the sub-humid zones increased crop water productivity by 20% due to the creation of canopy shades which lowered the soil surface evaporation. The reduced ability of dolichos to confer protective shade in the upper highland zone was attributed to its low adaptation to low temperature conditions (Cook et al. 2005). The deep root systems by the legumes further minimized soil water extraction within the topsoil as they had increased capacity to extract water from the subsoils.

Effect of Legume Intercropping on Radiation Interception

The increased light interception by intercrops relative to sole potato stands could be asserted to the increased canopy size. The intercrops generally attained maximum canopy above 3, a value that corresponds to full groundcover by a typical potato cropping system (Allen and Scott 1980). This was partly attributed to the increased number of leaves forming on lateral branches of legumes. Plants in intercropping systems were thus able to occupy all the empty niches thus contributing strongly to canopy size and radiation interception.

Because dolichos and lima bean leaves have similar leaf characteristics on their adaxial surfaces, corresponding light absorption would be expected to be identical. This wasn't the case in this study as sole stands of dolichos intercepted higher light than lima bean in the upper-midland and lower-highland zones. Dolichos put short, dense canopy with few interior leaves relative to lima bean which established tall, broad dense crown with many interior leaves which allowed very little light to pass directly through the canopy.

The reversal of radiation interception by dolichos relative to lima bean in the upper-highland zone indicated that differences in radiation interception among the cropping systems were influenced by agro-ecological zones. This observation could be explained by the fact that different crops have different thermotolerance limits (Wahid et al. 2007). Unlike legumes which indicated progressive growth with little response to prevailing heat stress, potato crop responded by developing leaves showing downward curvatures, similar to finding by Romero et al. (2017). This observation was confirmed by the consistently higher leaf extinction coefficient recorded in the sole potato plots. This mechanism greatly reduced leaf area exposure to solar radiation and thus reduced radiation interception. The mechanism was probably meant to avoid water loss by potato under extreme temperature conditions. In the upper-midland zone where crops suffered longer heat stress, potato leaves drooped followed by wilting that started from the lower strata leaves. Only leaves that exhibited some level of greenness recovered turgor and finalized their production cycle. These leaves however had limited capacity to absorb solar radiation, an observation affirmed by the proportional decrease of LAI with increasing soil and ambient temperatures.

Intercropping Effect on Biomass Accumulation

Intercropping accumulated higher biomass and was more light use efficient compared to potato monoculture system due to their more vertical leaves as was indicated by the relatively low leaf extinction coefficient. The invariably lower dry matter yield of potato intercropped with lima bean compared to potato intercropped with dolichos in the upper-midland and lower-highland zones is primarily due to the shading effect caused by the bushy canopy of lima bean. The quality of light in terms of the ratio of light intercepted to total solar radiation reaching the potato crop was thus compromised by the understory canopy of lima bean. Burke (2017) noted that shading prolongs the stolon elongation period and delays tuberisation. When shading reduced radiation by approximately 50% during the period of tuber initiation, tuber numbers decreased by 20%. These results strongly suggest that the amount of solar radiation intercepted by potato was indeed causal in determining dry matter accumulation.

Relation of Potato Yield, Crop Water Productivity and Radiation Use Efficiency to Temperature and Soil Water Content

Based on our observations, canopy and tuber growth were generally slowed during the periods of heat stress and increased thereafter when the soil temperature and soil moisture conditions improved to nearly optimal levels for potato growth. A direct consequence of this effect was shortening of the tuber bulking period. Burke (2017) noted that high soil temperatures coupled with the high ambient temperatures caused premature senescence in potato with yield reduction of 20–30%. In a study conducted by Radeni and Caesar (1986), heating the soil to 28 °C reduced the flow of assimilates to tubers. Similarly, Krauss and Marschner (1984) observed cessation of starch accumulation when developing tubers were subjected to soil temperature of 30 °C. It could also be possible that allocation of assimilated carbon into non-structural and structural carbon was altered by the high soil temperature (Arai-Sanoh et al. 2010).

For the legumes, the effects of high soil temperature were mediated in part by the deep roots coupled with their good adaptations to high temperatures. While potato crop was characterized by roots that rarely exceeded a vertical depth of 30 cm, dolichos roots were traced to 120 cm depth while lima bean roots penetrated to about 90 cm depth (data not shown). Legumes could therefore access cooler subsoil layers more easily than the potato crop. This is in agreement with the previous studies which have established that potato has shallow fibrous root systems which are concentrated in the topsoil layer making the crop highly sensitive to fluctuating soil moisture contents and high surface soil temperatures (Nyawade et al. 2018a; Aliche et al. 2018; Gitari et al. 2018b).

Moisture deficits during root initiation period induce lignification of adventitious root and hampers potato growth (Belehu and Hammes 2004). This process is exacerbated under high soil temperature conditions. It may therefore be concluded that the consequence of aiming for the highest tuber yields in potato production is a water demand in excess of that which can consistently be met by the plant from natural sources. This view was evident in the upper-midland zone that despite it receiving great irradiance, could not attain the high biomass yield primarily due to the low and poorly distributed rainfall.

Soil temperature interacted with soil moisture to influence the potato yield, crop water productivity and radiation use efficiency. High soil temperatures have been shown to increase the soil water flow resistance through the soil-plant-atmosphere continuum and hence reducing the plant root water uptake (Schwarz et al. 1997). Therefore, keeping soil water contents high at extreme soil temperature conditions would minimize the impact of high soil temperatures and increase the efficiency by which the intercepted light is converted into plant biomass. Prolonged heat and water stress results in root clumping, root deformations and shrinkage, and causes weak root-soil contact that limits root water uptake and transport (Trebejo and Midmore 1990). This effect is especially true if the heat stress is coupled with soil water deficit and/or an increase in soil temperature (Irmak 2016).

Night temperatures also showed a significant effect on potato yield, crop water productivity and radiation use efficiency. Intercropping lowered the night soil temperatures to an optimal range of 15–20 °C for tuber formation thus increasing tuber weight and yield. High night soil temperatures above the latter range may induce high gibberellin acid concentrations in the stolon tip, with consequent disruption of tuber growth (Wilkinson and Davies 2002). Onset of tuberization was generally delayed with night temperatures greater than 25 °C, an observation associated with accelerated metabolism and growth due to induction of specific inhibitory effects. Radiation use efficiency of potato has been shown to decrease during high ambient temperatures only if the partial stomatal closure is coupled with high night temperatures that lower net respiration (Burke 2017).

Agro-ecological zone showed significant effect on radiation use efficiency probably due to the spatial variability that existed in ambient temperatures, rainfall amounts and distributions. Rainfall amounts were generally well distributed and greatest in the upper-highland zone, intermediate in the lower-highland, and lowest in the upper-midland zone. The greater specific heat coupled with slower heating of a moist soil could have contributed to the yield increase associated with the upper-highland zones (Hunt et al. 2010).

Radiation use efficiency was significantly lower in the upper-midland zone relative to lower-highland zone partly as a consequence of reduced partitioning of dry matter to tubers under heat and water stress conditions. This effect was offset to some extent in intercrops due to legumes' ability to confer shade that optimized soil temperature and soil moisture conditions. The reduced efficiency by which the solar radiation was converted into tuber dry matter in the lower-highland zone appeared to be associated with the delay in the onset of tuber bulking and increased stem growth caused by the higher temperatures, an observation well explained by Bodlaender (1963). The lower soil temperatures within the optimal range for potato growth in the upper-highland zone favored rapid tuber initiation resulting in greater number of tubers formed. Prolongation and greater persistence of leaf area index in the upper-highland zone further contributed to extended radiation interception thus compensating for the radiation interception sacrificed earlier in the season when the low soil temperatures delayed tuber sprout.

The observed effect of season on radiation use efficiency is primarily due to variations in the amount and distribution of rainfall in relation to the potential demand for water. The larger amount and better distribution of rainfall during the long rains season increased the soil water content which in turn favored early establishment and growth of crops. On the contrary, potato suffered from the severe moisture stress conditions during flowering and tuber filling stages which greatly contributed to low vegetative growth and yield decreases during the short rains. Extremely dry soil not only restricts respiration, but also facilitates wilting due to depressed xylem and leaf tissues (Falah et al. 2010). In potatoes, this condition is generally manifest first in the newly formed leaves with consequent death if this condition continues throughout the plant.

Conclusion

These results demonstrate the potential role of legume intercropping in enhancing radiation interception and use efficiency of potato grown under heat and water stress conditions. Legume intercrops reduced soil temperature, hastened foliage development and canopy cover of the soil which in turn reduced soil temperature and favored tuber initiation. By extracting water from the deep soil layers and lifting it to the leaves via evapotranspiration, legumes enhanced leaf area index development under heat and water stress conditions. This enhanced radiation interception and subsequent conversion into biomass. These findings have implications with respect to potato production in tropical lowlands where high temperatures are amongst the major problems limiting the crop diversification. Farmers are likely to stabilize the potato yields and accrue high returns from systematic legume integration into potato cropping system. These benefits can only be realized if crop diversification is based on agro-ecological and system compatibility.

Acknowledgements This work was implemented and funded as part of the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS) and undertaken jointly with the CGIAR Research Program on Roots, Tubers and Bananas (RTB), which are carried out with support from CGIAR Fund Donors and through bilateral funding agreements. For details please visit https://ccafs.cgiar.org/donors. The views expressed in this document cannot be taken to reflect the official opinions of these organizations.

Compliance with Ethical Standards

Conflict of Interests The authors declare that they have no competing interests in this paper and the study as a whole.

References

Aliche, E.B., M. Oortwijn, T.P. Theeuwen, C.W.B. Bachem, R.G.F. Visser, and C.G. Linden. 2018. Drought response in field grown potatoes and the interactions between canopy growth and yield. *Agricultural Water Management* 206: 20–30.

Allen, B.J., and R.K. Scott. 1980. An analysis of growth of the potato crop. *Journal of Agricultural Science Cambridge* 94: 583–606.

Allen, R.G., L.S. Pereira, D. Raes, and M. Smith. 1998. Crop evapotranspiration. Guidelines for computing crop water requirements. FAO Irrig. Drain paper 56.FAO, Rome, 300 pp.

Arai-Sanoh, Y., I. Tsutomu, O. Ohsumi, and M. Kondo. 2010. Effects of soil temperature on growth and root function in Rice. *Plant Production Science* 13 (3): 235–242.

Belehu, T., and P.S. Hammes. 2004. Effect of temperature, soil moisture content and type of cutting on establishment of sweet potato cuttings. *South African Journal of Plant and Soil.* 212: 85–89.

Black, C., and C. Ong. 2000. Utilization of light and water in tropical agriculture. *Agricural Forestry for Meteorology* 104: 25–47.

Bodlaender, K.B.A. 1963. Influence of temperature, radiation and photoperiod on development and yield. In *The growth of the potato*, ed. J.D. Ivins and F.L. Milthorpe. London: Butterworths.

Burke, J.J., 2017. Growing the potato crop. Vita, equity house, upper Ormond quay, Dublin 7, Ireland.

Chaves, M., S. Pereira, J. Maroco, L. Rodrigues, P. Ricardo, and L. Osorio. 2002. How plants cope with water stress in the field. *Annals of Botany* 89: 907–916.

CIP. 2008. Catalogue of CIP potato varieties. https://research.cip.cgiar.org/germplasm-istribution/red_varie/brochure.php?variedad=392797.22. Accessed on 7th December, 2018.

Cook, B.G., Pengelly, B.C. Brown, J.L. Donnelly, D.A. Eagles, M.A. Franco, J. Hanson, B.F. Mullen, I.J. Partridge, I.J., Peters, and R. Schultze-Kraft. 2005. Tropical forages: An interactive selection tool. Lablab purpureus. CSIRO, DPI and F (Qld), CIAT, and ILRI, Brisbane, Australia. http://www.tropicalforages (accessed 28.12.18).

Ewert, F. 2004. Modelling plant responses to elevated CO_2: How important is leaf area index? *Annals of Botany* 93: 619–627.

Falah, M.A.F., T. Wajima, D. Yasutake, Y. Sago, and M. Kitano. 2010. Responses of root uptake to high temperature of tomato plants (*Lycopersicon esculentum* Mill.) in soil-less culture. *Journal of Agricultural Technology* 6 (3): 543–558.

FAO. 2012. Harmonized World Soil Database (version 1.2). Food Agriculture Organization, Rome, Italy and IIASA, Laxenburg, Austria (http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/.

Gee, G.W., J.W. Bauder. 1986. Particle-size analysis, in Klute, A.: Methods of soil analysis, Part 1. Agron. 9, 2nd edn., ASA, Madison, WI, pp. 383–411.

Gitari, H., N.N. Karanja, C.K.K. Gachene, S. Kamau, K. Sharma, and E. Schulte-Geldermann. 2018a. Nitrogen and phosphorous uptake by potato (*Solanum tuberosum* L.) and their use efficiency under potato-legume intercropping systems. *Field Crops Research* 222: 78–84.

Gitari, H.I., C.K.K. Gachene, N.N. Karanja, S. Kamau, S.O. Nyawade, and E. Schulte-Geldermann. 2018b. Optimizing yield and economic returns of rain-fed potato (*Solanum tuberosum* L.) through water conservation under potato-legume intercropping systems. *Agricultural Water Management* 208: 59–66.

Gitari, H.I., C.K.K. Gachene, N.N. Karanja, S. Kamau, S.O. Nyawade, and E. Schulte-Geldermann. 2019. Potato-legume intercropping on a sloping terrain and its effects on soil physico-chemical properties. *Plant Soil* 438–447.

Gough R.E., and B. Wolf 1996. Diagnostic techniques for improving crop production, Volume 1. CRC Press.

Hunt, H.W., A.G. Fountain, P.T. Doran, and H. Basagic. 2010. A dynamic physical modelfor soil temperature and water in Taylor Valley, Antarctica. *Antarctic Science* 22 (4): 414–419.

Irmak, Suat, 2016. Impacts of extreme heat stress and increased soil temperature on plant growth and development. UNL Extension Water Resources.

Jaetzold, R., B. Hornetz, C.A. Shisanya, and Schmidt H (Eds). 2012. Farm management handbook of Kenya. Vol. I-IV (Western, central, eastern, Nyanza, southern Rift Valley, Northern Rift Valley, Coast), Nairobi. Available at: https:// www.uni-trier.de/index.php?id=58581.

Karuku, G.N., C.K.K. Gachene, N.N. Karanja, N. Cornelisb, and H. Verplacke. 2014. Effect of different cover crop residue management practices on soil moisture content under a tomato crop (*Lycopersicon esculentum*). *Tropical and Subtropical Agroecosystem* 17: 509–523.

Keeney, D.R., D.W. Nelson. 1982. Nitrogen in organic forms. Pages 643–698 in a. L. Page et al., Eds. Methods of soil analysis. Part 2. Agronomy no. 9, *American Society of Agronomy*, Madison, WI.

Koocheki, A., M.N. Mahallati, H. Solouki, and S. Karbor. 2016. Evaluation of radiation absorption and use efficiency in substitution intercropping of sesame (*Sesamum indicum* L.) and mung bean (*Vigna radiata* L.). *Advanced Plants and Agricultural Research* 3 (5): 001–009.

Krauss, A., and H. Marschner. 1984. Growth rate and carbohydrate metabolism of potato tubers exposed to high temperatures. *Potato Research* 27: 297–303.

Lizaso, J.I., W.D. Batchelor, M.E. Westgate, L. Echart, and L. Echarte. 2003. Enhancing the ability of CERES-maize to compute light capture. *Agricultural Systems* 76: 293–311.

Ma, B., L. Yuxin, L. Xiaojun, M. Fan, W. Faqi, and L. Zhanbin. 2015. Soil splash detachment and its spatial distribution under corn and soybean cover. *Catena.* 127: 142–151.

Monteith, J.L. 1965. Radiation and crops. *Experimental Agriculture* 1 (4): 241–251.

Monteith, J.L. 1977. Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London* 281: 277–294.

Monteith, J.L. 1994. Validity of the correlation between intercepted radiation and biomass. *Agricultural and Forest Meteorology* 68: 213–220.

Monteith, J.L., and Unsworth, M. 1990. Principles of environmental physics (2nd Ed.). Edward. Arnold, London.

Murphy, J., and J.P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27: 31–36.

Muthoni, J., H. Shimelis, and R. Melis. 2013. Potato production in Kenya: Farming systems and production constraints. *Journal of Agricultural Science* 5: 182–197.

Mylavarapu, R.S., J.F. Sanchez, J.H. Nguyen, and J.M. Bartos. 2002. Evaluation of Mehlich-1 and Mehlich-3 extraction procedures for plant nutrients in acid mineral soils of Florida. *Communications in Soil Science and Plant Analysis* 33 (5–6): 807–820.

Nelson, D.W., and L.E. Sommers. 1996. Carbon and organic matter. In *Methods of soil analysis, part 3, Chemical Analysis*, ed. D.L. Sparks, A.L. Page, P.A. Helmke, R.H. Loeppert, P.N. Soltanpour, M.A. Tabatabai, C.T. Johnston, and M.E. Sumner, 961–1010. Madison: SSSA, ASA.

Nyawade, O.S., 2015. Effect of potato (*Solanum tuberosum* L.) cropping systems on soil and nutrient losses through runoff in a humic nitisol. MSc. Thesis. University of Nairobi, Kenya.

Nyawade, S.O., N.N. Karanja, C.K.K. Gachene, E. Schulte-Geldermann, and M. Parker. 2018a. Effect of potato hilling on soil temperature, soil moisture distribution and sediment yield on a sloping terrain. *Soil and Tillage Research* 184: 24–36.

Nyawade, S.O., N.N. Karanja, C.K.K. Gachene, M. Parker, and E. Schulte-Geldermann. 2018b. Susceptibility of soil organic matter fractions to soil erosion under potato-legume intercropping systems in Central Kenya. *Journal of Soil and Water Conservation* 73: 568–577.

Nyawade, S.O., C.K.K. Gachene, N.N. Karanja, H.I, Gitari, E. Schulte-Geldermann, and M.L. Parker. 2019a. Controlling soil erosion in smallholder potato farming systems using legume intercrops. *Geoderma Regional.* 15 e00225.

Nyawade, S.O., N.N. Karanja, C.K.K. Gachene, H.I., Gitari, E. Schulte-Geldermann, and M. Parker. 2019b. Short-term dynamics of soil organic matter fractions and microbial activity in smallholder legume intercropping systems. *Applied Soil Ecology.* 142: 123–135.

Radeni, G., and K. Caesar. 1986. Effects of soil temperature on the carbohydrate status in the potato plant. *Journal of Agronomy and Crop Science* 156: 217–224.

Romero, A.P., A. Alarcón, R.I. Valbuena, and C.H. Galeano. 2017. Physiological assessment of water stress in potato using spectral information. *Frontier of Plant Science* 8: 1608.

Rykaczewska. 2015. The effect of high temperature occurring in subsequent stages of plant development on potato yield and tuber physiological defects. *American Journal of Potato Research* 92: 339–349.

Schwarz, P.A., T.J. Fahey, and T.E. Dawson. 1997. Seasonal air and soil temperature effects on photosynthesis in red spruce (*Picea rubens*) saplings. *Tree Physiology* 17 (3): 187–194.

Shah, S.F.A., B.A. McKenzie, R.E. Gaunt, J.W. Marshall, and C.M. Frampton. 2004. Effect of production environments on radiation interception and radiation use efficiency of potato (*Solanum tuberosum* L.) grown in Canterbury, New Zealand, New Zealand. *Journal of Crop and Horticultural Science* 32 (1): 113–119.

Sinclair, T.R. 2000. Model analysis of plant traits leading to prolonged crop survival during severe drought. *Field Crops Research* 68: 211–217.

Sinclair, T.R., and R.C. Muchow. 1999. Radiation use efficiency. *Advances in Agronomy*: 215–265.

Struik, P.C., J. Geertsema, and C.H.M.G. Custers. 1989. Effects of shoot, root and stolon temperature on the development of potato (*Solanum tuberosum* L.) plant. Development of tubers. *Potato Research.* 32: 151–158.

Thornton, M.K., N.J. Malik, and R.B. Dwelle. 1996. Relationship between leaf gas exchange characteristics and productivity of potato clones grown at different temperatures. *American Journal of Potato Research* 73: 63–77.

Trebejo, and J. Midmore. 1990. Effect of water stress on potato growth, yield and water use in a hot and a cool tropical climate. *Journal of Agricultural Science, Cambridge* 114: 321c334.

Wahid, A., S. Gelani, M. Ashraf, and M. Foolad. 2007. Heat tolerance in plants: An overview. *Environmental and Experimental Botany* 61 (3): 199–223.

Wilkinson, S., and J. Davies. 2002. ABA-based chemical signaling: The coordination of responses to stress in plants. *Plant Cell Environment* 25: 195–210.

Zahoor, A., M. Riaz, S. Ahmad, H. Ali, M.B. Khan, K. Javed, M.A. Anjum, M. Zia-Ul-Haq, and M.A. Khan. 2010. Growth and radiation use efficiency of pearl millet as affected by hybrids, nitrogenous regimes and planting geometry under irrigated arid conditions. *Pakistan Journal of Botany* 42: 3197–3207.

Affiliations

Shadrack O. Nyawade[1,2] • **Nancy N. Karanja**[2] • **Charles K. K. Gachene**[2] • **Harun I. Gitari**[3] • **Elmar Schulte-Geldermann**[4,5] • **Monica L. Parker**[1,4]

1 The CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS), International Potato Center (CIP), Sub-Saharan Africa Regional Office, ILRI Campus, Old Naivasha Road, P.O. Box 25171, Nairobi 00603, Kenya

2 Department of Land Resource Management and Agricultural Technology, College of Agriculture and Veterinary Sciences, University of Nairobi, P.O. Box 29053-00625, Nairobi, Kenya

3 Department of Agricultural Science and Technology, School of Agriculture and Enterprise Development, Kenyatta University, P. O. Box 43844-00100, Nairobi, Kenya

4 The CGIAR Research Program on Roots, Tubers and Bananas (RTB), International Potato Center (CIP), Sub-Saharan Africa Regional Office, ILRI Campus, Old Naivasha Road, P.O. Box 25171, Nairobi 00603, Kenya

5 University of Applied Science Bingen (TH Bingen), Berlinstrasse 109, 55411 Bingen, Germany