CSIRO PUBLISHING
Crop & Pasture Science, 2017, **68**, 442–456
http://dx.doi.org/10.1071/CP16416

Understanding growth and development of three short-season grain legumes for improved adaptation in semi-arid Eastern Kenya

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Abstract. Short-season grain legumes play an important role in smallholder farming systems as source of food and to improve soil fertility through nitrogen fixation. However, it is not clearly understood how these diverse legumes contribute to the resilience of such systems in semi-arid environments. We describe the growth, development and resource-use efficiency (focusing on radiation, RUE) of three promising short-season grain legumes: common bean (*Phaseolus vulgaris* L.), cowpea (*Vigna unguiculata* (L.) Walp.) and lablab (*Lablab purpureus* (L.) Sweet). Two field experiments were conducted during the short rains of 2012–13 and 2013–14 in Eastern Kenya. In the first experiment, the legumes were grown at three plant densities (low, medium, high); in the second experiment, they were subjected to three water regimes (rainfed, partly irrigated, fully irrigated). Phenological development was monitored and biomass accumulation, leaf area index and fractional radiation interception were measured repeatedly during growth; grain yield was measured at maturity. Harvest index and RUE were calculated from these data. Common bean had the shortest growing period (70 days), the most compact growth habit and relatively high RUE but limited grain yield (1000–1900 kg ha^{-1}), thereby proving more suitable for cultivation in areas with restricted cropping windows or in intercropping systems. Cowpea had a longer growing period (90 days) and a spreading growth habit leading to high light interception and outstanding grain yields under optimal conditions (1400–3050 kg ha^{-1}). Lablab showed stable RUE values (0.76–0.92 g MJ^{-1}), was relatively unaffected by limited water availability and had a comparatively long growing period (100 days). Lablab grain yields of ~1200–2350 kg ha^{-1} were obtained across all water regimes, indicating a high potential to cushion climatic variability. Planting density strongly influenced the production success of cowpea and lablab, with high plant densities leading to vigorous growth habit with low podset establishment. Such information on temporal and spatial differences in growth, development and resource-use efficiency is highly valuable for crop-modelling applications and for designing more resilient farming systems with short-season grain legumes.

Additional keywords: climate-smart agriculture, phenology, plant physiology, resource-use efficiency.

Received 15 June 2016, accepted 22 May 2017, published online 26 June 2017

Introduction

Eastern Africa, including the semi-arid areas of Eastern Kenya, is one of the most vulnerable regions to the impacts of climate change (Slingo *et al.* 2005; Boko *et al.* 2007; Challinor *et al.* 2007; Thornton *et al.* 2011). Analysis of future climate scenarios indicates that high variability of rainfall and increased occurrence of extreme weather events (e.g. prolonged dry spells) are further aligned with changes in growing-season characteristics (Boko *et al.* 2007; Stern 2007; van de Steeg *et al.* 2009). This means that the start, end and length of a growing season have become less predictable. Coping with such variability is challenging for farmers who aim to optimise their farming activities, and it requires agronomists to re-think how diverse germplasm may fit into these farming systems for both enhanced food production and resilience (Cooper *et al.* 2009).

Legumes possess great genetic diversity, and the right selection and promotion of drought-resistant species and varieties may help to overcome these challenges (Daryanto *et al.* 2015). Furthermore, legume production has been widely promoted to address the demands of resource-poor farmers in semi-arid areas. Grain legumes, in particular, offer great potential to diversify existing cropping systems and are highly regarded for their multiple benefits. They provide food and nutritional security in rural areas (Vance *et al.* 2000), improve soil fertility through biological nitrogen fixation, and, thus, contribute to sustainable intensification of agricultural systems (Onduru *et al.* 2001; Graham and Vance 2003; Ojiem *et al.* 2007). Challenges associated with climate change make short-season grain legumes a viable option owing to their ability to complete their life cycle before the onset of terminal drought (Loss and Siddique 1994).

The present study focused on three grain legumes: common bean (*Phaseolus vulgaris* L.) and cowpea (*Vigna unguiculata* (L.) Walp.), which are widely utilised in Eastern Kenya; and lablab (*Lablab purpureus* (L.) Sweet), a previously widespread, but now less studied, 'neglected legume' with great potential for semi-arid areas (Maass *et al.* 2010). Common bean and cowpea are among the main sources of protein and cash income for farmers in semi-arid areas of Eastern Kenya (Muhammad *et al.* 2010). However, average yields are generally low at 530 kg ha^{-1} for cowpea and 600 kg ha^{-1} for common bean (FAOSTAT 2014), and below the potential yield (Abberton 2010; Foyer *et al.* 2016). Lablab is well suited to semi-arid areas and its tolerance to drought stress is well established (Maundu *et al.* 1999; Maass *et al.* 2010).

In order to understand the phenological development of these grain legumes, a thermal time model was applied in this study (Monteith 1977; Sinclair and Muchow 1999). Dry matter (DM) production over the growing period, and final grain yield, are essential agronomic measures to quantify growth and evaluate the production potential. Furthermore, harvest index (HI) and the biomass partitioning coefficient are ratios used to express the reproductive efficiency of grain crops and the biomass allocation among different crop organs (Hay 1995). Understanding resource capture, particularly the utilisation of light and water over the growing period, is critically important to identifying possible niches for different short-season grain legumes. The spatial interception of radiation by crops can be described by the leaf area index (LAI) and the fraction of intercepted light. Finally, the radiation-use efficiency (RUE) is defined as the amount of biomass accumulated per unit radiation intercepted, in particular photosynthetically active radiation (PAR), and the key indicator to estimate the photosynthetic performance (Monteith 1977; Muchow *et al.* 1993). When evaluating the production potential and resource use of different legumes, plant density is one of the major adjustments for insights into resource capture with respect to time and space. Furthermore, the response to water availability is of central interest in rainfed agricultural systems and has been a component of several scientific studies (e.g. Muchow 1985; Turner *et al.* 2001).

The number of comprehensive and comparable studies on legume growth, development and resource use from semi-arid areas in Sub-Saharan Africa is limited. Most studies focus on a single legume (e.g. Turpin *et al*. 2002; Uarrota 2010) or a single trait such as RUE (e.g. Tesfaye *et al.* 2006). Understanding the expressions of agronomic traits in response to environment and management remains a central aim for adapting to a changing climate. Moreover, the interpretation of important agronomic measures regarding resource availability can contribute to defining breeding targets that will lead to improved adaptation in these challenging environments. In addition, defining key physiological parameters is essential for parameterising crop models to simulate the cropping systems of semi-arid areas (Keating *et al.* 2003).

The objectives of this study were: (*i*) to describe the growth and development of three short-season grain legumes (common bean, cowpea, lablab) under semi-arid conditions in Eastern Kenya in response to plant density and water availability and evaluate their production potential; (*ii*) to estimate resource use and use efficiency, with focus on radiation; and (*iii*) to consider the phenological, morphological and physiological characterisation of the three legumes and thereby assess their usefulness for improved adaptation in semi-arid environments in the context of climate change.

Material and methods

Study site

The experiments were conducted during the short rains of 2012–13 and 2013–14 at the Kenya Agricultural Research Institute (KARI; now Kenya Agricultural and Livestock Research Organisation, KALRO), Katumani, Machakos county, Kenya (1°34′55.84″S, 37°14′42.95″E; elevation 1592 m a.m.s.l.). The site is in a semi-arid environment with mean annual total rainfall of 700 mm with bimodal pattern. The short rains occur from October to December with a mean of ~350 mm, and the long rains from March to May with ~300 mm. Inter-seasonal rainfall variation is large with coefficient of variation 45–58% (Keating *et al.* 1992). Annual temperatures vary from a mean minimum of 15°C to a mean maximum of 26°C, with the hottest months being October and February and the coolest month July (Jaetzold *et al.* 2006).

Soil characterisation

The soil at the experimental site is characterised as a moderately well drained, reddish brown chromic Luvisol with a clay texture throughout the profile but with an increased sand content at the surface layer (Jaetzold *et al.* 2006). The soil is low in nitrogen, phosphorus, calcium and zinc and with a low organic matter content (OC $\leq$1%) (Table 1). The pH is slightly acidic to neutral, range 5.5–7. Prior to sowing (October 2012), pH, soil texture (hydrometer method) and soil fertility status were analysed. Ten samples per layer (0–15, 15–30, 30–60 and 60–90 cm) were randomly taken across a diagonal of the experimental site (Dalgleish and Foale 1998) and analysed at the KARI National Agricultural Research Laboratories in Nairobi, Kenya.

Experimental design

There were two separate field experiments: the first, a plant-density trial; and the second, a water-response trial. Locally

Table 1. Summary of soil texture and fertility analysis before sowing at KARI, Katumani, Kenya

	Soil depth (cm)			
	0–15	15–30	30–60	60–90
Soil texture analysis (%)				
Sand	68.0	69.0	62.5	50.5
Clay	25.3	23.5	31.5	40.0
Silt	6.7	7.5	6.0	9.5
Soil fertility analysis[A]				
pH	6.5	6.5	6.2	6.0
Organic carbon (%)	0.90	0.80	1.00	0.70
Total nitrogen (%)	0.08	0.07	0.06	0.05
Available phosphorus (mg kg^{-1})	33.75	31.25	20.00	15.00
Exchangeable potassium (cmol kg^{-1})	0.87	0.81	0.65	0.35

[A] Horwitz and Latimer (2005).

adapted and commonly used short-season varieties recommended by KARI (2006) for cultivation in the region were used in the experiments. The cultivars for common bean were KAT/B-1 and KAT X56, for cowpea M66 and KVU27-1, and for lablab DL1002 and Highworth. Because of similar growth and development patterns of both varieties within every species, data are represented for only one variety of each: KAT X56 for common bean, M66 for cowpea, and DL1002 for lablab. Cowpea and bean seeds were inoculated with *Rhizobium phaseoli* strain CIAT 899, whereas lablab was inoculated with USDA 3605 strain before sowing.

Plant-density trial

The legumes were grown at three plant densities. Medium density was 10 plants m^{-2} for common bean and cowpea, and 4.2 plants m^{-2} for lablab, following the recommendations by KARI (2006). High density (20 plants m^{-2} for common bean and 8.4 plants m^{-2} for cowpea and lablab) was double and low density (5 plants m^{-2} for common bean and 2.1 plants m^{-2} for cowpea and lablab) was half the recommended medium density. All plots received additional water of up to 50 mm $week^{-1}$ through drip irrigation throughout the growing period, which represented the fully irrigated treatment of the water-response trial.

Water-response trial

The water response trial consisted of three treatments: (*i*) purely rainfed; (*ii*) partly irrigated, total of 50 mm water $week^{-1}$ with additional drip irrigation until bud formation, i.e. onset of flowering; and (*iii*) fully irrigated, total of 50 mm water $week^{-1}$ with additional drip irrigation throughout the growing period (Table 2). All plants were established using medium density, as described for the plant-density trial.

Experimental layout and crop management

The two experiments were independent of each other. However, experimental design, crop management and data collection were partly similar. The experiments were arranged in main blocks representing the main treatments (different densities for the plant-density trial, and different water regimes for the water-response trial) with legume species and varieties as subplots, completely randomised and replicated four times within each main block. Individual subplot sizes were 5 m by 2.5 m for common bean and cowpea (row spacing 0.5 m) and 5 m by 3.2 m for lablab (row spacing 0.8 m) in order to provide sufficient plants for destructive sampling for biomass determination.

Seeds were sown at 3 cm depth on 14 November 2012 for the 2012–13 short rains, and on 5 November 2013 for the 2013–14 season. At planting, triple superphosphate (46% P_2O_5) fertiliser was applied at a rate of 20 kg P ha^{-1} and urea at a rate of 10 kg N ha^{-1}. Two seeds were planted per hill and later thinned to the required density after the appearance of the first true leaf. Weeds were controlled with a pre-plant knockdown herbicide (Roundup, a.i. 2% glyphosate; Monsanto, St. Louis, MO, USA) before planting and manually during the growing period to minimise competition for water, nutrients and sunlight. The following insecticides were applied to control leaf-eating insects and aphids on cowpea and lablab: Duduthrin (lambda-cyhalothrin 17.5 g L^{-1}; Twiga, Nairobi), Thunder (imidacloprid 100 g + Beta-cyfluthrin 45 g L^{-1}; Bayer, Leverkusen, Germany), and Marshal (35% carbosulfan; Syngenta, Basel, Switzerland).

Data collection

Meteorological data

Meteorological data recorded during the experimental period included rainfall and daily minimum and maximum temperatures. Records of solar radiation were obtained from the meteorological station at KARI Katumani, ~150 m from the experimental field.

Biomass and LAI sampling

For both experiments, plants were destructively harvested for aboveground biomass determination every second week after

Table 2. Summary description of the treatments included in the water-response trial at KARI, Katumani, Kenya, during the short rains of 2012–13 and 2013–14

Season	Species	Water regime	Irrigation	In-crop rainfall (mm)	Irrigation + rainfall
2012–13	Common bean	Fully irrigated	270	156	426
		Partly irrigated	150	156	306
		Rainfed	–	156	156
	Cowpea	Fully irrigated	300	190	490
		Partly irrigated	225	190	415
		Rainfed	0	190	190
	Lablab	Fully irrigated	345	190	535
		Partly irrigated	210	190	400
		Rainfed	–	190	190
2013–14	Common bean	Fully irrigated	240	259	499
		Partly irrigated	60	259	319
		Rainfed	–	259	259
	Cowpea	Fully irrigated	330	259	589
		Partly irrigated	180	259	439
		Rainfed	–	259	259
	Lablab	Fully irrigated	345	339	684
		Partly irrigated	180	339	519
		Rainfed	–	339	339

plant establishment (2 weeks after planting). Because of their distinct development times, different numbers of samples were taken for each legume and in each season. During the 2012–13 season, the number of samples was 5 (common bean), 6 (cowpea) and 7 (lablab), and in the 2013–14 season, 6 (common bean), 7 (cowpea) and 8 (lablab). A sample was also taken at 50% flowering and physiological maturity. On each sampling date, two plants were randomly cut immediately above the soil surface from one of the middle rows of each subplot in all replications and manually separated into leaves, stems, flowers, pod-walls and grains. The plant parts were dried at 60°C to constant weight for DM determination. LAI and PAR above and below the canopy were measured at 7–10-day intervals (depending on daily cloudiness) after plant establishment until complete leaf senescence by using an AccuPAR LAI ceptometer (model LP-80; Decagon Devices, Pullman, WA, USA). For the spot measurement, the LAI ceptometer was placed at right angle to the crop rows at the soil surface covering the representative middle rows. Ten repeated-measurements were taken between 12 : 00 and 14 : 00 local time (GMT+3) for all replications.

Phenological development

Data on phenology, including first bud formation, flowering, end of flowering and maturity, were recorded as days after planting (DAP). Flowering was defined as 50% of plants with open flowers, podset was 50% of plants with visible pods, end of flowering was 50% of plants with no more flowers, and physiological maturity when 90% of the pods were dry.

Calculated variables

Thermal time. The time from and between different developmental stages was determined in thermal time expressed in degree-days (T_t). The concept of thermal time is based on the assumption that growth is a positive linear process between base temperature and optimal temperature. At optimal temperature, processes proceed at their maximum rate. From the optimal temperature towards the maximum temperature, there is a declining negative relationship (Monteith 1977). Thermal time was computed by using the algorithms used in CERES-Maize, which divides each day into eight 3-h periods on the basis of daily inputs of maximum and minimum temperatures (Jones and Kiniry 1986). Base, optimal and maximal temperatures (T_b, $T_{optimal}$, T_{max}, °C) were assumed to be 9°C, 25°C and 37°C, respectively, for common bean; 10°C, 34°C and 44°C for cowpea; and 10°C, 30°C and 40°C for lablab (Robertson *et al.* 2002; Turpin *et al.* 2003; Hill *et al.* 2006).

Biomass partitioning. The distribution of leaves was described by using the biomass partitioning coefficient, which was determined by the regression of the biomass of green leaves against the total aboveground vegetative biomass. The slope of the regression was estimated to be the biomass partitioning coefficient (Robertson *et al.* 2002; Soltani *et al.* 2006). This represents the allocation of biomass distributed to different organs as implemented in crop simulation models such as APSIM.

Harvest index. HI represents the ratio of grain yield to total aboveground biomass (TDM). The denominator, i.e. TDM, was compared both at flowering (maximum biomass production) and at harvest. Because grain legumes often drop their leaves towards the end of the growing period, HI calculated from biomass at flowering can give a more representative and better comparable value.

Radiation-use efficiency. From the measured PAR values, the radiation interception fraction (*f*) was calculated by taking into account the assumption that only 6% of visible light is reflected by green canopy (Dingkuhn *et al.* 1999). According to Lambert-Beer's law, f is related to LAI, with k being the extinction coefficient:

$$f = 1 - \exp^{(-k\mathrm{LAI})}$$

The PAR transmitted is consequently $\mathrm{PAR}_{\mathrm{transm}} = 1 - f$ and extinction coefficient can be estimated by least-square regression analysis—calculating the slope of the relationship between the natural logarithm of the transmitted PAR $\ln(\mathrm{PAR}_{\mathrm{transm}})$ and LAI (Szeicz 1974; Dingkuhn *et al.* 1999). For each day after emergence, the incoming solar radiation measured by the meteorological station was summed to determine cumulative intercepted radiation based on the respective PAR fraction assuming that 45% of solar radiation is PAR (Meek *et al.* 1984). RUE was calculated as the slope of the regression of the accumulated biomass (aboveground biomass, including leaves and stem as DM in $\mathrm{g\,m^{-2}}$) and cumulative intercepted radiation (Sinclair and Muchow 1999). The accumulated PAR was calculated from the cumulative daily PAR and the previously estimated k by Lambert-Beer's law. Values for RUE were assessed for the three legumes and different density and water regimes included in the two experiments.

Statistical analyses

Yield and HI data were analysed by analysis of variance (ANOVA), and tests of significance were conducted by using post-hoc multiple comparison Tukey test to identify effects of plant density and water regime within species. A test of homogeneity was conducted to compare the regression coefficient RUE. Significant differences among treatments were compared with the critical difference at $P = 0.05$. All statistical analyses were computed using R 2.15.1 (R Core Team 2014).

Results

Seasonal conditions

Temperature patterns were fairly similar in the two short rainy seasons, 2012–13 and 2013–14 (15 October–15 March), with mean minimum temperatures of 15°C, mean maximum temperatures of 31°C and an average temperature of 23°C (Fig. 1). Rainfall intensity and distribution were, however, different in both seasons. In the 2012–13 season, rainfall (262 mm) was below the long-term average (Rao and Okwach 2005) and relatively evenly distributed between November and January. In 2013–14, total rainfall (354 mm) was above the long-term average (Rao and Okwach 2005); however, its distribution was comparatively uneven, with 220 mm falling between the end of November and the end of December, and a long dry spell from 22 December to 6 February.

Phenological development

Pronounced temporal differences were observed in the phenological development of common bean, cowpea and

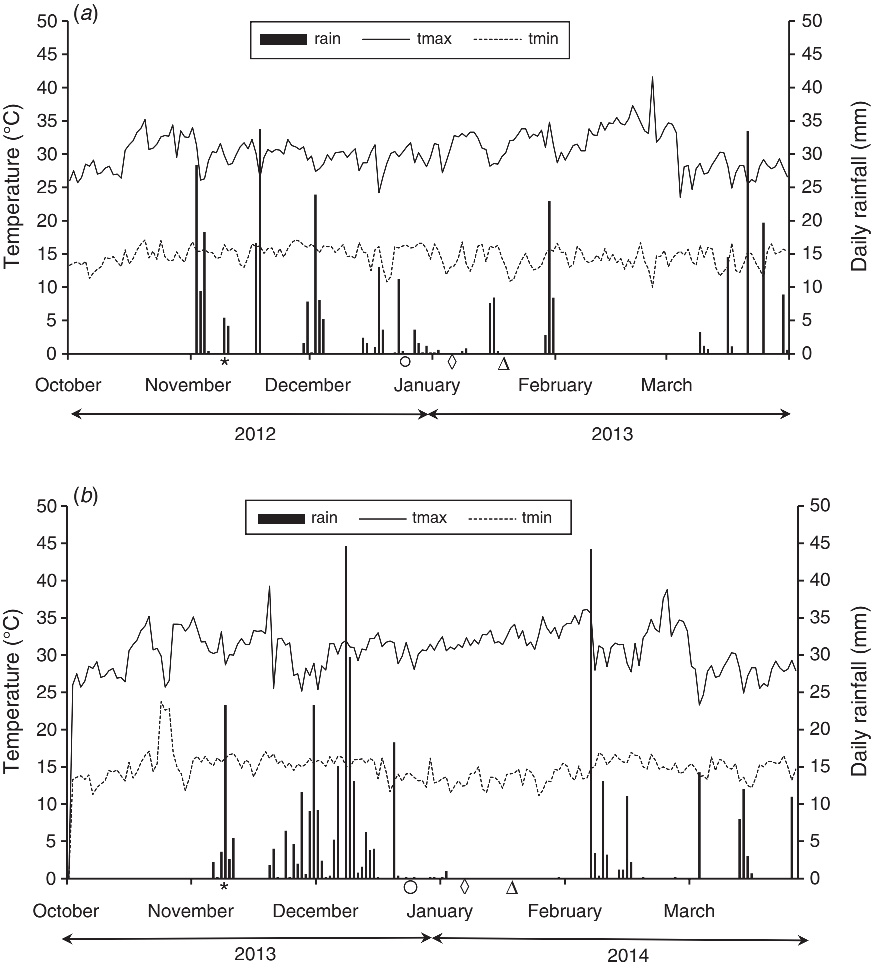

Fig. 1. Daily minimum (tmin) and maximum (tmax) temperatures and rainfall during the short rains at KARI, Katumani, Kenya: (*a*) 2012–13 and (*b*) 2013–14. Planting date (*); harvest dates for common bean (○), cowpea (◇), lablab (Δ).

lablab (Fig. 2). Bud formation in common bean started around 24–28 DAP and flowering at 31–41 DAP, with grain maturity at 69–78 DAP. Cowpea was characterised by a long vegetative phase, with flowering at 50 DAP, but with a relatively short grain filling period (87–95 DAP). Lablab started flowering earlier than cowpea, but did not reach physiological maturity until ~100 DAP.

Similar trends were observed for phenological development expressed in thermal time (Table 3). Compared with the 2012–13 season, flowering and physiological maturity were delayed for all legumes during the short rains in 2013–14 by ~7 days or 50–100 degree-days. However, no significant differences were observed in thermal time of phenological development between the different treatments (density and water regime) (data not presented). In contrast to the development time expressed as DAP, the development time expressed in degree-days was longer for common bean than cowpea, owing to the different cardinal temperatures used for their calculation.

LAI and fraction of PAR intercepted

In both experiments, differences in (spatial) development and growth characteristics of common bean, cowpea and lablab became obvious in their differences in LAI and fraction of intercepted PAR (Figs 3 and 4). LAI increased from planting to the end of flowering and decreased rapidly from the beginning of grain filling to physiological maturity. Interestingly, the speed of increase and reduction in LAI over time varied among the legumes because of differences in leaf appearance rate and overall canopy structure. The LAI of cowpea dropped rapidly immediately after flowering; however, lablab seemed to maintain almost maximum LAI for some time even after 50% flowering (Fig. 3). A strong effect of plant density on LAI was detected for common bean, with a faster increase in LAI and higher LAI values at high plant density than at medium and low densities. By contrast, the effect of plant density on LAI was weak for cowpea, indicating a growth compensation ability in space (Fig. 3). The response to the different water treatments was comparatively low in 2013–14 (Fig. 4). In 2012–13, the LAI

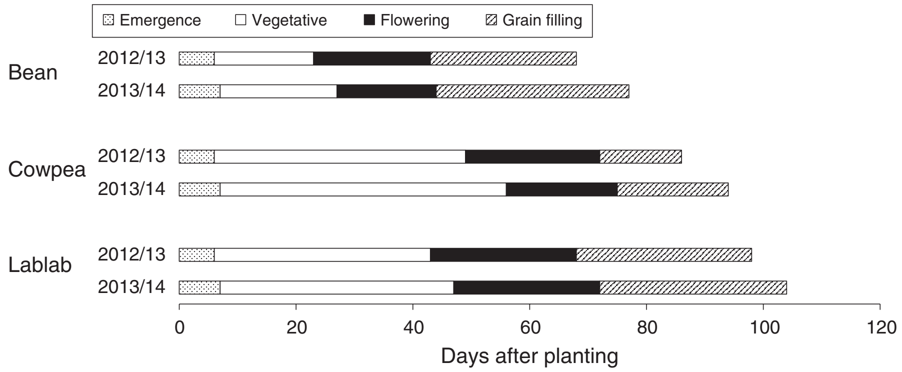

Fig. 2. Phenological development including emergence, vegetative phase, flowering and maturity of common bean, cowpea and lablab for the 2012–13 and 2013–14 growing periods at KARI, Katumani, Kenya.

Table 3. Phenological development of common bean, cowpea and lablab expressed as thermal time (degree-days) for seasons 2012–13 and 2013–14 at KARI, Katumani, Kenya

Thermal time to:	Common bean		Cowpea		Lablab	
	2012–13	2013–14	2012–13	2013–14	2012–13	2013–14
Emergence	93.09	95.11	43.71	55.12	74.60	91.29
Bud formation	326.59	370.78	493.13	577.34	536.35	586.43
First flowering	421.98	477.29	564.13	648.87	635.93	681.36
50% flowering	499.18	543.78	643.96	700.70	707.54	740.14
End of flowering	593.01	592.13	734.54	774.10	841.08	882.59
Maturity	911.64	985.98	887.46	988.06	1203.64	1270.77

of common bean reached almost 2 and was below 1 under rainfed conditions. In general, the highest LAI values (>4) were recorded for cowpea for the fully irrigated treatment at early flowering (56 DAP). The plants responded differently when supplementary irrigation was stopped at bud formation, also depending on rainfall distribution over the growing period (Figs 3 and 4).

Trends similar to those observed for the change in LAI were reflected in the change in the fraction of intercepted PAR (Fig. 5). Cowpea intercepted almost 100% of incoming PAR during the flowering period from early bud formation at 40 DAP to the start of grain filling at ~70 DAP, indicating a very high potential for aboveground biomass production and surface coverage. Lablab maintained fairly high ratios of intercepted PAR (0.8) for a relatively long period (40–85 DAP) covering flowering and grain filling. All legumes when planted at high densities reached maximum levels of fractional intercepted PAR earlier, indicating a fast canopy closure and good leaf coverage of soil at high planting densities. However, higher densities affected only the early stages of seasonal fractional PAR interception. At later stages, f levelled off and was similar for all plant densities, indicating some compensation by the low-density crop through greater branching and increased leaf area production per plant. Water treatment influenced the seasonal fractional PAR interception at later developmental stages from flowering onwards. For example, under rainfed conditions, the decrease in seasonal fractional PAR interception from bud formation onwards was evident and most severe for common bean (Fig. 5). For lablab, f continuously increased until the end of flowering (>80 DAP) even under rainfed conditions; however, levels did not reach the maximum of the fully irrigated plants (Fig. 5). Stopping the supplementary irrigation (partly irrigated treatment) at bud formation had little impact on seasonal fractional PAR interception, indicating that water stress was more important in early reproductive stages than in later reproductive stages.

Biomass development and partitioning

The dimensions of LAI and light interception were also reflected in aboveground biomass accumulation (Tables 4 and 5). In 2012–13, total aboveground biomass production at maturity was highest for cowpea (2600–5600 kg DM ha^{-1}), followed by lablab (2500–3800 kg DM ha^{-1}), and lowest for common bean (2200–3700 kg DM ha^{-1}). Plant density had a significant ($P < 0.05$) effect on the aboveground biomass accumulation of cowpea and lablab, but not common bean (Fig. 4). This indicates a vigorous growth habit and higher degree of phenological plasticity of cowpea and lablab. However, the effect of plant density on cowpea and lablab growth and development was not clear and differed between seasons. Final biomass production at maturity of cowpea, for instance, was similar (in 2013–14) or higher (2012–13) with planting at medium density compared with high density. Even if canopy closure and light interception were similar for common bean and cowpea at low densities compared with medium densities, total aboveground biomass and grain yields were reduced. Interestingly, a high plant density of lablab led to significantly higher biomass production at flowering; however, this trend levelled off towards maturity, indicating a high investment in vegetative plant organs and a low podset if planted at high density (Tables 4 and 5).

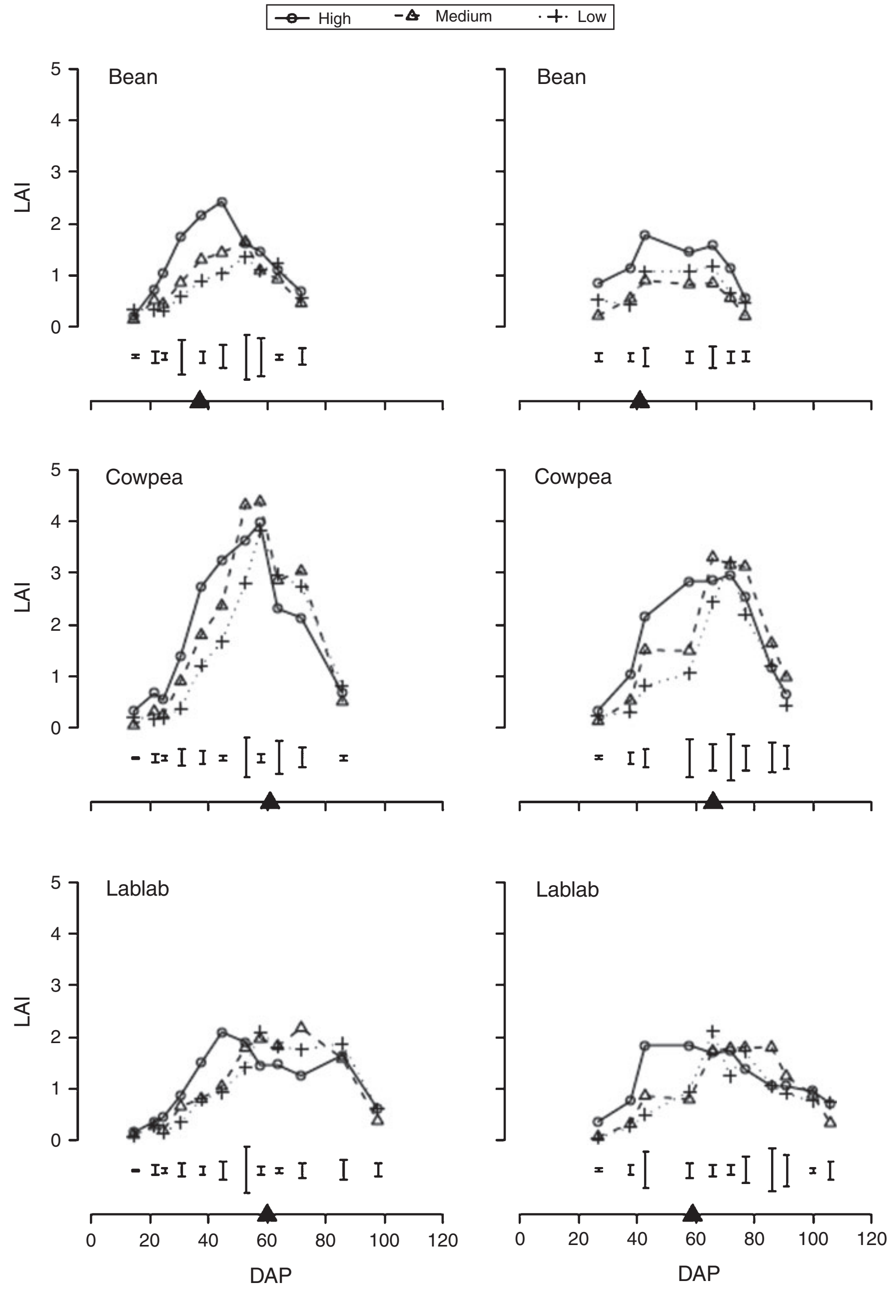

Fig. 3. Change in leaf area index (LAI) over the growing periods 2012–13 (left) and 2013–14 (right) for common bean, cowpea and lablab at three planting densities at KARI, Katumani, Kenya. Standard deviation is presented for the medium-density treatment. DAP, Days after planting. ▲, 50% flowering.

The effect of supplementary irrigation on biomass accumulation varied among legumes and between seasons. In cowpea, for instance, the aboveground biomass production at maturity more than doubled (5600 kg DM ha^{-1}) and significantly increased in 2012–13 under the fully irrigated treatment compared with the rainfed. For lablab, the increase was lower but still significant (Table 5).

Maximum biomass was not determined by leaf area and fraction of PAR interception alone, but influenced by the allocation of biomass among plant organs. Common bean had the highest biomass partitioning coefficient (Appendix 1, 0.48) on average across all plant-density treatments. Cowpea partitioned, on average, 43% of the total biomass to the leaves, whereas lablab partitioned only 35% (Appendix 1 and 2). The partitioning coefficient represents the biomass allocation among plant organs, indicative of the plant architecture and growth habit. Common bean for example was characterised by large leaves, whereas the spreading cowpea displayed longer stems and smaller leaves. The large and strong lablab plants also had generally more stem biomass in relation to leaf biomass,

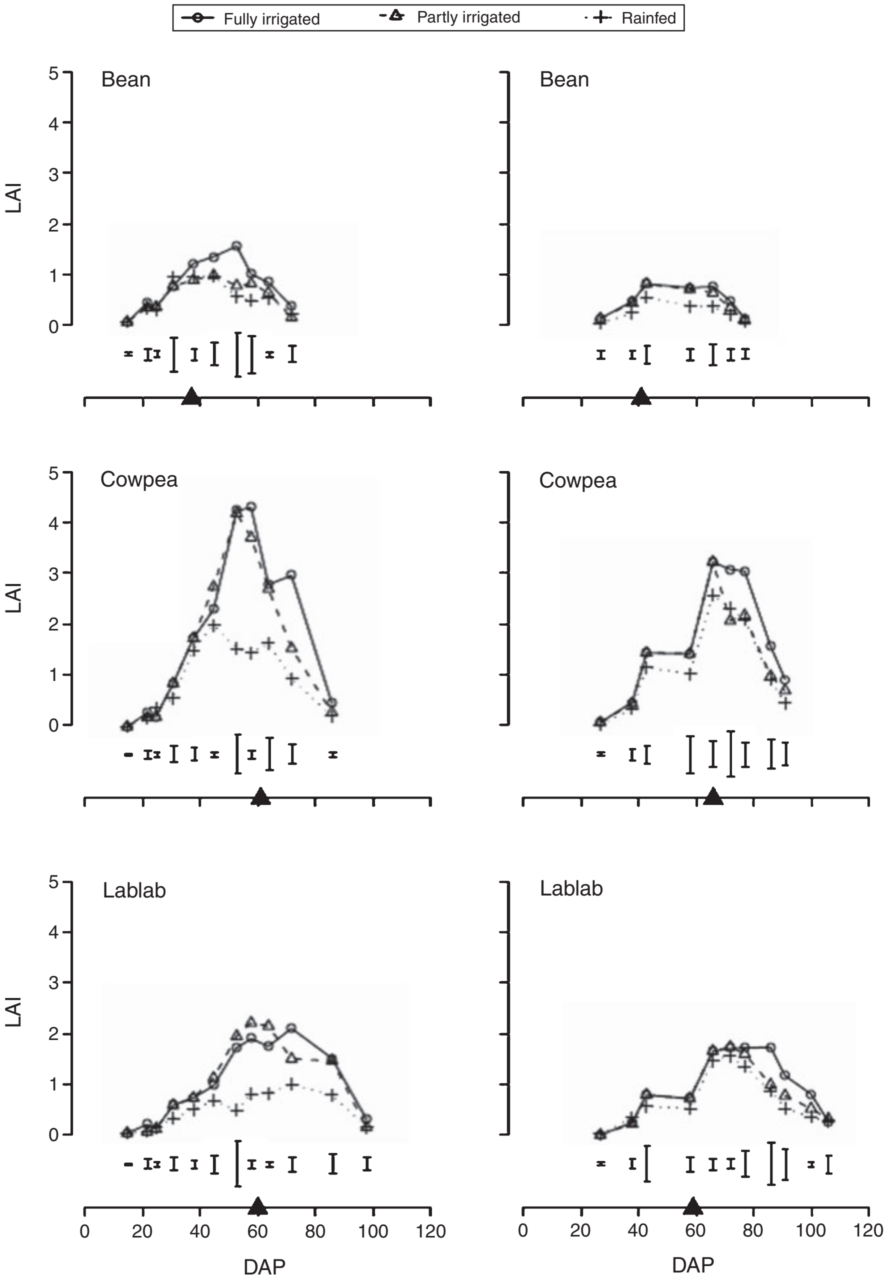

Fig. 4. Change in leaf area index (LAI) over the growing periods 2012–13 (left) and 2013–14 (right) for common bean, cowpea and lablab for three watering regimes at KARI, Katumani, Kenya. Standard deviation is presented for the fully irrigated treatment. DAP, Days after planting. ▲, 50% flowering.

represented in the low partitioning coefficient during early development stages. However, in general, plant density had no significant effect on biomass partitioning for all three legumes (Appendix 1 and 2, Table 4). For common bean and lablab, a significant reduction in the biomass partitioning coefficient was observed for the fully irrigated treatment compared with the rainfed treatment, indicating a greater investment in vegetative plant organs relative to reproductive plant parts during later development (Table 5).

Radiation-use efficiency (RUE in g MJ^{-1} PAR) was predicted from the interpolation of cumulative PAR against biomass production, with the coefficient of determination being fairly high for species, plant density and water regime ($R^2 > 0.65$) (Tables 6 and 7). Best fits were estimated for lablab with $R^2 > 0.76$. RUE estimates differed significantly ($P < 0.05$) among plant densities (Table 6) and water regimes (Table 7). For common bean, RUE was generally high and ranged from 0.92 g MJ^{-1} PAR under high plant density to 1.73 g MJ^{-1} PAR under low plant density (Table 6). Lablab had the lowest RUE, ranging from 0.62 to 0.92 g MJ^{-1} PAR for low to high plant density, respectively. Water regime had a significant effect on RUE only in common bean and cowpea (Table 7); under rainfed

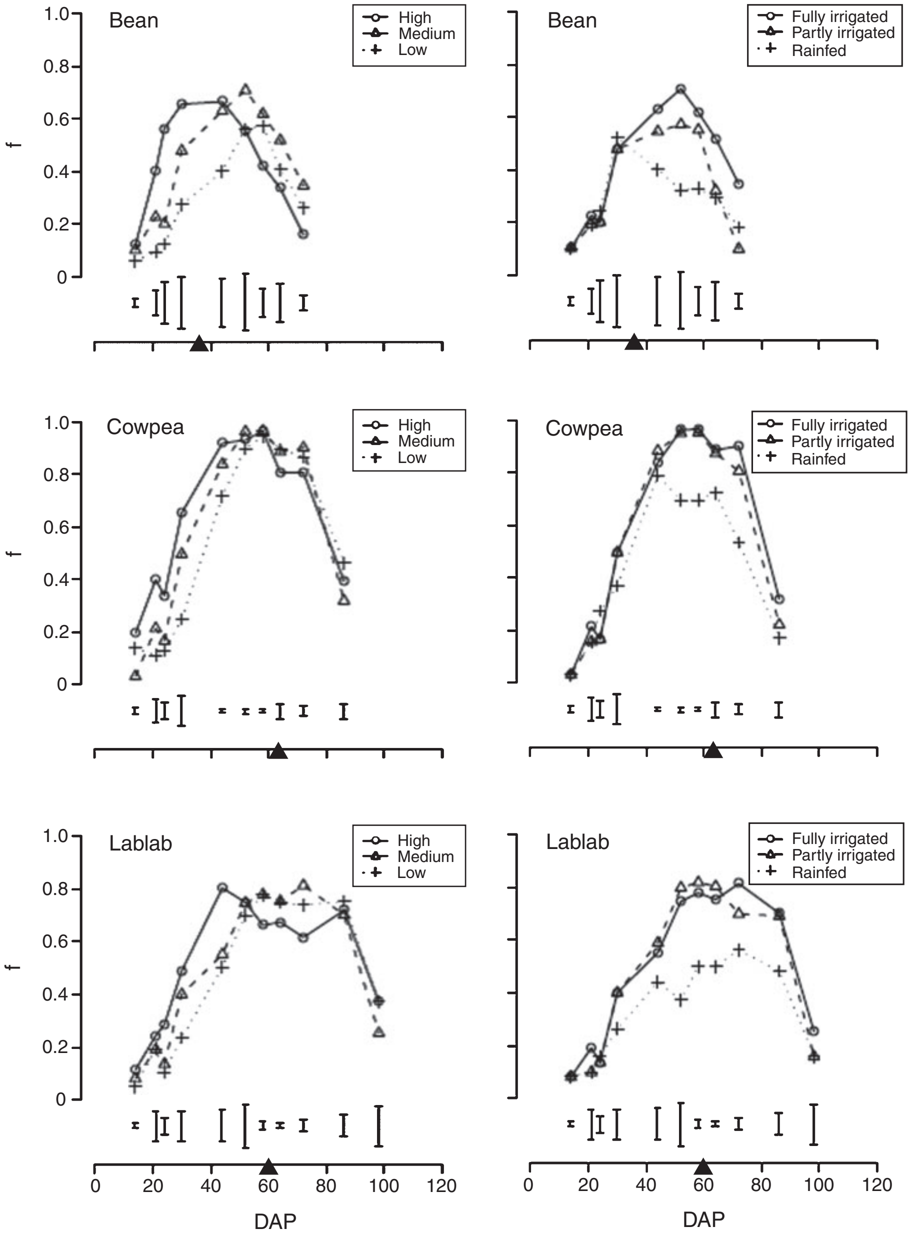

Fig. 5. Fraction of photosynthetically active radiation intercepted (*f*) over the growing period of 2012–13 for common bean, cowpea and lablab for three plant densities (left) and three water regimes (right) at KARI, Katumani, Kenya. Standard deviation is illustrated for the medium-density treatment (right) and the fully irrigated treatment (left). DAP, Days after planting. ▲, 50% flowering.

conditions, RUE was significantly lower than fully irrigated, reaching only 0.49 and 0.54 g MJ^{-1} PAR for common bean and cowpea, respectively.

Grain yield and harvest index

Grain yield varied strongly between the two seasons. At all planting densities, common bean and cowpea had higher grain yields in 2012–13 than in 2013–14. By contrast, lablab had higher yield in 2013–14 than in 2012–13. The effect of planting density varied among species within individual seasons (Table 8). In 2012–13, planting density had no significant effect on yield of common bean, whereas in 2013–14 yields were reduced by almost 20% at low planting density compared with medium and high densities. In cowpea, yields were reduced at low plant density (by 28% and 25% in 2012–13 and 2013–14, respectively). For lablab, yields were significantly reduced at low and high planting densities in 2012–13, but only at high density in 2013–14. The significant decrease in lablab grain yield (–27%) at high planting density indicated continuous investment in vegetative growth throughout the growing period, as reflected in the comparatively low biomass

Table 4. Total aboveground biomass as dry matter (kg ha^{-1}) at flowering and physiological maturity for common bean, cowpea and lablab for three planting densities from 2012–13 and 2013–14 seasons at KARI, Katumani, Kenya

Within columns, values followed by the same letter are not significantly different according to Tukey's multiple-comparison test ($P > 0.05$)

Plant density	Biomass at flowering			Total biomass at maturity		
	Common bean	Cowpea	Lablab	Common bean	Cowpea	Lablab
			2012–13			
Low	1185b	3974a	1178b	3306a	4319ab	2546b
Medium	2433a	4553a	2559a	3638a	5629a	3652a
High	2350a	3641a	2851a	3741a	3494b	3829a
Mean	1989	4056	2196	3562	4481	3342
			2013–14			
Low	1943ab	3019a	2367b	2771a	3425b	4682ab
Medium	1423b	3862a	3047b	3335a	4487a	5474a
High	2553a	3428a	4611a	3455a	4572a	4152b
Mean	1973	3436	3342	3187	4161	4769

Table 5. Total aboveground biomass as dry matter (kg ha^{-1}) at flowering and physiological maturity for common bean, cowpea and lablab for three water regimes in 2012–13 and 2013–14 seasons at KARI, Katumani, Kenya

Within columns, values followed by the same letter are not significantly different according to Tukey's multiple-comparison test ($P > 0.05$)

Water regime	Biomass at flowering			Total biomass at maturity		
	Common bean	Cowpea	Lablab	Common bean	Cowpea	Lablab
			2012–13			
Fully irrigated	2433a	4553a	2559a	3638a	5629a	3652a
Partly irrigated	1504b	3030b	2529a	2940ab	4068b	2937b
Rainfed	1219b	2156c	2466a	2182b	2574c	2966b
Mean	1719	3246	2518	2920	4090	3185
			2013–14			
Fully irrigated	1423a	3862a	3047a	3335a	4487a	5474a
Partly irrigated	879a	3446a	2477ab	2628ab	3431b	3965b
Rainfed	1332a	2219b	2002b	1762b	3030b	3906b
Mean	1211	3175	2509	2575	3649	4448

Table 6. Radiation-use efficiency derived from the regression analysis of aboveground biomass in dry matter and cumulative photosynthetically active radiation for common bean, cowpea and lablab for three plant densities calculated from the dataset derived from the growing period of 2012–13 at KARI, Katumani, Kenya

Values in parentheses represent R^2

Plant density	Common bean	Cowpea	Lablab
Low	1.73 (0.79)	1.26 (0.88)	0.62 (0.76)
Medium	1.40 (0.66)	1.06 (0.85)	0.90 (0.91)
High	0.92 (0.81)	1.31 (0.81)	0.92 (0.91)
Mean	1.35	1.21	0.81

Table 7. Radiation-use efficiency derived from the regression analysis of aboveground biomass in dry matter and cumulative photosynthetically active radiation for common bean, cowpea and lablab for three water regimes calculated from the dataset derived from the growing period of 2012–13 at KARI, Katumani, Kenya

Values in parentheses represent R^2

Water regime	Common bean	Cowpea	Lablab
Fully irrigated	1.40 (0.66)	1.06 (0.85)	0.90 (0.91)
Partly irrigated	1.42 (0.87)	1.02 (0.86)	0.81 (0.90)
Rainfed	0.49 (0.65)	0.54 (0.65)	0.76 (0.79)
Mean	1.10	0.87	0.82

partitioning coefficient and high share of leaf biomass. Yields were highest under fully irrigated treatments and declined under rainfed condition by ~50%, 30–50% and 20–30% for common bean, cowpea and lablab, respectively (Table 9). The effects of plant density and watering regime on grain yield were not reflected in HI. In 2012–13, the share of grain biomass in total biomass at harvest was >50% for common bean, cowpea and lablab, except for lablab at high planting density or under water-limited conditions.

The hypothesis of increased vegetative growth in dense plant stands was supported only in lablab, where the mean HI decreased under high planting density compared with medium and low densities in both years. The different water regimes did not change the HI of common bean and cowpea. Surprisingly, supplementary irrigation resulted in highest HI for lablab in 2012–13 but the lowest in 2013–14, indicating a high phenological plasticity aligned with environmental conditions. When grain yield was set in relation to maximum TDM at flowering, calculated values of HI were lower than for HI determined from TDM at harvest (Tables 8 and 9). Because biomass production of cowpea was highest at flowering in relation to grain yield, calculated HI (0.37 and 0.36 in 2012–13 and 2013–14, respectively) was lower than for beans (0.49 and 0.48 in 2012–13 and 2013–14, respectively) and lablab (0.43 and 0.39 in 2012–13 and 2013–14, respectively).

Discussion

Growth and development

The selection of crops and their varieties should aim to align the plant growth cycle with environmental conditions to allow the optimal use of available resources with the ability to adapt to environmental changes (Thomson and Siddique 1997; Cooper *et al.* 2008). Early emergence and fairly short vegetative periods of the selected short-season grain legumes allowed flowering and, most importantly, podset during the rainy period when soil moisture conditions are most favourable. The phenological development of the studied short-season grain legumes seemed to match the environmental conditions prevalent in semi-arid Eastern Kenya. However, the predicted warming trend for many parts of Eastern Africa (Boko *et al.* 2007; Stern 2007) suggests that varieties currently available will mature more quickly as the climate warms (Cooper *et al.* 2009). Furthermore, published studies report that severe drought can lead to accelerated ripening and, therefore, shortened development times (Hall 2004; Cooper *et al.* 2009). In particular, an earlier switch from vegetative to reproductive phase and accelerated ripening of the already short-season common bean might lead to reduced yields in the future, unless physiologically efficient varieties are developed that mature even earlier than currently (Beebe 2012). This requires further investigation and/or the application of crop-growth simulation models as suggested by Whitbread *et al.* (2010).

Table 8. Grain yield and harvest index calculated from total aboveground biomass at harvest and maximal aboveground biomass at flowering (in parentheses) for common bean, cowpea and lablab for three plant densities from 2012–13 and 2013–14 seasons at KARI, Katumani, Kenya

Within columns, values followed by the same letter are not significantly different according to Tukey's multiple-comparison test ($P > 0.05$)

Plant density	Grain yield (kg ha^{-1})			Harvest index		
	Common bean	Cowpea	Lablab	Common bean	Cowpea	Lablab
			2012–13			
Low	1822a	2192b	1271b	0.55a (0.61a)	0.51a (0.36ab)	0.50a (0.52a)
Medium	1888a	3061a	1933a	0.52a (0.44b)	0.54a (0.40a)	0.53a (0.43b)
High	1859a	1864b	1464b	0.50a (0.44b)	0.53a (0.34b)	0.38b (0.34c)
Mean	1857	2372	1556	0.52a (0.49)	0.53 (0.37)	0.47 (0.43)
			2013–14			
Low	1597b	1647b	2139a	0.58a (0.45b)	0.48a (0.35a)	0.43a (0.47a)
Medium	1956a	2210	2352a	0.59a (0.58a)	0.49a (0.36a)	0.43a (0.44a)
High	1882a	2189a	1707b	0.55a (0.42b)	0.48a (0.39a)	0.41a (0.27b)
Mean	1812	2015	2066	0.57 (0.48)	0.48 (0.37)	0.43 (0.39)

Table 9. Grain yield and harvest index calculated from total aboveground biomass at harvest and maximal aboveground biomass at flowering (in parentheses) for common bean, cowpea and lablab for three water regimes from 2012–13 and 2013–14 seasons at KARI, Katumani, Kenya

Within columns, values followed by the same letter are not significantly different according to Tukey's multiple-comparison test ($P > 0.05$)

Water regime	Grain yield (kg ha^{-1})			Harvest index		
	Common bean	Cowpea	Lablab	Common bean	Cowpea	Lablab
			2012–13			
Fully irrigated	1888a	3061a	1933a	0.52a (0.44b)	0.54a (0.40a)	0.53a (0.43a)
Partly irrigated	1557b	1968b	1438b	0.53a (0.51a)	0.49a (0.39a)	0.49a (0.36ab)
Rainfed	1107c	1385c	1234b	0.51a (0.48ab)	0.54a (0.39a)	0.42b (0.33b)
Mean	1518	2138	1535	0.52 (0.47)	0.52 (0.40)	0.48 (0.38)
			2013–14			
Fully irrigated	1956a	2210a	2352a	0.59a (0.58a)	0.49a (0.36ab)	0.43c (0.44a)
Partly irrigated	1460b	1541b	1996b	0.56a (0.62a)	0.45a (0.31b)	0.50a (0.45a)
Rainfed	978c	1513b	1873b	0.55a (0.42b)	0.50a (0.41a)	0.48b (0.48a)
Mean	1465	1754	2074	0.57 (0.54)	0.48 (0.36)	0.47 (0.46)

Besides temperature, the most critical parameter influencing growth and development in semi-arid areas is the availability of water. Results show that yield variability was very high for all three short-season grain legumes tested. Yield variability is generally high for grain legumes (e.g. Muchow 1985; Sinclair and Ludlow 1986; Ayaz *et al.* 2004*b*; Hall 2004; Tesfaye *et al.* 2006). In general, increased water supply leads to higher biomass and grain yield accumulation (Muchow 1985; Graham and Vance 2003; Hall 2004). However, the magnitude of the increase and the threshold of biomass and grain production differed significantly among the three legumes studied. Cowpea recorded the highest grain yields with supplementary irrigation, up to 3000 kg ha^{-1}, compared with rainfed conditions (1300–1500 kg ha^{-1}). The observed yields of cowpea were higher than those reported by Tesfaye *et al.* (2006) (1700 kg ha^{-1}) under well-watered conditions, or Uarrota (2010), who recorded only up to 800 kg ha^{-1} with adequate P fertilisation. The yield increase with increased water supply under fully irrigated conditions was less pronounced for common bean and lablab in the present study. Lablab, in particular, achieved comparatively high grain yields under rainfed conditions, especially in the 2013–14 season. Lablab seemed to cope best with the long dry spell in 2013–14 by making good use of the high rainfall during its vegetative period, suggesting some degree of drought tolerance and high phenological plasticity (Maundu *et al.* 1999; Maass *et al.* 2010).

Furthermore, all three legumes were characterised by pronounced leaf senescence towards the end of the growing period, leading to high HI values based on total biomass at maturity (Ayaz *et al.* 2004*b*). This led to increased biomass partitioning towards the grain and ensured comparatively high returns despite the relatively short growing period for all three short-season grain legumes. However, the HI, as a key determinant for potential yield accumulation, did not change significantly with different plant densities or water regimes either for cowpea or for common bean. This indicates that translocation to reproductive organs was not significantly affected by water availability (Unkovich *et al.* 2010). This result concurs with findings of Muchow *et al.* (1993) and Craufurd and Wheeler (1999), confirming the conservative nature of biomass partitioning. Consequently, grain yield of common bean and cowpea is primarily determined by the ability to accumulate biomass even under dry conditions (e.g. Hay 1995; Subbarao *et al.* 1995).

Light interception and radiation use efficiency

In terms of LAI and light interception, the strongest influence of plant density was observed for common bean owing to its fairly small size and compact canopy structure (characterised by comparatively low LAI <2). Higher plant density led to increased LAI and light interception during the vegetative growth phase. However, even if light interception was increased by increasing planting density, final grain yield was relatively stable, indicating a determined yield potential. By contrast, cowpea, because of its spreading growth habit and relatively big plants, reached high surface coverage (LAI <5) independent of plant density (Craufurd and Wheeler 1999), indicating a high ability for growth compensation. Surprisingly, increased planting density (high-density treatment) in cowpea and lablab led to vigorous vegetative growth and significantly increased biomass production but decreased podset and grain yield accumulation. This phenomenon is not well described in the literature, but was also observed on farmers' fields in Machakos, Kenya, where lablab was planted at densities similar to common bean (Grotelüschen, unpubl. data). Therefore, plant density can be considered critically important for successful grain production in these legumes.

Differences in canopy architecture and, consequently, differences in light interception (Fig. 5) (Huyghe 1998; Ayaz *et al.* 2004*a*) are also reflected in the distinct ability to convert intercepted radiation into DM as represented by the estimated RUE. The effect of water scarcity during crop growth was conspicuous for common bean and cowpea, where RUE was reduced by almost 70% and 50%, respectively. The RUE values reported by Tesfaye *et al.* (2006) were higher, estimating maxima of 2.44 and 2.16 g MJ^{-1} for common bean and cowpea, respectively; even under water stress in Ethiopia, RUE remained relatively high, reaching 1.5 and 1.59 g MJ^{-1}, respectively, owing to much higher estimated DM accumulation for the varieties used in their study. The present findings, however, are consistent with those of Muchow *et al.* (1993), who report RUE of 1.05–1.16 g MJ^{-1} for cowpea under non-stressed conditions and 0.64 g MJ^{-1} in a water-limited environment. Craufurd and Wheeler (1999) concluded that drought in early stages of cowpea growth affects f more than RUE, whereas the opposite is true for drought during the reproductive stage, because leaf senescence is not as sensitive to drought as leaf development. Cowpea adjusts f through decreased leaf development if drought is experienced in early vegetative stages and through moderate leaf senescence if drought occurs at reproductive development (Craufurd and Wheeler 1999). This strategy to regulate source–sink dynamics may be favourable under optimal water supply, but is risky if frequent droughts are experienced. Lablab seemed to follow a fairly conservative strategy, with maximum RUE lower than in common bean or cowpea; however, no significant reduction in RUE was observed under rainfed conditions, indicating better assimilation efficiency under dry conditions and better adaptation to a semi-arid environment. Moreover, lablab was observed to be able to change the leaf angle position when sun exposure changed (paraheliotropism). This is an adaptation strategy to optimise radiation interception and water loss through transpiration. Pastenes *et al.* (2004) proved that paraheliotropism can help to minimise water loss and heat stress in common bean, thus allowing better radiation use under water-limited conditions. These findings are in agreement with the hypothesis by Pengelly *et al.* (1999), who stated that a high RUE can be advantageous under non-water-limiting conditions but may indicate high drought susceptibility and, consequently, high production risk in drier years. On the other hand, low RUE might reflect a conservative agro-morphological plasticity, challenging the crop to respond to superior, favourable conditions in periods of higher rainfall (Pengelly *et al.* 1999; Black und Ong 2000). Consequently, high RUE should not necessarily be the primary breeding goal if drought resistance is the major trait of interest. In summary, RUE is one of the key indicators for describing plant development and resource use. It was found to be strongly influenced by plant density and water availability. This interaction with management and environmental factors must, therefore, be considered necessary information in plant growth models.

Towards improved adaptation in semi-arid environments

Common bean had the shortest life cycle, reaching maturity in <80 days. This is advantageous for cropping systems with short rainy season and useful for adaptation to climate change (Muchow *et al.* 1993; Tesfaye *et al*. 2006). Furthermore, growth of common bean was characterised by its relatively low total leaf area due to a rather compact growth habit. The recommended varieties of common bean are therefore suitable for intercropping with cereals because of their optimal and less competitive use of light in space and time. Its disadvantage is the low biomass production compared with cowpea and lablab, which reduces the potential benefit from both biological nitrogen fixation and nutrient recycling.

Cowpea was characterised by a comparatively long vegetative phase (~50 days) and a relatively short grain-filling period. Consequently, cowpea can benefit more from favourable soil moisture under optimal conditions. The dense leaf surface (high LAI) decreases possible water loss through soil evaporation and helps to conserve soil moisture. This can be advantageous in decreasing water loss through soil evaporation and increasing the water-use efficiency of the system. At the same time, very high yield losses are recorded if in-season droughts are experienced (Tesfaye *et al.* 2006; Uarrota 2010), because cowpea leaf appearance and expansion are extremely sensitive to drought (Uarrota 2010). Furthermore, the vigorous growth habit under favourable conditions and possible competiveness would make timing of sowing of cowpea critically important if incorporated in intercropping systems in association with non-legume crops. Watiki *et al*. (1993) further highlight that plant densities adjusted to the location-specific resource availability, especially water availability, are of great importance in reaching optimal light interception to produce high grain yield in maize–cowpea intercropping systems. Nevertheless, cowpea leaves are a highly valued African vegetable (Dube and Fanadzo 2013) and high leaf productivity is a major feature of many cowpea varieties with the potential to add to smallholders' food and nutrition security, health and income.

Time to maturity for lablab was comparatively long (<100 days), resulting from a combination of long flowering time and grain-filling period. However, lablab still has the potential to return seeds within one season in semi-arid Eastern Kenya, even if the season is short and the rain stops earlier than expected (Whitbread *et al.* 2011). Lablab seemed the most consistent and robust among the three legumes, with stable RUE, even under water-limited conditions. The comparatively long growing period allowed lablab to buffer environmental shocks, leading to fairly stable biomass production and grain yield. Relatively high grain yields of lablab, even under dry conditions, are in agreement with observations by Maundu *et al*. (1999) and the review by Maass *et al*. (2010). Moreover, lablab herbage can be used as a quality animal feed, helping to boost milk production if obtained in sufficiently large quantities (Njarui *et al.* 2004). On the other hand, lablab cultivars that are compact and of ultra-short duration are known from India, Bangladesh and China (Maass *et al.* 2010); their suitability should be tested in the Eastern African environment.

This study has highlighted the potential for exploiting differences in morphology and phenology. Other research has confirmed pronounced phenological plasticity of legumes and their distinctive ability to respond to changing environmental conditions (Acosta-Gallegos and White 1995; Jeuffroy and Ney 1997; Ayaz *et al.* 2004*b*). Diversity in common bean is known to be among the highest for food crops around the world, with very high levels of variation in development time and growth habit (Jones 1999). Similarly, lablab is one of the agro-morphologically most diverse tropical legumes (Maass *et al.* 2010). The differences described here are, therefore, rather characteristic of the selected varieties instead of true species differences.

Conclusions

In summary, the studied legumes followed different adaptation strategies to cope with short growing periods and restricted water availability. This study revealed important differences in growth and development of three legume species and varieties and characterised the usefulness of certain traits such as short growing periods and compact canopy architecture for different application within the smallholder farming systems. This can be exploited to fill niches for short-season grain legumes and to design strategies for improved adaptation in the small-scale farming systems of Eastern Kenya and other semi-arid environments with similar climate and soil types. Furthermore, the information generated is particularly valuable for use in crop modelling to advise agronomists and plant breeders on management and genetic options for semi-arid areas.

Acknowledgements

We thank the technical staff of KALRO, Katumani, Kenya for their continuous support and encouragement during the on-station field research. The German academic exchange service (DAAD) supported this research by providing a travel scholarship enabling the senior author to conduct field research in Kenya. Operational expenses were funded by the University of Göttingen via the chair group position of Tropical Plant Production and Agricultural Systems Modelling. The CGIAR Research Program (CRP) on Dryland Systems is acknowledged for partly funding the time of AM Whitbread, and CRP on Livestock and Fish for partly funding BL Maass.

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Appendix 1. Biomass partitioning coefficient for common bean, cowpea and lablab calculated for three plant densities at KARI, Katumani, Kenya

Calculated from combined data over two growing seasons (2012–13 and 2013–14). Values within a column followed by the same letter are not significantly different according to Tukey's multiple-comparison test ($P > 0.05$)

Plant density	Common bean	Cowpea	Lablab
Low	0.49a	0.45a	0.34a
Medium	0.47a	0.41a	0.37a
High	0.47a	0.43a	0.34a
Mean	0.48	0.43	0.35

Appendix 2. Biomass partitioning coefficient for common bean, cowpea and lablab calculated for three water regimes at KARI, Katumani, Kenya

Calculated from combined data over two growing seasons (2012–13 and 2013–14). Values within a column followed by the same letter are not significantly different according to Tukey's multiple-comparison test ($P > 0.05$)

Water regime	Common bean	Cowpea	Lablab
Fully irrigated	0.47b	0.41a	0.37b
Partly irrigated	0.53a	0.43a	0.41a
Rainfed	0.52a	0.42a	0.39ab
Mean	0.51	0.42	0.39