How weather during development of common bean (*Phaseolus vulgaris* L.) affects the crop's maximum attainable seed quality

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Abstract

Weather conditions affect the seed quality of major crops including common bean. This study aimed to evaluate whether seed quality is affected through weather effects on the quality achievable at the end of seed filling (PM) or through changes in quality during maturation drying in the period between PM and harvest maturity (HM). The research also aimed to establish relationships between seed yield and seed quality. Twenty-four common bean (*Phaseolus vulgaris* L.) crops from two cultivars were sown on different dates in Eldoret and Kitui, Kenya. Seed quality was quantified as the percentage of viable seeds determined with a tetrazolium test, and as vigour measured by electrical conductivity (EC). Over the range of weather conditions during our study, high temperatures were more detrimental to seed quality than little rainfall. The two cultivars differed in susceptibility to high temperatures. High temperatures and little rainfall seemed to reduce seed quality mainly through reducing maximum quality attainable during the course of crop development. The quality in general did not change significantly between PM and HM, but in some cases the proportion of viable seeds increased between PM and HM, especially when ambient temperatures were relatively low. For seed samples free from mechanical damage, EC appeared to be an unsuitable criterion to detect quality differences at HM, because in almost all seed lots quality was indiscriminately classified as 'good', whereas viability varied between 69 and 100%. Production conditions leading to low seed yields or seeds of low weight resulted in a low percentage of viable seeds but conditions resulting in fairly high yields or heavy seeds did not guarantee a high percentage of viable seeds.

Additional keywords: crop development, drought, heat, rainfall, seed viability, seed vigour, seed yield, temperature

Introduction

Poor quality seeds resulting from variable weather conditions before and during seed formation can hinder the production of major food crops including common bean. Maximum seed quality of field crops is reported to be obtained around physiological maturity (PM), i.e., at the end of seed filling when seed dry weight is maximum (Egli, 1998). The seeds of most crops that are harvested as dry seeds attain maximum viability and vigour at PM (TeKrony & Egli, 1997), but this moment of obtaining maximum seed quality can also be later, depending on the seed quality test used, the method of seed drying before testing, or the season (e.g., Sanhewe & Ellis, 1996a, b; Muasya *et al.*, 2002a). The crop is harvested at harvest maturity (HM) when the seeds have dried to a moisture content at which harvesting is possible without considerable damage. The final seed quality at HM may be influenced by the growing conditions before PM and during maturation drying between PM and HM. The main environmental factors involved are rainfall (drought) and temperature (heat).

In soya bean, drought during vegetative growth causes large reductions in vegetative plant size and reduces leaf area, eventually impeding seed filling and leading to seeds of low weight (Meckel *et al.*, 1984). In common bean, drought at flowering results in flower abortion (Calvache *et al.*, 1999), and drought stress during pod set in faba bean decreases the number of pods and seed yield (Mwanamwenge *et al.*, 1999). In soya bean, drought during seed filling leads to shortening of the seed filling period, incomplete filling, reduction in individual seed weight and eventually in forced maturation drying of the seed (Meckel *et al.*, 1984; Dornbos & Mullen, 1991; Egli, 1998; Egli & Bruening, 2004). Drought stress in soya bean during seed filling also decreases seed vigour, and results in shrivelled, flat and underdeveloped seeds (Vieira *et al.*, 1992; Bandeh & Jalilian, 1997).

In common bean high temperatures during flowering result in shedding of flowers, leading to the formation of fewer pods (Gross & Kigel, 1994), whereas in soya bean high temperatures near the end of pod set reduce seed numbers (Spears *et al.*, 1997; Egli, 1998). Soya bean seeds exposed to high temperatures during seed filling tend to be less viable and less vigorous (Spears *et al.*, 1997; Egli *et al.*, 2005).

When maturation drying is in progress, high rainfall can cause embryo damage because of uptake of water by the seed (e.g., Tu *et al.*, 1988). High temperatures during maturation drying reduced seed viability and vigour in soya bean (e.g., Spears *et al.*, 1997). In glasshouse experiments with common bean higher temperatures (27/22 °C or 33/28 °C) during maturation drying led to a lower percentage of seeds producing normal seedlings than lower temperatures (18/13 °C or 21/16 °C) (Siddique & Goodwin, 1980).

This study aims to evaluate whether temperature and rainfall under field production conditions affect seed viability and vigour through effects on the quality achievable at PM or through influencing the change in quality during maturation drying of the seeds between PM and HM. In addition we shall test the general notion that production conditions favourable for seed yield are also favourable for seed quality.

Materials and methods

Experimental sites, experimental set-up and crop and seed management

Different seed lots of common bean (*Phaseolus vulgaris* L.) were produced by growing 2 cultivars sown on 3 dates in 2 seasons and at 2 locations (Kitui and Eldoret, Kenya) (Table 1). At each site and in each season the experimental design was a split plot with 4 replications. The 2 cultivars, Rosecoco and Mwezi Moja, were assigned to main plots. Both are determinate cultivars, but Rosecoco is characterized by prolonged flowering whereas the flowering period of Mwezi Moja is short. Sowing dates were assigned to subplots. Each plot measured 16 m^2. Temperature and rainfall were recorded throughout the growing periods.

At planting, the plots were fertilized with calcium ammonium nitrate (26% N), triple super phosphate (48% P_2O_5) and muriate of potash (60% K_2O), at rates of 80 kg N, 100 kg P and 40 kg K per hectare, respectively. Two seeds were planted per hill, with hills spaced at 0.5 m × 0.1 m. After emergence the seedlings were thinned to one per hill. The moment of PM was estimated by change of pod colour from green to green yellow and seed colour from green yellow to 100% red purple (Muasya *et al.*, 2002b). HM was determined by the moment at which all pods had changed colour from green yellow to straw yellow (Muasya *et al.*, 2002b). Colours were assessed using Munsell colour charts (Anon., 1972).

Within the net experimental area of each subplot, two areas of 2 m^2 (40 plants) were used for quality determinations at PM and HM. From one area all pods were harvested. Seeds were removed by hand and only normal looking seeds were selected and further dried at 30 °C in a continuous flow dryer until a moisture content of 14% was reached. The seeds were then stored in airtight containers at 2 °C for on average three months, followed by sampling for the determination of electrical conductivity and the percentage of viable seeds. The second area of 2 m^2 was used for yield and seed weight determinations at HM.

Developmental periods

The period of vegetative mass accumulation was the period from seedling emergence (7 days after sowing) until there was no further increase in ground cover by the leaves. To establish the pattern of flower and pod development over time, all flowers in a row of 20 plants were counted every two days starting on the first day of anthesis. Flowering duration was the time interval in days between the opening of the first and the last flower. The number of pods that had reached a length of 12 cm or more was recorded every two days. The duration of pod set was defined as the period from the day the first pod of 12 cm was recorded until the day when there was no further increase in pod number. Seed filling duration was defined as the period from the day the first pods were 12 cm until and including the day of PM. Maturation drying was the time interval in days from the day of PM until and including the day of HM.

Table 1. Sowing and harvesting dates, growth duration, temperature sum and total rainfall for the common bean crops grown for seed quality assessment in different seasons at Kitui and Eldoret, Kenya.

	Cultivar	Kitui		Eldoret	
		Season 1	Season 2	Season 1	Season 2
First sowing date					
Date of sowing	Rosecoco	05.11.1998	11.03.1999	01.07.1998	11.03.1999
	Mwezi Moja	05.11.1998	11.03.1999	01.07.1998	11.03.1999
Date of harvesting	Rosecoco	28.01.1999	03.06.1999	12.10.1998	24.06.1999
	Mwezi Moja	27.01.1999	02.06.1999	12.10.1998	17.06.1999
Growth duration (days)	Rosecoco	84	84	103	105
	Mwezi Moja	83	83	103	98
Total rainfall (mm)	Rosecoco	845	382	535	364
	Mwezi Moja	845	382	535	321
Temperature sum (°Cd) [1]	Rosecoco	2122	1911	1369	1497
	Mwezi Moja	2094	1890	1369	1403
Second sowing date					
Date of sowing	Rosecoco	19.11.1998	25.03.1999	21.07.1998	26.04.1999
	Mwezi Moja	19.11.1998	25.03.1999	21.07.1998	26.04.1999
Date of harvesting	Rosecoco	17.02.1999	17.06.1999	27.10.1998	17.08.1999
	Mwezi Moja	16.02.1999	16.06.1999	27.10.1998	10.08.1999
Growth duration (days)	Rosecoco	90	84	98	113
	Mwezi Moja	89	83	98	106
Total rainfall (mm)	Rosecoco	420	264	486	636
	Mwezi Moja	420	264	486	503
Temperature sum (°Cd)	Rosecoco	2318	1872	1334	1554
	Mwezi Moja	2296	1853	1334	1460
Third sowing date					
Date of sowing	Rosecoco	08.12.1998	09.04.1999	20.08.1998	15.05.1999
	Mwezi Moja	08.12.1998	09.04.1999	20.08.1998	15.05.1999
Date of harvesting	Rosecoco	27.02.1999	30.06.1999	25.11.1998	30.09.1999
	Mwezi Moja	26.02.1999	29.06.1999	25.11.1998	24.09.1999
Growth duration (days)	Rosecoco	81	82	97	138
	Mwezi Moja	80	81	97	132
Total rainfall (mm)	Rosecoco	117	144	287	547
	Mwezi Moja	117	144	287	544
Temperature sum (°Cd)	Rosecoco	2135	1778	1359	1888
	Mwezi Moja	2112	1759	1359	1802

[1] Base temperature: 0 °C.

Electrical conductivity test

Electrical conductivity was determined after equilibrating the seeds from cold storage for 3 days at room temperature (19–25 °C). Their moisture content was then constant at 12%. Per treatment combination 4 replicate samples (one from each block) of 50 seeds were weighed and incubated in 250 ml of distilled water at 20 °C for 24 hours. A control was included, consisting of an equivalent amount of distilled water but without seeds. Electrical conductivity (μS cm^{-1}) was measured using a Fieldlab LF conductivity meter and an LF 513T electrode dip type cell (Schott Gerate Glass Company, Mainz, Germany). The conductivity per gram of seed weight (μS cm^{-1} g^{-1}) at 12% moisture content at PM and HM was then calculated to estimate vigour (Hampton & TeKrony, 1995).

Tetrazolium test

Per treatment combination four replicate samples (one from each block) of 20 seeds were taken from the cold storage and kept at room temperature (19–25 °C) for one day before soaking in water at room temperature for 24 hours. The seeds were cut longitudinally through the middle of the embryonic axis and soaked in a 0.5% tetrazolium (2,3,5-triphenyltetrazolium chloride) solution at 30 °C for 3 hours, briefly washed in distilled water and examined under hand lens magnification (Hampton & TeKrony, 1995). The staining of the embryo was examined per seed. Seeds with sound tissues and those with no staining in small, non-critical parts – mainly in the cotyledons – (weakly viable seeds) were combined to calculate viability, i.e., the percentage of viable seeds.

Statistical analysis

Replicated values were averaged to derive one value for each of the 24 seed crops grown under a given set of conditions. These averages were used in the further analysis. Linear correlation coefficients were calculated to establish associations between different seed quality parameters over seed lots. T-tests were used to determine whether there were quality differences between sites, cultivars or harvesting moments. Single and multiple linear regression analyses were carried out using Genstat 5 (Release 4.1) to establish associations between weather data and seed quality and yield. Average rainfall and average temperatures data were used as explanatory variates (x), the other parameters as response variates (y). The statistical significance of associations was established using the adjusted R^2. First, linear associations were established over all seed lots. Next, the factors site and cultivar were added individually and in combination to the regression model. When addition of these factors significantly ($P < 0.05$) increased R^2, regression curves were also calculated for the individual combinations of site and/or cultivar.

Results

Seed quality at physiological maturity and harvest maturity

At physiological maturity (PM), the percentage of viable seeds of the seed lots produced under different conditions varied between 51 and 99%, and the bulk electrical conductivity (EC) ranged from 7 to 42 μS cm^{-1} g^{-1} (Figure 1A). Across seed lots, a lower percentage of viable seeds was closely associated with a higher EC value (Figure 1A).

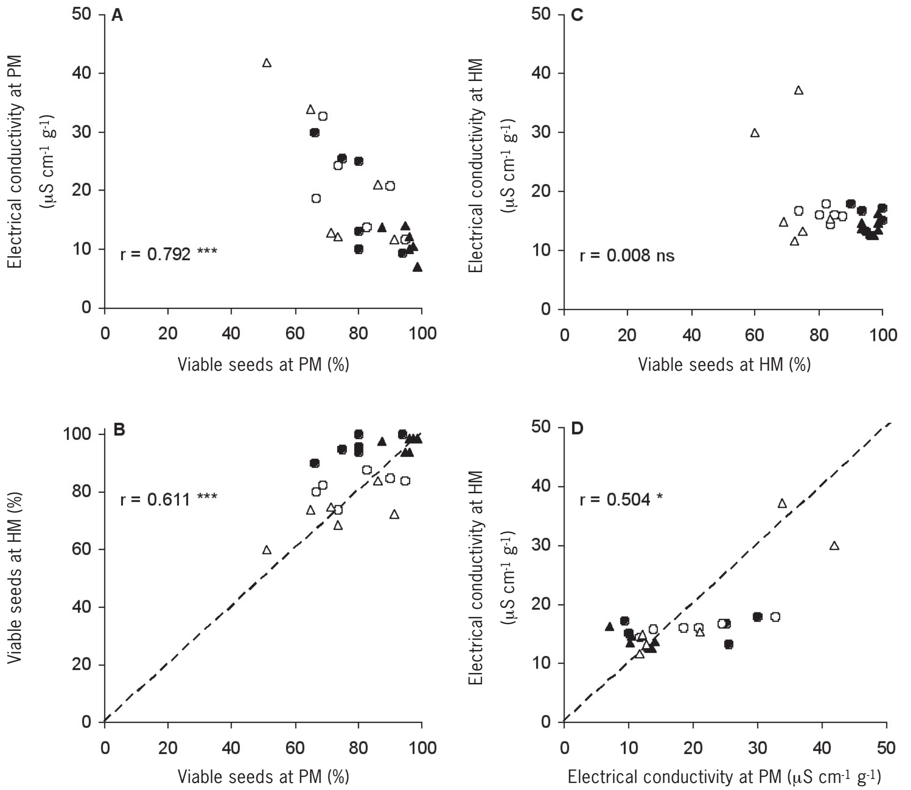

Figure 1. Associations between percentage viable seeds (determined with the tetrazolium test) and electrical conductivity (EC) for seeds from 24 common bean crops of the cultivars Rosecoco and Mwezi Moja, grown at Eldoret and Kitui, Kenya, and harvested at physiological maturity (PM) or harvest maturity (HM). A: between percentage viable seeds and EC, both at PM; B: between percentage viable seeds at HM and at PM; C: between percentage viable seeds and EC, both at HM; D: between EC at PM and at HM. Dashed lines in B and D indicate equal seed quality at PM and HM. Eldoret: closed symbols; Kitui: open symbols; cv. Rosecoco: ●, ○ ; cv. Mwezi Moja: ▲, Δ. ***: $P < 0.001$, *: $0.01 \leq P < 0.05$, ns: $P \geq 0.05$. Correlation coefficients (r) were calculated over 22 seed lots, i.e., two deviating lots were excluded.

Table 2. Percentage of viable seeds and electrical conductivity at physiological and harvest maturity for the common bean cultivars Rosecoco and Mwezi Moja grown in six periods at Eldoret and Kitui, Kenya (n = 6; values per cultivar per site per harvest time).

	Physiological maturity				Harvest maturity				Harvest time effect		
	Eldoret	Kitui	Average over sites	Site effect	Eldoret	Kitui	Average over sites	Site effect	Eldoret	Kitui	Average over sites
Percentage viable seeds											
cv. Rosecoco	79.2	79.7	79.4	ns [1]	95.8	82.3	89.1	***	**	ns	**
cv. Mwezi Moja	95.3	73.0	84.2	**	97.2	72.5	84.8	***	ns	ns	ns
Average over cultivars	87.3	76.3	81.8	*	96.5	77.4	87.0	***	**	ns	*
Cultivar effect	**	ns	ns		ns	*	ns				
Electrical conductivity (μS cm^{-1} g^{-1})											
cv. Rosecoco	18.8	20.3	19.6	ns	15.5	16.1	15.8	ns	ns	ns	ns
cv. Mwezi Moja	11.2	22.2	16.7	ns	14.2	20.4	17.3	ns	ns	ns	ns
Average over cultivars	15.0	21.3	18.1	ns	14.8	18.3	16.6	ns	ns	ns	ns
Cultivar effect	*	ns	ns		ns	ns	ns				

[1] Statistical significance. ns = not significant ($P \geq 0.05$) ; * = significant at $0.01 \leq P < 0.05$; ** = significant at $0.001 \leq P < 0.01$; *** significant at $P < 0.001$, according to the t-test.

The percentage of viable seeds was higher for Eldoret than for Kitui, which was entirely accounted for by the better performance of cv. Mwezi Moja in Eldoret (Table 2). EC values were not significantly different between the two sites (Table 2).

At harvest maturity (HM), the seed lots produced under different conditions still varied greatly in percentage viable seeds (Figure 1C), but little variation was found in EC, which in most seed lots was around 15 μS cm^{-1} g^{-1} (Figure 1C). Only 2 out of the 24 seed lots had a higher EC. Consequently, lower percentages of viable seeds were no

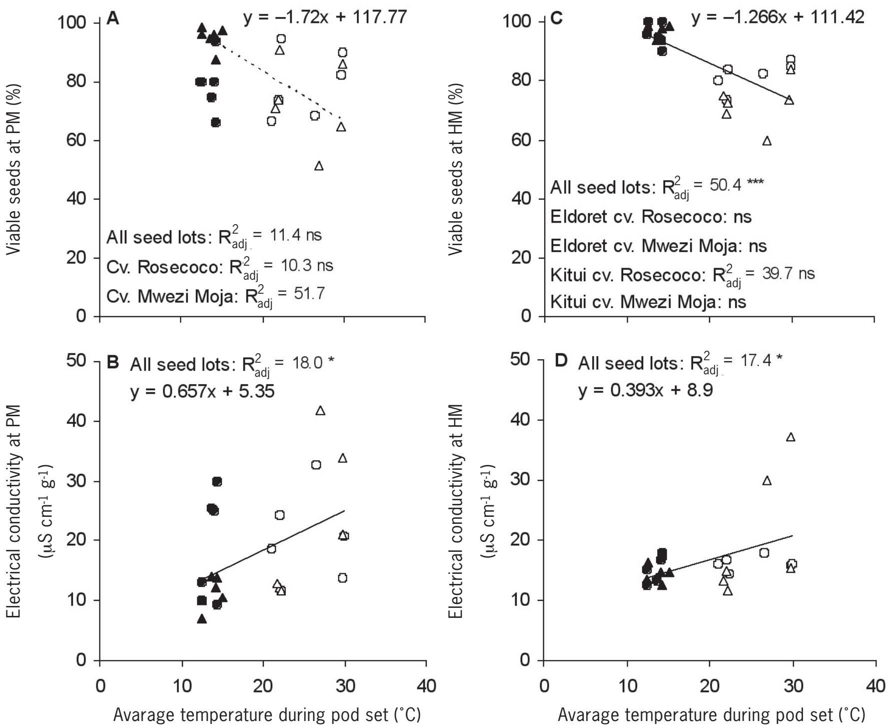

Figure 2. Associations between average daily temperature during pod set and percentage viable seeds (A, C) or electrical conductivity (EC) (B, D) for seeds from 24 common bean crops of the cultivars Rosecoco and Mwezi Moja, grown at Eldoret and Kitui, Kenya, and harvested at physiological maturity (PM) or harvest maturity (HM). Eldoret: closed symbols; Kitui: open symbols; cv. Rosecoco: ●, ○ ; cv. Mwezi Moja: ▲, Δ. Uninterrupted lines indicate statistically significant ($P < 0.05$) regression lines over all seed lots. Dotted line indicates statistically significant regression line for specific site and/or cultivar combinations. The latter were calculated when adding site or cultivar to the regression model significantly ($P < 0.05$) improved the R^2 of the model. R^2 values presented are for the regression model over all seed lots and for individual site and/or cultivar combinations when relevant. When no value is presented for the R^2, the residual variance exceeded the variance of the response variate; ***: $P < 0.001$, **: $0.001 \le P < 0.01$, *: $0.01 \le P < 0.05$, ns: $P \ge 0.05$.

longer associated with high EC values (Figure 1C). The percentage of viable seeds was higher for Eldoret than for Kitui for both cultivars (Table 2).

Across all crops, a higher percentage of viable seeds at PM was associated with a higher percentage of viable seeds at HM (Figure 1B). Higher EC values at PM were weakly associated with higher EC values at HM, even when the two deviating seed lots were excluded from the analysis (Figure 1D), which is ascribed to the small variation in bulk EC at HM.

Between PM and HM, seed quality of individual crops could still change (Figures 1B and D). On average, the percentage of viable seeds increased, but this was almost exclusively accounted for by cv. Rosecoco in Eldoret (Table 2). On average, EC did not change significantly between PM and HM (Table 2).

Table 3. Slope and statistical significance of the adjusted R^2 (R^2_{adj}) between the average daily temperature and rainfall in different growth phases (x) and percentage of viable seeds and electrical conductivity at physiological and harvest maturity (y) as established by linear regression analysis over all seeds lots (df_{total} = 23).

	Physiological maturity				Harvest maturity			
	Viable seeds (%)		Electrical conductivity (μS cm^{-1} g^{-1})		Viable seeds (%)		Electrical conductivity (μS cm^{-1} g^{-1})	
	Slope	R^2_{adj}	Slope	R^2_{adj}	Slope	R^2_{adj}	Slope	R^2_{adj}
Average temperature (°C) *during*:								
Vegetative mass accumulation	−1.271	* [1] [c]	0.767	* [s]	−1.896	*** [cs]	0.408	ns
Flowering	−0.729	ns [c]	0.594	*	−1.451	*** [cs]	0.361	*
Pod set	−0.767	ns [c]	0.657	*	−1.266	*** [cs]	0.393	*
Seed filling	−0.833	ns [c]	0.699	*	−1.382	*** [cs]	0.427	*
Maturation drying					−1.916	*** [cs]	0.506	*
Average daily rainfall (mm) *during*:								
Vegetative mass accumulation	−0.126	ns [s]	0.341	ns	−1.363	ns [s]	0.186	ns
Flowering	1.057	ns	−0.468	ns	2.437	** [s]	−0.520	ns
Pod set	0.855	ns	−0.833	ns	1.470	** [s]	−0.173	ns
Seed filling	2.400	*	−1.450	ns	2.801	** [s]	−0.402	ns
Maturation drying					2.530	*** [s]	−0.569	ns

[1] Statistical significance of associations: ns = not significant ($P \geq 0.05$); * = significant at $0.01 \leq P < 0.05$; ** = significant at $0.001 \leq P < 0.01$; *** = significant at $P < 0.001$.

[c] Adding cultivar (c) to the regression model significantly improved R^2_{adj}.

[s] Adding site (s) to the regression model significantly improved R^2_{adj}.

[cs] Adding cultivar and site (cs) to the regression model significantly improved R^2_{adj}.

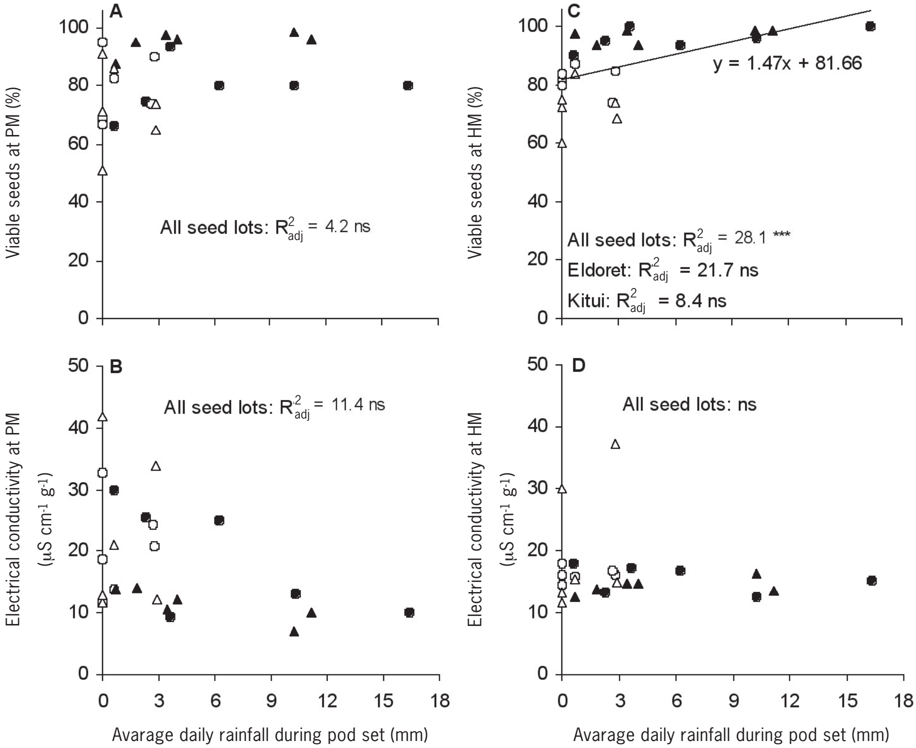

Figure 3. Associations between average daily rainfall during pod set and percentage viable seeds (A, C) or electrical conductivity (B, D) for seeds from 24 common bean crops of the cultivars Rosecoco and Mwezi Moja, grown at Eldoret and Kitui, Kenya, and harvested at physiological maturity (PM) or harvest maturity (HM). Eldoret: closed symbols; Kitui: open symbols; cv. Rosecoco: ●, ○; cv. Mwezi Moja: ▲, Δ. For explanation of R^2, regression line and statistical significance, see Figure 2.

Associations between temperature and seed quality

Per crop the temperatures during the different – but partly overlapping – development phases (vegetative mass accumulation, flowering, pod set, seed filling and maturation drying) were positively correlated with each other ($P < 0.01$), indicating temperatures had been higher or lower throughout the growing periods. The differences in average temperature between the two sites were much larger than the differences over time within the sites, with average temperatures being higher at Kitui than at Eldoret.

At PM, higher average temperatures during all preceding development phases were associated with lower percentages of viable seeds, but the effect was usually not statistically significant across all seed lots (Table 3). Within cultivars, the effect was

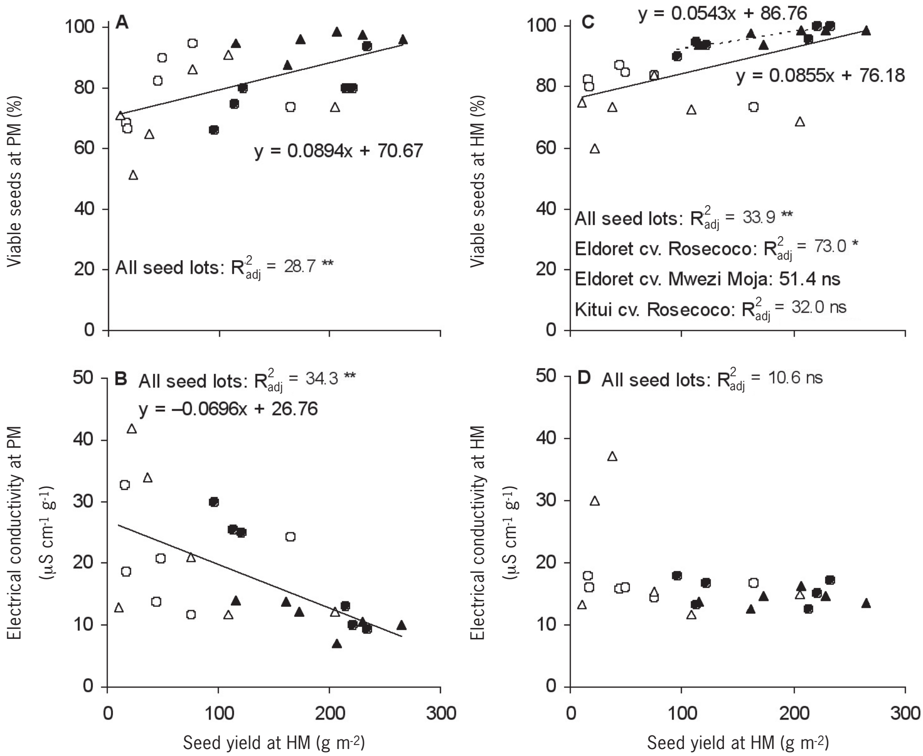

Figure 4. Associations between seed yield (dry weight basis) at harvest maturity (HM) and percentage viable seeds (A, C) or electrical conductivity (B, D) for 24 common bean crops of the cultivars Rosecoco and Mwezi Moja, grown at Eldoret and Kitui, Kenya, and harvested at physiological maturity (PM) or harvest maturity (HM). Eldoret: closed symbols; Kitui: open symbols; cv. Rosecoco: ●, ○; cv. Mwezi Moja: ▲, Δ. For explanation of R^2, regression lines and statistical significance, see Figure 2.

only statistically significant for cv. Mwezi Moja. This is illustrated in Figure 2A for the temperature during pod set. The cultivar Mwezi Moja appeared to benefit more from low temperatures and suffer more from higher temperatures than cv. Rosecoco. EC increased with increasing temperature over all seed lots (Table 3; Figure 2B).

Also at HM, higher temperatures were associated with lower percentages of viable seeds (Table 3; Figure 2C). The effect was confounded with the site effect: both cultivars had a higher percentage of viable seeds at low temperature (Eldoret) and a lower one at high temperature (Kitui). Within cultivars and sites, the temperature effects on the percentage of viable seeds were not statistically significant. EC was higher when temperatures were higher (Table 3), but this positive trend was only found because two seed lots of cv. Mwezi Moja had much higher EC values than the other ones (Figure 2D).

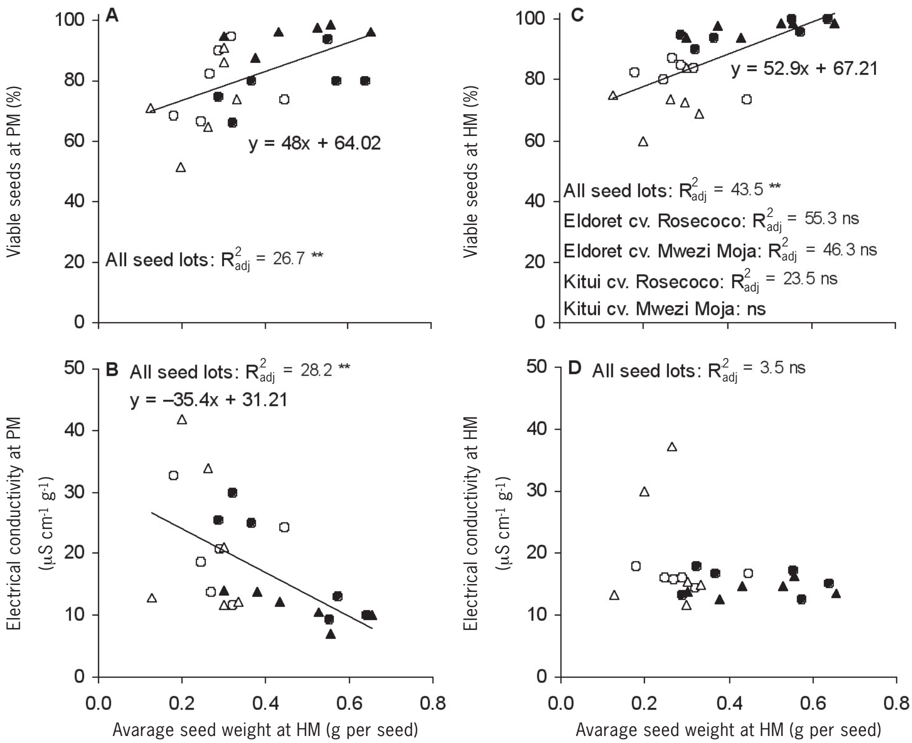

Figure 5. Associations between average weight per seed (dry weight basis) at harvest maturity (HM) and percentage viable seeds (A, C) or electrical conductivity (B, D) of seeds at physiological maturity (PM) or harvest maturity for 24 common bean crops of the cultivars Rosecoco and Mwezi Moja, grown at Eldoret and Kitui, Kenya. Eldoret: closed symbols; Kitui: open symbols; cv. Rosecoco: ●, ○; cv. Mwezi Moja: ▲, Δ. For explanation of R^2, regression lines and statistical significance, see Figure 2.

Associations between rainfall and seed quality

At PM, a statistically significant association was found between average daily rainfall during seed filling and percentage viable seeds only: a higher rainfall was associated with a higher percentage of viable seeds (Table 3). No statistically significant associations were found between daily rainfall in any of the preceding phases and the percentage of viable seeds or EC (Table 3; Figures 3A and B).

At HM, the percentage of viable seeds was higher when average daily rainfall during flowering, pod set, seed filling or maturation drying was higher (Table 3). These effects were mainly due to site effects (Table 3; Figure 3C). Within a site no statistically significant associations were found. EC was not significantly associated with rainfall (Table 3; Figure 3D).

Associations between seed quality and seed yield or weight

A high seed quality at PM, indicated by a high percentage of viable seeds and a low EC, was associated with high seed yields per m^2 (Figures 4A and B) and with high individual seed weights (Figures 5A and B). The same was found for the percentage of viable seeds at HM (Figures 4C and 5C), but for yield the effects were confounded with site and cultivar effects. A positive association between yield and seed quality within a cultivar was only found for cv. Rosecoco in Eldoret. No associations were found between EC at HM and seed yield (Figure 4D) or weight per seed (Figure 5D).

Discussion

Effects of temperature and rainfall on seed quality

The lower seed quality found at higher growing temperatures (Table 3; Figure 2) and low rainfall (Table 3; Figure 3) is in accordance with the well described effects on seed quality of high temperatures (e.g., Siddique & Goodwin, 1980; Gibson & Mullen, 1996; Spears *et al.*, 1997) and drought (e.g., Dornbos & Mullen, 1991). The purpose of this study was to explain whether these weather conditions exerted their effects mainly through influencing the quality attainable at PM, or through change of quality during the period between PM and HM.

On the basis of the results, we consider the seed quality attainable around PM a more important explanatory factor for quality differences at harvest than quality changes between PM and HM (Figure 2). In most cases quality did not improve significantly between PM and HM, so that the quality at PM was predictive for the quality at HM. However, also under the conditions encountered in this study the concept that quality is highest at PM (Harrington, 1972; Egli, 1998) proved not always tenable: in some cases the percentage viable seeds still increased after PM (Table 2). This occurred especially under the more favourable production conditions in Eldoret. At this site the percentage of viable seeds for cv. Rosecoco, with its non-uniform flowering habit, increased from 79.2 at PM to 95.8 at HM (Table 2), likely because especially the later developing seeds still increased in quality. The more uniform cultivar Mwezi Moja already had attained a high percentage of viable seeds at PM in Eldoret and did not significantly increase in quality anymore between PM and HM (Table 2). An increase in the percentage of viable seeds until well after PM was reported before by Zanakis *et al.* (1994) for soya bean and Sanhewe & Ellis (1996a) and Muasya *et al.* (2002a) for common bean. Nevertheless, a high seed quality at PM was positively associated with high quality at HM over all crops (Figures 1B and D). Seed quality sometimes appeared to decrease between PM and HM, but this could not be proven statistically for individual seed lots.

Relative importance of temperature and rainfall in different periods

As the crops were exposed to natural conditions, temperature and rainfall effects cannot be separated from each other. Because development phases were also partly overlapping, and temperatures during the different phases within one crop were strongly correlated it is difficult to identify the most critical phases. In addition, temperature effects were confounded with site effects, and factors other than only temperature may have exerted their influence as well. The negative effect of a higher temperature was nevertheless obvious and was found at both PM and HM for percentage of viable seeds and for EC. The positive effect of sufficient rainfall, however, was mainly expressed at HM and only for the parameter percentage of viable seeds (Table 3; Figure 3). We therefore surmise that within the range of conditions studied, temperature effects are more decisive for seed quality than rainfall effects.

Irrigation as a means of improving seed quality when temperatures are high and rainfall is little, may therefore not be successful. This is supported by the fact that when conditions in the warm area of Kitui still allowed a reasonable yield to be achieved (Figure 4C) seed quality was still relatively poor.

Electrical conductivity versus tetrazolium

The electrical conductivity (EC) test and the tetrazolium test seem to produce conflicting results when used for assessing seed quality at HM (e.g., Figure 1C). At HM, EC appeared to be a less appropriate parameter to characterize seed quality differences between seed lots, because it classified almost all seed lots as good and thus was not very discriminating. EC values of 10–20 μS cm^{-1} g^{-1} are generally regarded to indicate good seed quality (Hampton & TeKrony, 1995). In our study the EC values of all seed lots except two were within this range, whereas the percentages of viable seeds as determined with the tetrazolium test varied between 69 and 100 for the same seed lots (Figure 2B). However, because sites and sowing dates were chosen to cover a range from good to bad production conditions, the tetrazolium test results better reflected the expected future performance of the seed lots produced than the EC values. The reason for the poor discriminating value of the EC test at HM remains unknown. Because of the hand harvesting in our experiments, there was no leakage caused by mechanical seed coat damage. Also no hard-seededness occurred in the samples tested and therefore this could not have been the cause of the low electrolyte leakage. EC tests test differences in seed vigour and also in common bean the test results were shown to correlate with field emergence under favourable and unfavourable conditions (Kolasinska *et al.*, 2000). It should detect differences between seed lots in ranges where germination tests do not yet differentiate (cf. Gibson & Mullen, 1996), although Sanhewe & Ellis (1996a) found a good correlation between normal germination and electrical conductivity. We have no germination test data because of malfunctioning of the equipment. However, germination tests might also have resulted in overall high values that may not have been discriminative at harvest maturity.

Relationship between seed quality and seed yield and seed size

A general notion in seed production is that conditions conducive to high yields are also conducive to a high seed quality. However, Adam *et al.* (1989) showed for soya bean crops grown in different periods, that the highest seed quality was not always attained when yield was highest. Our results confirm the general trend, but at the same time show that under production conditions where the yield was low or seed weights were low, seed quality in general was not good either (Figures 4 and 5). On the other hand, fairly good yields and fairly high seed weights were no guarantee for a good seed quality. The crops deviating from the trend, i.e., those with a fairly high yield but a poor seed quality (Figure 4C), were not the ones produced under the most extreme conditions since in that case also yield would have been reduced (results not shown).

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