Potato Crop Response to Genotype and Environment in a Subtropical Highland Agro-ecology

L. Molahlehi • J. M. Steyn* • A. J. Haverkort

Abstract Potato response to environment, planting date and genotype was studied for different agro-ecological zones in Lesotho. Field experiments were conducted at four different sites with altitudes ranging from 1,655 to 2,250 m above sea level during the 2010/2011 and 2011/2012 summer growing seasons. Treatments consisted of three cultivars that varied in maturity type, two planting dates and four sites differing in altitude and weather patterns. Various plant parts were measured periodically. To understand and quantify the influence of abiotic factors that determine and limit yields, the LINTUL crop growth model was employed which simulated potential yields for the different agro-ecological zones using weather data collected per site during the study period. Observed actual crop yields were compared with model simulations to determine the yield gap. Model simulations helped to improve our understanding of yield limitations to further expand potato production in subtropical highlands, with emphasis on increasing production through increased yields rather than increased area. Substantial variation in yield between planting date, cultivar and site were observed. Average tuber dry matter (DM) yields for the highest yielding season were above 7.5 t DM ha^{-1} or over 37.5 t ha^{-1} fresh tuber yield. The lowest yield obtained was 2.39 t DM ha^{-1} or 12 t ha^{-1} fresh tuber yield for cultivar Vanderplank in the 2011/2012 growing season at the site with the lowest altitude. Modelled potential tuber yields were 9–14 t DM ha^{-1} or 45–70 t ha^{-1} fresh yield. Drought stress frequently resulted in lower radiation use efficiencies and to a lesser degree harvest indices, which reduced tuber yield. The site with the lowest altitude and highest temperatures had the lowest yields, while the site with the highest altitude had the highest yields. Later maturing cultivars yielded more than earlier maturing ones at all sites. It is concluded that the risk of low yields in rain-fed subtropical

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highlands can be minimised by planting late cultivars at the highest areas possible as early as the risks of late frosts permit.

Keywords Harvest index · Potential yield · Radiation use efficiency · Subtropical highlands · Tuber dry matter · Yield gap analysis

Introduction

The Kingdom of Lesotho is a small (30,000 km^2), landlocked country which is an enclave surrounded by South Africa (Fig. 1). Potatoes are widely grown in Lesotho and it is an important food crop. However, the area cropped with potato is still far below that of other staple crops such as maize, wheat, sorghum and pulses (Bureau of Statistics 2008). Potato production takes place mainly under subsistence farming

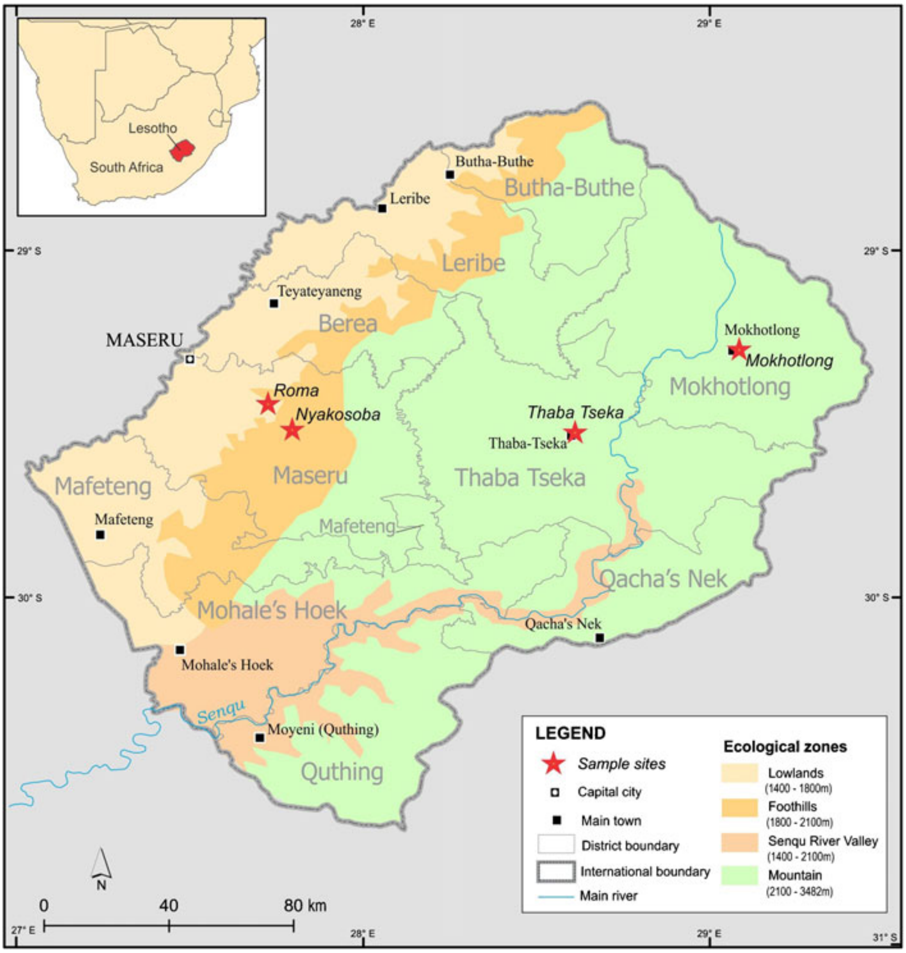

Fig. 1 Map of Lesotho showing the four agro-ecological zones and the four experimental sites (Department of Geography, University of Pretoria, Pretoria, South Africa)

practices with low levels of input use and under rain-fed conditions. Farming practices such as planting, ridging and harvesting are done manually and with the use of draught animals in some incidences. The use of mechanisation is very minimal as there is no large-scale commercial production. The crop is grown in the lowlands and highlands of Lesotho (above 2,000 m a.s.l.) in summer, as winters are too cold with frequent snow and night frost due to the high altitude. Weather patterns are extremely erratic with periods of excessive rainfall and prolonged droughts, which are both deleterious to crop growth. The former lead to periods with low solar radiation and leaching of nutrients, especially nitrogen, and the latter lead to lack of water available to the plants (Vos and MacKerron 2000). As a result, Lesotho is not self-sufficient in potato and a substantial proportion of the potatoes consumed in the country is imported.

Despite these limitations, the climatic conditions that prevail in the country are considered to be suitable and have the potential for high yields when the crop is managed adequately (Bureau of Statistics 2008). Lisinska and Leszczynski (1989) stated that the effect of locality on potato tuber yield and quality is generally connected to climatic conditions prevailing in a given area. Lesotho can be divided into four agro-ecological zones: the lowlands, foothills, Maluti mountains and Senqu River Valley (Fig. 1).

The climatic conditions of Lesotho, of warm summers and cold winters, allow for only one production season throughout the whole country. Potato is grown as a summer crop and planting can start anytime from mid-September to December, although there is a risk of late frost incidence up to the beginning of October. However, planting normally only starts in October since summer rains usually only occur from then. The country has a typical monsoon or Sahel-type climate, with dry winters and rainy summers. Although potatoes are produced in all parts of the country, the most suitable growing conditions—with relatively low temperatures—are those at the higher altitude mountain zones rather than the foothills and lowlands. Seed potato production, which is considered of economic importance in the country, is confined to isolated areas in the cooler high mountain valleys. Advantages of the subtropical highland summer crop compared to subtropical lowland winter crop is that the low night temperatures assure adaptation of the crop while the long days assure high levels of solar radiation and as such potentially high dry matter production (Haverkort 1990). The relatively cool conditions also mean that there is relatively low incidence of diseases and pests.

Seed production is mainly carried out by farmer groups who normally buy their seed stock together. The seed potatoes are obtained from South Africa and farmers usually buy generation two or three, and in some cases generation four seed, and then multiply the seed for one season. The seed produced is then sold to farmers who produce ware potato. The cultivars commonly used are BP1 and Up-to-date, with BP1 having higher preference. Ware potato is commonly produced in the foothill and lowland areas, with generally low typical yields (Zones of Production 2008). According to FAOSTAT DATA (2013), the area planted to potato increased from less than 500 ha in 1961 to 6,850 ha in 2011, while for the same period the average yield has not increased significantly and is currently at about 14 t ha^{-1} (fresh tuber yield). With a total annual production of around 85,000 t and a population of 1.7 million, the average consumption is 50 kg per person per annum of potato grown in

Lesotho itself. In addition, a considerable amount is imported from South Africa, but this amount is not known.

Given the availability of suitable climatic conditions that exist in the country, consumer preferences and the desire to be more self-reliant regarding food, there is a need to further expand and improve potato production in Lesotho with more emphasis on increasing production through increased yields rather than through increased area. To understand and quantify the influence of abiotic factors that determine and limit yields (Van Oort et al. 2012), there was a need to elaborate the potato crop ecology and physiology through field trials and a modelling approach for the various agro-ecological conditions prevailing in the country. The methodology followed would enable us to establish actual and potential yield (Caldiz et al. 2001) and quality levels and allow us to analyse the yield and quality gaps. The knowledge of these yield levels and how they are established as interaction between genotype and environment will help to establish the role of cultivars, environments and management practices that can be employed to enhance production.

Based on this background, the current study was conducted for different agro-ecological zones, planting dates and different cultivars. The aim was to establish the actual yields that can be achieved using best practices under the different environments and weather conditions. Secondly, the study could help identify which production and management practices need to be optimised to make the crop more robust in erratic environmental conditions. To this end, we planted three cultivars varying in maturity type in two different years, which experienced different weather conditions, at four sites differing in altitude and weather patterns, and on two planting dates to further increase variation in the conditions crops were subjected to. The seed for the two planting dates was acquired at the same time and this further enhanced variation in genotype response, since the second planting was a month later and therefore the seed was physiologically older. Observed crop parameters were compared with those of the LINTUL-Potato model (Kooman and Haverkort 1994) which calculates the potential yield. This study is significant as it was the first crop ecological analysis for this agro-ecology. It will help to design more robust potato cropping systems for Lesotho in terms of planting time, cultivar selection and management practices for the different agro-ecological zones, in order to enhance potato yields. The results of the study will also be significant for other potato cropping systems with sub-tropical highlands similar to that of Lesotho, such as the Southern Sahel in North Africa.

Materials and Methods

Environments of the Field Experiments

Field experiments were conducted during the 2010/2011 and 2011/2012 summer growing seasons at four different sites, representing the four agro-ecological zones in Lesotho. All experiments were planted under dry-land conditions, as almost no irrigation is practiced in the country. The experiments were planted on research stations and farms of the National Agricultural Research Institute (Department of

Agricultural Research) and the National University of Lesotho (NUL). Given that the terrain of the country does not allow off-road exploration, the sites—besides being representative of the various zones—were selected based on accessibility to allow frequent monitoring and data collection. The four sites (Fig. 1) are geographically separated from each other and have different micro-climates in terms of temperature, rainfall and solar radiation intensity. Rainfall and temperatures tend to decrease with increasing altitude. Table 1 shows the names of the sites, their altitude, coordinates, soil type and pH, and which zone they represent.

The long-term monthly weather data (daily maximum and minimum temperatures and total monthly precipitation) of each site are shown in Fig. 2. The long-term data lack evapotranspiration data, which was not available. The lowland and foothill area, represented by Roma and Nyakosoba, respectively, clearly have the highest temperatures, while temperatures in the highland areas of Thaba Tseka and Mokhotlong are slightly lower (Table 1; Fig. 2). Temperatures can drop below zero during winter months, especially in the highlands (Fig. 2). The total monthly precipitation is highest in the lowland and foothill areas of Roma and Nyakosoba, compared with the highlands (Table 1).

Daily weather data between planting and final harvest of the trials for each of the two seasons were collected with an automatic weather station (AWS) located within about 100 m from each of the trial sites, except for Roma where data were supplied by the Geography Department at NUL. The location details of each weather station are given in Table 1. The AWS instruments consisted of an LI200X silicon pyranometer (LI-COR, Lincoln, Nebraska, USA) to measure solar irradiation, an electronic cup anemometer (R.M. Young, Inc., USA) to measure wind speed, an electronic tipping bucket rain gauge (TE525 Texas Instruments, USA), a Vaisala HMP50 electronic temperature and humidity sensor and a CR10X datalogger (Campbell Scientific, Inc., Logan, Utah, USA). Weather data were offloaded once every 3 weeks using a laptop computer.

Table 1 Trial sites with their respective agro-ecological zoning, altitudes, soil characteristics and long-term average annual temperature and rainfall

Site name	Agro-ecological zone and altitude (m a.s.l.)	Coordinates		Soil type	Soil pH	Long-term average annual temperature (°C)	Long-term average annual rainfall (mm)
		Latitude	Longitude				
Roma	Lowland; 1,655	29.443° S	27.723° E	Sandy Loam	5.0	Max. 22.40 Min. 8.80	779
Nyakosoba	Foothill; 2,034	29.522° S	27.778° E	Clay Loam	4.7	Max. 22.08 Min. 7.56	778
Thaba Tseka	Highland; 2,250	29.526° S	28.612° E	Sandy Clay Loam	6.6	Max 19.01 Min 5.48	631
Mokhotlong	Highland; 2,170	29.289° S	29.079° E	Clay Loam	6.9	Max 20.02 Min 4.78	596

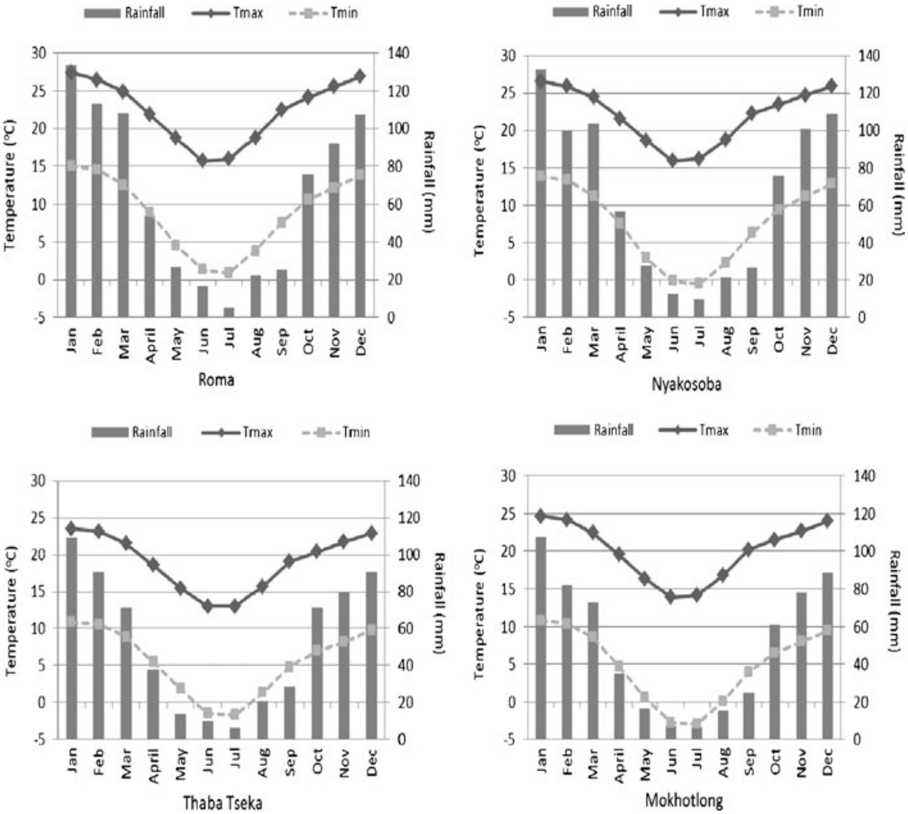

Fig. 2 Long-term monthly rainfall, maximum temperature (T_{max}) and minimum temperature (T_{min}) patterns for the four trials sites (Roma, 26-year temperature and rainfall averages, 1985–2011; Nyakosoba, 44-year temperature averages, 1967–2011; 61-year rainfall averages, 1950–2011; Thaba Tseka, 35-year temperature and rainfall averages, 1976–2011; Mokhotlong, 44-year temperature averages, 1967–2011; 81-year rainfall averages, 1930–2011) (Lesotho Meteorological Services 2012)

Experimental Details

Field experiments were laid down in a randomised complete block design with four replicates during the 2010/2011 and the 2011/2012 growing seasons. The treatments consisted of three cultivars (BP1, Mondial and Vanderplank) and two planting dates: the first in mid-November and the second planting 1 month later in mid-December. Cultivars were selected based on their maturity types as follows: Vanderplank (short growth cycle), Mondial (medium to long cycle) and BP1 (long cycle cultivar) (Visser 2012). BP1, a South African cultivar, is the most commonly planted cultivar in Lesotho because of its good adaptability and relatively high yields. The soils were fertilised with mineral fertilisers according to soil analysis results and fertilisation guidelines (Steyn and Du Plessis 2012). Plants were sprayed three-weekly with fungicides to control late blight caused by *Phytophthora infestans*.

Plots were 30 m^2 in size (6×5 m) and plant spacing was 100 cm between the rows and 25 cm within the row. Each plot consisted of five rows and 24 plants per row (120 plants per plot). The seed tubers, which originated from seed producers in South Africa, ranged in mass between 60 and 90 g each and were well sprouted.

Periodic harvests for growth analyses were carried out three-weekly throughout the growing season and the final harvest was conducted at the end of March for both planting dates and seasons. At each periodic harvest, ten plants per plot (two plants per row) were sampled, leaving a single guard plant between samples. No guard rows were left between adjacent plots due to the limited number of plants available for sampling. Although this could have affected the results, the effect was assumed to be consistent across all cultivars. Fewer plants were sampled when plants were missing due to non-emergence. The following crop characteristics were observed at each periodic harvest: number of main stems; stem length and number; fresh and dry mass of leaves, stems and tubers; and tuber number. Subsamples of about 300 g each were taken from the fresh foliage, stems and tubers. These were then weighed, dried at 70 °C for 48 h and re-weighed to determine their dry matter contents. After decline of the foliage had commenced, no further above-ground samples were taken. At crop maturity, the tubers of 20 plants per plot (four per row) were harvested to determine final tuber yield.

The percentage ground cover with green leaves was determined every 3 weeks at three spots in each plot. A transparent plastic grid of 19×27.5 cm (GC calculator), which is divided into 100 rectangles with black lines, was used to estimate the percentage cover of green leaves, as described by Kooman et al. (1996). The grid was handheld and pointed downward at such distance from the eye that a representative area of about 1 m^2 was observed and the number of rectangles with over 50% of leaves were counted.

Crop Model

The LINTUL crop growth model used in the present study is similar to that used by Franke et al. (2011). The model calculates potential potato dry matter production from the amount of solar radiation intercepted by the green foliage and a conversion factor (radiation use efficiency, RUE) (Spitters 1990), and follows the approach of Kooman and Haverkort (1994) to calculate temperature-dependent phenological development of the potato crop. Higher temperatures lead to earlier crop emergence and a more rapid initial leaf growth, resulting in increased interception of solar radiation at early stages of crop growth, a rapid maturation of the crop and a reduced length of the growing cycle from planting to harvest. Unfavourably high temperatures reduce photosynthesis and thereby biomass accumulation (Levy and Veilleux 2007).

We simulated shoot growth, foliar expansion, biomass accumulation and tuber growth on a day-to-day basis. Climate input data required by the model include daily minimum and maximum temperatures, incoming solar radiation and rainfall and reference evapotranspiration. Management input data include the depth and date of planting. Accumulated degree days from planting (with a base temperature of 2 °C) determines the time to crop emergence, leaf area development and the time of crop termination. The leaf area index (LAI) increases exponentially from crop emergence until a leaf area index of 0.75 is achieved; whereafter, development rate depends on temperature and water availability until a full crop cover is reached (LAI >3). Daily biomass growth is calculated from the LAI, solar radiation interception (using an extinction coefficient of 1 (Spitters and Schapendonk 1990)) and RUE (1.25 g dry matter MJ^{-1} of intercepted solar radiation). In the model, photosynthesis capacity is reduced when the average daily temperature falls below 16 °C or when the maximum temperature exceeds 30 °C and is completely halted at temperatures below 2 °C and above 35 °C (Kooman and Haverkort 1994). The harvest index for all cropping situations was set at 0.75 (Kooman and Haverkort 1994) and simulated yields are presented as tuber dry and fresh matter, assuming a dry matter concentration of 20%.

Daily Penman–Monteith grass reference evapotranspiration (ETo) values were calculated using measured daily weather data as input parameters (Smith et al. 1996). Daily potential evapotranspiration (PET) for potatoes was calculated by multiplying ETo with a crop-specific coefficient (K_c) according to the procedure recommended by Allen et al. (1996). Actual (water-limited) crop transpiration rate (T) was calculated as the PET multiplied by a drought stress factor, which is a function of the plant available water in the soil, as described by Franke et al. (2011).

Evaporation from the soil (E) was quantified following the procedure of Ritchie (1972), who calculated that a soil with an average water holding capacity that is wetted every 4 days by irrigation or rain has an evaporation rate that is one third of ETo until emergence of the crop. Thereafter, evaporation from the soil decreases linearly with ground cover (calculated from LAI) to 10% of ET at full ground cover (LAI >3).

Data Analysis

Data analyses were conducted using the SAS software computer programme (SAS 9.3). ANOVA was carried out to determine significant differences, and where there were differences, mean separations were done using LSD. Correlations were also done to show relationship between the different variables (Gomez and Gomez 1984; Petersen 1994).

Results and Discussion

The weather data recorded from planting until harvest for the two cropping seasons and four sites are presented in Fig. 3 and Table 2. For both planting seasons, the lowest altitude site—Roma—usually had the highest day and night temperatures compared to sites at the foothills (Nyakosoba) and higher elevations (Thaba Tseka and Mokhotlong).

The solar radiation levels were higher in the highland areas than at the foothills and lowland sites and seasonal averages varied between 19 and 25 MJ m^{-2} day^{-1}. For both seasons, there was more precipitation in the lowland and foothills than in the highlands. Precipitation levels for both seasons ranged between 300 and 900 mm during the growing seasons and there was more precipitation in the first season than in the second for all the sites. ETo was higher in the highland areas, especially for Mokhotlong, compared to the lowlands and foothills.

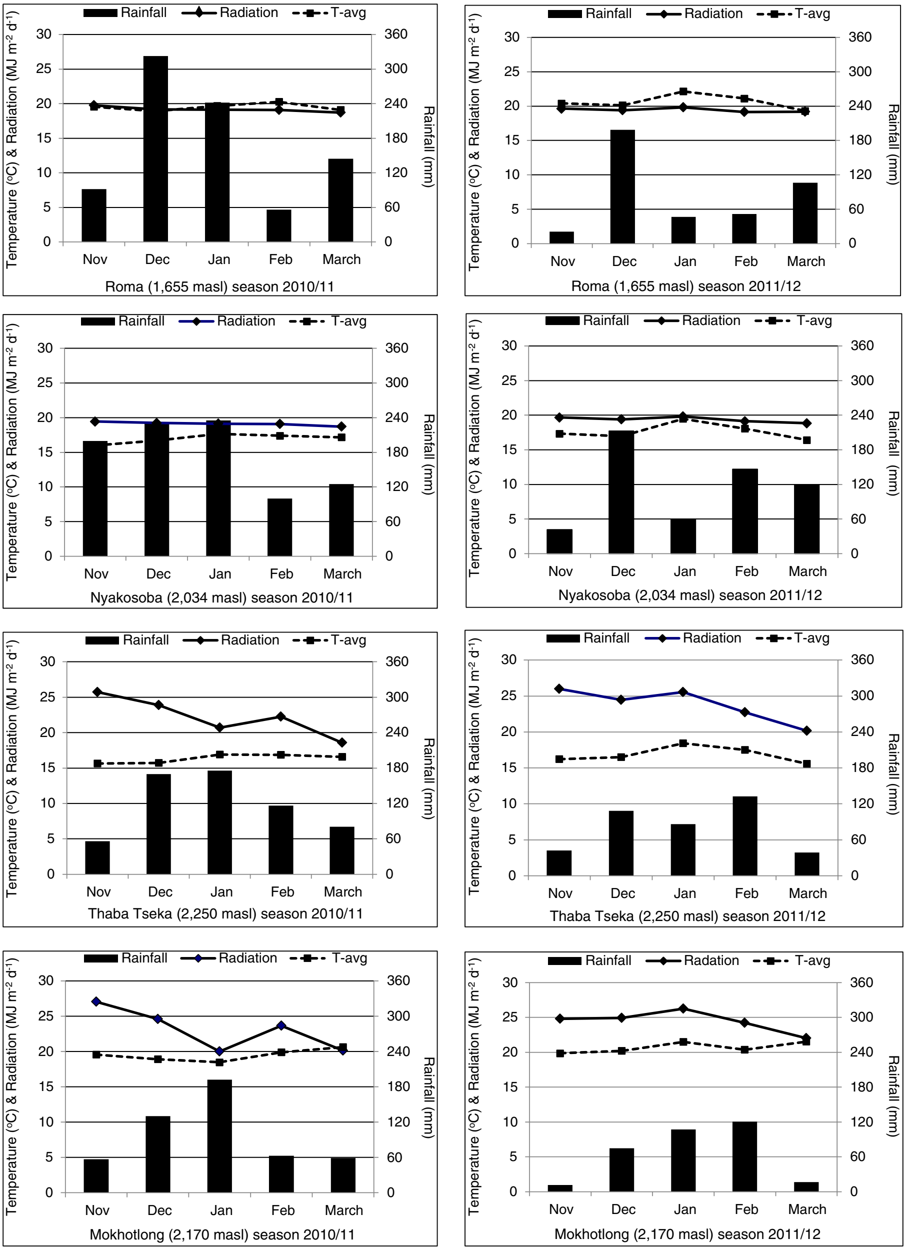

Fig. 3 Actual weather data (total rainfall, average radiation and temperature (T-avg)) recorded from planting until harvest date during the 2010/2011 and 2011/2012 planting seasons for the four localities. Altitudes of localities in metres above sea level are given in *parentheses*

Observed and modelled yields and other parameters recorded in the field trials are presented in Table 3. In the first season (2010/2011; S1) total dry matter and tuber yields were significantly higher for the first planting than the second planting at all sites, except for Nyakosoba (Table 3). Average tuber dry matter (DM) yields across

Table 2 Actual weather data recorded from planting until harvest date during the 2010/2011 and 2011/2012 planting seasons for each of the four localities

Parameter	Site				Site			
	Roma	Nyakosoba	Thaba Tseka	Mokhotlong	Roma	Nyakosoba	Thaba Tseka	Mokhotlong
	Planting 1				Planting 2			
Season 1, 2010/2011								
T_{max} °C	25.4	22.9	23.1	24.5	25.4	23.2	23.2	24.6
T_{min} °C	13.5	11.1	9.7	10.0	13.9	11.4	10.0	10.2
Rad MJ	19.1	19.1	22.0	22.8	19.0	19.0	20.2	21.7
Rain mm	857	891	598	502	637	625	482	358
ETo mm	615	589	628	793	465	447	468	549
Planting date	12 November 2010	08 November 2010	10 November 2010	11 November 2010	16 December 2010	13 December 2010	14 December 2010	15 December 2010
Final harvest date	15 April 2011	12 April 2011	20 April 2011	18 April 2011	15 April 2011	12 April 2011	20 April 2011	18 April 2011
Season 2, 2011/2012								
T_{max} °C	27.3	24.4	24.6	25.3	27.1	24.5	24.7	25.6
T_{min} °C	13.9	11.2	9.2	9.2	14.3	11.4	9.4	9.5
Rad MJ	19.4	19.4	23.7	24.8	19.4	19.4	23.1	24.3
Rain mm	425	508	408	333	386	403	335	310
ETo mm	625	589	635	726	487	466	496	585
Planting date	07 November 2011	08 November 2011	09 November 2011	10 November 2011	05 December 2011	06 December 2011	07 December 2011	08 December 2011
Final harvest date	26 March 2012	27 March 2012	29 March 2012	28 March 2012	26 March 2012	27 March 2012	29 March 2012	28 March 2012

sites were in the range of 6.96–8.65 t ha^{-1} (average 7.60 t ha^{-1}) for the first planting (P1), while the range was 3.60–6.07 t ha^{-1} (average 4.57 t ha^{-1}) in the second planting (P2). No significant differences in harvest index (HI) values occurred between the first and second plantings. HI values ranged between 72.4 and 76.7% (average of 73.8%) for P1 and 67.8–79.3% (average of 71.5%) for P2 (across all sites). There was also little variation in the calculated average RUE across sites in P1 (range of 0.84–0.91 g MJ^{-1} and average of 0.88 g MJ^{-1}) and between the two planting dates. However, a wide range of RUE values was recorded between localities in the second planting (range 0.53–1.22 g MJ^{-1} and average of 0.83 g MJ^{-1}). Tuber dry matter contents (DM%) were quite stable across planting dates, with no significant differences recorded, except for Nyaksoba where the values were lower in the second planting. Average tuber dry matter contents across sites were in the range of 19.4–20.9% (average 20.3%) for P1 and 19.2–21% (average 20.1%) for P2.

In the second season (2011/2012; S2), there were no differences in average tuber yields between the first and second plantings. Tuber yields across localities ranged from 3.60 to 5.52 t DM ha^{-1} (average 4.64 t DM ha^{-1}) for P1, and for P2, the range was similar (3.23–5.86 t DM ha^{-1} and average 4.64 t DM ha^{-1}). The same trend was observed for harvest index (range 60.4–72.6% and average 68.0% for P1; range 57.1–75.7% and average 68.8% for P2) and radiation use efficiency (range 0.45–0.62 g MJ^{-1} and average 0.52 g MJ^{-1} for P1; range 0.41–0.57 g MJ^{-1} and average 0.51 g MJ^{-1} for P2). There were no differences in tuber DM% between plantings, with a range of 19.5–22.9% (average of 21.1%) for P1, and 19.5–23.4% (average 21.3%) for P2.

Overall, the tuber yields were highest in the first season (S1 average 6.1 t DM ha^{-1}), and yields were especially high for P1 (average 7.6 t DM ha^{-1}), compared to the second season (S2, average 4.6 t DM ha^{-1}). The same pattern was observed for radiation use efficiencies, which were relatively high in S1 (average 0.85 g MJ^{-1}) compared to S2 (0.51 g MJ^{-1}). There was little variation in harvest indices between the two seasons (average 72.6% in S1 and 68.4% in S2). The lowest HI of 57% was recorded for Roma in S2. Similarly, average tuber DM% showed little variation, with an average of 20.2% in S1 and 21.2% in S2. The radiation use efficiencies achieved in this study were generally low, probably because production was under dry-land conditions and the crops were frequently exposed to stress periods, similar to the findings of Kooman and Rabbinge (1996).

Arab et al. (2011) found that planting date influences leaf area index and, therefore, also the amount of intercepted solar radiation, which is an important factor that determines potato yield. Planting date directly affects the weather conditions that a crop will be exposed to, for example the rainfall, temperature and amount of solar radiation (Kawakami et al. 2005). Hassanpanah et al. (2009) found that marketable tuber yields were affected by planting date and that early planting leads to more time for plant growth and higher yields. The long-term weather data for Lesotho (Fig. 2) show that for all four of our sites substantial summer rains that would allow for early planting only start from October onwards. November to March are the months with the highest rainfall that will best support dry-land crop production. The best period for planting therefore seems to be between mid-October (after the first good rains) and mid-November. Later planting may firstly pose a risk of too wet soils that will result in rotting of tubers in poorly drained or heavier soils. For example, the low yields recorded for Roma (P2 in S1) (Fig. 3) resulted from erratic intense rainfall in

Table 3 Observed total dry matter (DM) yield, tuber dry matter yield, LINTUL model simulated potential tuber dry matter yield, tuber dry matter content, harvest index (HI) and radiation use efficiency (RUE) per site, planting time and season (average values across cultivars)

Parameter	Unit	Roma Planting		Nyakosoba Planting		Thaba Tseka Planting		Mokhotlong Planting	
		1	2	1	2	1	2	1	2
Season 1, 2010/2011									
Total DM yield	t ha^{-1}	9.64 a	4.70 b	9.55 a	8.55 a	10.08 a	7.23 b	11.70 a	5.29 b
Tuber DM yield	t ha^{-1}	7.43 a	3.70 b	6.96 a	6.07 a	7.36 a	4.91 b	8.65 a	3.60 b
Tuber dry matter	%	20.1 a	20.5 a	20.9 a	19.6 b	20.8 a	21.0 a	19.4 a	19.2 a
HI	%	76.7 a	79.3 a	72.4 a	70.8 a	72.8 a	68.2 a	73.1 a	67.8 a
Calculated RUE	g MJ^{-1}	0.89	0.53	0.91	1.22	0.84	0.74	0.87	0.83
Potential yield	t ha^{-1}	13.74	11.67	13.51	10.32	14.34	9.47	14.33	9.66
Actual/potential		0.54	0.32	0.52	0.59	0.51	0.52	0.60	0.37
Season 2, 2011/2012									
Total DM yield	t ha^{-1}	5.80 a	5.49 a	6.37 a	6.41 a	7.57 a	7.76 a	7.22 a	6.98 a
Tuber DM yield	t ha^{-1}	3.60 a	3.23 a	4.52 a	4.75 a	5.52 a	5.86 a	4.91 a	4.72 a
Tuber dry matter	%	19.5 a	19.8 a	20.4 a	19.5 a	21.5 a	22.3 a	22.9 a	23.4 a
HI	%	60.4 a	57.1 a	70.8 a	74.4 a	72.6 a	75.7 a	68.2 a	68.0 a
Calculated RUE	g MJ^{-1}	0.62	0.57	0.53	0.52	0.47	0.52	0.45	0.41
Potential yield	t ha^{-1}	9.14	6.75	12.81	10.21	13.15	10.49	12.99	11.27
Actual/potential yield		0.39	0.48	0.35	0.47	0.42	0.56	0.38	0.42

For each parameter, means followed by the same letter within the same row (across planting dates) for each site and season are not significantly different at the $p \leq 0.05$ level of probability, according to the LSD test

December 2010, which resulted in hampered emergence, rotting of seed tubers and leaching of nitrogen from the soil. This was followed by a period of prolonged drought in both seasons at the time of the sensitive tuber bulking stage (Adams and Stevenson 1990; Onder et al. 2005).

Secondly, late planting results in a shorter growth period, which results in less radiation intercepted (Hassanpanah et al. 2009) and increased frost and drought risk from April onwards, which will decrease tuber yield. Therefore, farmers planting later than these prescribed dates (mid-October–mid-November) are facing an increased risk of yield loss. In the present study, late planting indeed resulted in a higher drought risk towards the end of the growing season. This was especially evident in S1, when yields were substantially lower for the second planting, partly due to the drier second half of the growing season, resulting in water stress during the sensitive tuber bulking stage (Van Loon 1981; Steyn et al. 1998).

The S2 of the present study was generally substantially drier than S1 and the long-term average (Figs. 2 and 3), especially early in the growing season (November 2011), which resulted in delayed crop emergence, development and radiation interception (data not presented). Van Loon (1981) also reported that the planting of tubers in a dry soil could delay emergence and root growth and, accordingly, shorten the vegetative and tuber formation periods, which will reduce production. As a result of the much lower rainfall early in S2 (Table 2; Fig. 3), yields recorded for P1 in S2 were substantially lower than those recorded for P1 in S1 (Table 3).

RUE is a measure of how efficiently the solar radiation intercepted by the canopy is converted into dry matter (Hammer and Wright 1994; Kooman and Rabbinge 1996; Lindquist et al. 2005). In this study, the average RUE values recorded were substantially lower (0.85 g MJ^{-1} in S1 and 0.51 g MJ^{-1} in S2), compared to the value of 1.25 g MJ^{-1} solar radiation (or 2.5 g MJ^{-1} PAR), which was used in our model, and which is typically cited for potato (Kooman and Haverkort 1994). Since all production aspects, except for water, were optimised, the lower RUE values recorded here could probably be attributed to water stress that interfered with normal production (Kooman and Rabbinge, 1996). Similarly, the HI gives an indication of the proportion of dry matter that was allocated to reproductive organs (tubers) (Vos 1997). A low harvest index is usually indicative of a remarkably shortened growth cycle as the crop was not allowed to grow to maturity (Kooman et al. 1996). In this study, HI values were mostly close to typical values (70–80%) reported in literature (Kooman 1995; Victorio et al. 1986), except for S2, when HI values were substantially lower for both planting dates (P1 and P2) at Roma and Nyakosoba (Table 3). It is therefore clear that the very dry conditions towards the end of the growing season (January–March 2012) at these sites (Fig. 3) resulted in premature crop senescence and lower HI values.

Regarding cultivars, in S1, there were significant differences in their total yields per site, except for Mokhotlong, where no differences occurred between cultivars (Table 4). In this season, tuber yield differences between cultivars were significant at all sites, except Thaba Tseka. BP1 and Mondial produced higher yields than Vanderplank at all the other sites. Average tuber DM yields across sites were in the range of 6.44–7.35 t ha^{-1} for BP1 (average 6.91 t ha^{-1}), 5.52–7.20 t ha^{-1} (average 6.49 t ha^{-1}) for Mondial and 4.80–5.50 t ha^{-1} (average 5.20 t ha^{-1}) for Vanderplank.

Harvests indices, radiation use efficiencies and tuber dry matter contents per site hardly differed between cultivars, except for Nyakosoba, where DM% values were the lowest for Mondial. Harvest indices ranged between 65 and 74.5% (average 70.3%) for BP1, 68.0 and 82.4% (average 74.0%) for Mondial, and 71.9 and 79.0% (average 74.2%) for Vanderplank. Radiation use efficiencies were in the range of 0.72–1.02 g MJ^{-1} (average of 0.81 g MJ^{-1}) for BP1, 0.60–1.00 g MJ^{-1} (average 0.83 g MJ^{-1}) for Mondial and 0.78–1.16 g MJ^{-1} (average 0.92 g MJ^{-1}) for Vanderplank. Tuber dry matter contents tended to be highest for BP1 (range 20.0–21.2%, average 20.6%), followed by Vanderplank (19.3–21.5%, average 20.5%) and Mondial (range 18.7–20.3%, average 19.3%).

In S2, tuber yields were substantially lower than in S1 and significant cultivar differences occurred. In almost all instances, except for Nyakosoba, Vanderplank again had lower tuber yields (range 2.4–5.4 and average 4.1 t DM ha^{-1}), compared to BP1 (range 3.7–5.7 and average 4.8 t DM ha^{-1}) and Mondial (range 4.1–6.0 and average 5.0 t DM ha^{-1}) (Table 4). Harvest index values of cultivars did not differ for all the sites (except for Thaba Tseka). The HI ranged from 55.6 to 76.9%. Mondial had the highest average HI (70.7%), followed by Vanderplank (68.5%) and BP1 (66.1%). Radiation use efficiencies showed little variation per site and ranged between 0.41 and 0.58 g MJ^{-1} (average 0.51 g MJ^{-1}) for BP1, 0.39 and 0.56 g MJ^{-1} (average 0.47 g MJ^{-1}) for Mondial and

Table 4 Observed total dry matter (DM) yield, tuber dry matter yield, LINTUL model simulated potential tuber dry matter yield, tuber dry matter content, harvest index (HI) and radiation use efficiency (RUE) per cultivar, site and season (average values across planting times)

		Season 1, 2010/2011			Season 2, 2011/2012		
Parameter	Unit	BP1	Mondial	Vanderplank	BP1	Mondial	Vanderplank
Roma							
Total DM yield	t ha^{-1}	9.21 a	6.81 ab	5.94 b	6.35 a	6.61 a	3.98 b
Tuber DM yield	t ha^{-1}	6.85 a	5.52 a	4.80 a	3.73 a	4.12 a	2.39 b
Tuber DM	%	20.5 a	19.4 a	20.6a	20.6 a	18.2 b	20.2 a
HI	%	74.5 a	82.4 a	79.0 a	58.3 a	62.3 a	55.6 a
RUE	g MJ^{-1}	0.75	0.60	0.78	0.55	0.56	0.67
Potential yield	t ha^{-1}	13.48	13.48	11.16	7.94	7.94	7.94
Actual/potential yield		0.51	0.41	0.43	0.47	0.52	0.30
Nyakosoba							
Total DM yield	t ha^{-1}	10.43 a	9.80 a	7.22 b	7.24 a	6.61a	5.31 b
Tuber DM yield	t ha^{-1}	7.35 a	7.20 a	5.22 b	5.06 a	4.77 ab	4.07 b
Tuber DM	%	21.2 a	18.8 b	20.8 a	20.7 a	18.9 b	20.1 ab
HI	%	69.8 a	72.6 a	72.4 a	69.5 a	71.9 a	76.3 a
RUE	g MJ^{-1}	1.02	1.00	1.16	0.58	0.45	0.54
Potential yield	t ha^{-1}	13.10	11.79	10.85	11.51	11.51	11.51
Actual/ potential yield		0.56	0.61	0.48	0.44	0.41	0.35
Thaba Tseka							
Total DM yield	t ha^{-1}	9.55 a	9.27 a	7.15 b	7.92 a	7.87 a	7.20 a
Tuber DM yield	t ha^{-1}	6.44 a	6.68 a	5.28 a	5.67 a	6.04 a	5.36 a
Tuber DM	%	20.8 a	20.3 a	21.5 a	23.8 a	20.9 b	21.0 b
HI	%	65.0 a	73.1 a	73.5 a	71.4 b	76.9 a	74.3 ab
RUE	g MJ^{-1}	0.73	0.83	0.81	0.48	0.49	0.50
Potential yield	t ha^{-1}	12.09	12.09	11.52	11.82	11.82	11.82
Actual /potential yield		0.53	0.55	0.46	0.48	0.51	0.45
Mokhotlong							
Total DM yield	t ha^{-1}	9.70 a	8.97 a	7.73 a	7.58 a	7.09 ab	6.62 b
Tuber DM yield	t ha^{-1}	7.01 a	6.56 a	5.50 a	4.90 ab	5.07 a	4.47 b
Tuber DM	%	20.0 a	18.7 a	19.3 a	24.0 a	23.4 ab	22.1 b
HI	%	71.7 a	68.0 a	71.9 a	65.0 a	71.5 a	67.7 a
RUE	g MJ^{-1}	0.72	0.90	0.92	0.41	0.39	0.49
Potential yield	t ha^{-1}	12.45	12.45	11.08	12.13	12.13	12.13
Actual /potential yield		0.56	0.53	0.50	0.40	0.42	0.37

For each parameter, means followed by the same letter within the same row (across cultivars) for each site and season are not significantly different at $p \leq 0.05$ probability level, according to the LSD test

0.49 and 0.67 g MJ^{-1} (average 0.55 g MJ^{-1}) for Vanderplank. Significant differences in tuber DM% occurred at Roma and Thaba Tseka, where Mondial had the lowest values. Like in S1, BP1 had the highest average DM% values (range 20.6–24.0% and average 22.3%), followed by Vanderplank (range 20.1–22.1% and average 20.9%), while Mondial had the lowest DM% values (range 18.2–23.4% and average 20.4%).

Tuber DM% gives an indication of quality and is generally dependent on the cultivar and environment—especially high temperatures can affect DM% negatively (Haverkort and Verhagen 2008). In this study, locality (as an indicator of environment) did not have a clear effect on DM% in S1, but in S2, Roma tended to have lower DM% values. This could be explained by the fact that the average daily maximum temperatures at Roma were the highest of all sites (over 25 °C), while night temperatures were about 4 °C higher than at the other sites. Cultivar clearly played the dominant role in determining the DM%, with BP1 having the highest average DM% values and Mondial the lowest.

As was the case with planting date, tuber yields per cultivar were slightly lower in S2, than in S1 (Table 4). In the first season average yields across sites were 6.91 t DM ha^{-1} for BP1, 6.49 t DM ha^{-1} for Mondial and 5.20 t DM ha^{-1} for Vanderplank (overall average of 6.20 t DM ha^{-1} for all three cultivars), while in S2, the average yield for BP1 was 4.84 t DM ha^{-1}, 5.00 t DM ha^{-1} for Mondial and 4.07 t DM ha^{-1} for Vanderplank (overall average of 4.64 t DM ha^{-1} for all three cultivars).

In the second season, tuber yields did not vary much among cultivars for the different sites. BP1 and Mondial were not that different to Vanderplank in yield levels. As already mentioned, early planting was affected by water stress at the beginning of the season and also during the critical stages of crop development. The delayed establishment affected the long season cultivars as they started late and their yields were reduced as their growth period was shortened.

Selection of appropriate cultivars for planting in a given region is of vital importance for production of high yields and quality (Dehdar et al. 2012). In general, the longer season cultivars (BP1 and Mondial) performed better in terms of total and tuber dry matter yields. Similar to the findings of Hassanpanah et al. (2009), these longer season cultivars were able to establish well at the beginning of the season and had a longer time to develop and mature (especially for P1). White and Sanderson (1983) found that early establishment of medium to long season cultivars such as Mondial and BP1 gives sufficient time for full bulking after tuberisation. They indicated that shorter season cultivars (such as Vanderplank) were still able to reach its potential even when established later. However, in the present study, Vanderplank lost its leaves, matured before the end of the growing season and always had the lowest yields, independent of planting date.

Even when planted later (P2) and under dry conditions (e.g. in S2), Vanderplank was not able to escape drought (a well-known drought avoidance mechanism of early cultivars) to produce better yields. Kooman and Rabbinge (1996) mentioned a self-destruction process where at the end of the season when the root zone is depleted from nutrients, tubers start to withdraw nitrogen from the foliage. They found that since early cultivars have a shorter leaf longevity, this reallocation of nitrogen from foliage is faster in early maturing cultivars with smaller foliage than in late cultivars with a large amount of foliage and longer leaf longevity.

Simulated potential tuber yields for each season and planting date are presented in Tables 3 and 4. For calculation of the theoretical potential yields, a default RUE value of 1.25 g MJ^{-1} intercepted solar radiation and a HI of 0.75 were used. Subsequently, the ratio of actual tuber yield observed was divided by the simulated yield for both planting date and cultivars per site, which gave the fraction of potential yield achieved for each treatment combination (cultivar × plant date × season). When actual observed yields are close to the values calculated with the crop growth model, the observed harvest index should be close to 0.75 and the observed RUE should be close to 1.25 g MJ^{-1}. Table 3 shows the average values per planting across cultivars. The first planting (P1) of S1 showed a HI of about 0.74 and RUE of 0.88 g MJ^{-1}. The second planting (P2), which was planted a month later showed similar, but slightly lower HI (0.72) and RUE values (0.83 g MJ^{-1}). During the second planting, plants apparently suffered more from adverse drought conditions and as a result the RUE and HI values were lower, resulting in lower actual/potential yield ratios for P2 (0.45), compared with P1 (0.54).

In S2 (2011/2012), planting date had no effect on HI and RUE, and almost identical values were recorded for P1 and P2. However, both the average HI and RUE were substantially lower in S2 (HI 0.68 and RUE 0.51 g MJ^{-1}), compared to S1 (HI 0.73 and RUE 0.85 g MJ^{-1}). This resulted in lower average actual/potential yield ratio (0.43) for S2, compared to S1 (0.50).

Table 4 shows actual and potential yields, HI, RUE values and actual/potential yield ratios per cultivar for different seasons and sites. The lowest yield of Vanderplank was to be expected, since it was the earliest maturing cultivar of the three. Vanderplank also showed the lowest relative performance with actual/potential ratios of 0.45 in the 2010/2011 and 0.35 in the 2011/2012 season (average of 0.42). This is also expected as earlier maturing cultivars suffer more from transient drought stress periods than later maturing cultivars. BP1 and Mondial showed similar average actual/potential yield ratios of 0.50. The actual/potential yield ratio depends on various environmental and management factors, but typically it is in the range of 0.6 (i.e. actual yields are about 60% of the potential). The lower values reported here could probably be attributed to the less favourable growing conditions and water stress under dry-land production.

The extensive data set of 3 cultivars × 2 planting times × 4 replicates × 4 sites × 2 seasons gave a total of 196 observations per crop and plant characteristic (variable). When averaging the four replicates, 48 data points remain, allowing a useful correlation exercise among some of these variables. Figure 4 shows the relationship between RUE and tuber yield of the three cultivars planted at four sites, two years and two planting times. It was expected that there would be a good correlation between these variables, as yield is one of the components needed to calculate RUE (auto-correlation). However, the correlation per variety was low for BP1 (R^2=0.37) and even lower for the two other varieties. This shows that factors other than the RUE affected final yield, implying that the calculated RUE is influenced by factors not included in the model. One possibility is that nitrogen was leached due to intense rainfall events, leading to variation in the ability of leaves to photosynthesise adequately. Similarly, prolonged periods of drought negatively affected the RUE. Moreover, there seems to be two clusters of points in Fig. 4; across clusters, there is a positive correlation, but within the clusters it is negative. The lower left cluster is associated with season 2 and the upper right cluster is associated with season 1. The negative correlation between RUE and yield within a cluster can probably be attributed to the fact that higher yields are associated with a longer growing period (later varieties), which also means longer exposure to possible negative influences such as nitrogen depletion and drought on RUE.

An example of a very good correlation is that between tuber dry matter yield and total dry matter yield (Fig. 5a, b). The slope (0.7765) represents the harvest index. Figure 5a clearly shows that the first planting (filled symbols) generally gave higher yields than the second planting (open symbols), due to better rainfall distribution. Site differences were less distinct (Fig. 5a), except for Roma with the majority of observations at the low end. Figure 5b shows that cultivar Vanderplank had the lowest yields and BP1 the highest, whereas Mondial yields were least stable and cover the whole range between 250 and 1,050 g m^{-2}. The first season (filled symbols) clearly showed higher yields than the second season (open symbols), due to higher rainfall (Fig. 5b).

The 48 data points (when the average value of the four replicates were taken) of each observation allowed for a meaningful regression analysis. Table 5 presents correlations between the various parameters that were measured or calculated. Correlations are shown for all cultivars and all plantings at all sites (bold text), and for one cultivar only (BP1 as an example). There were relatively good correlations (R^2>0.5) among several of the different parameters for both BP1 and for all the cultivars together in both seasons. Significant positive correlations were shown for

- Stem length versus foliar dry mass, tuber yield, total dry matter and tuber number per plant
- Total dry matter versus foliar dry mass, tuber yield and tuber number per plant
- Tuber yield versus tuber number per plant and harvest index
- Radiation use efficiency and stem length, tuber yield, tuber dry matter concentration, total dry matter and tuber number per plant.

Apparently conditions that lead to higher radiation use efficiency (more rain, lower light intensity), to longer stems and to higher leaf and stem mass lead to higher tuber yields. With unchanged or increased HI, this is well expected and explained. The relationship with a higher tuber number is also expected as in these rain-fed conditions higher yields are associated with more rain and favourable soil water conditions during stolon and tuber formation, leading to higher stolon and tuber numbers, as was demonstrated by Haverkort et al. (1990) in controlled and field conditions. The similarity of the data for BP1 and for all cultivars together (bold) in Table 4 shows that these correlation values also hold for each individual cultivar.

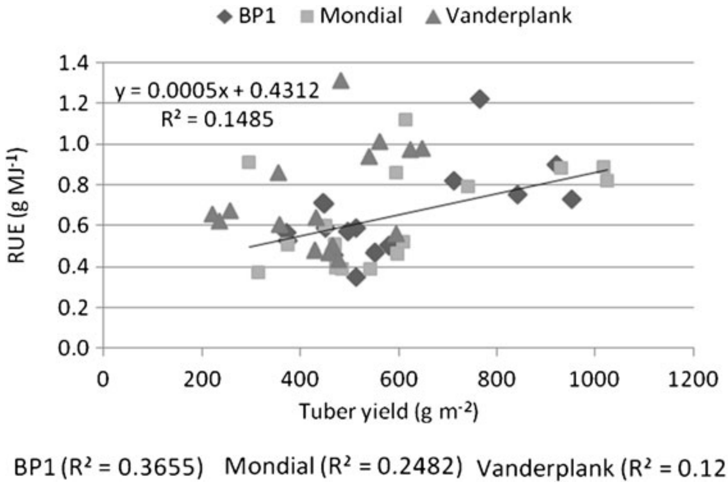

Fig. 4 Relationship between actual tuber dry matter yields and RUE for the different cultivars across sites, planting dates and seasons

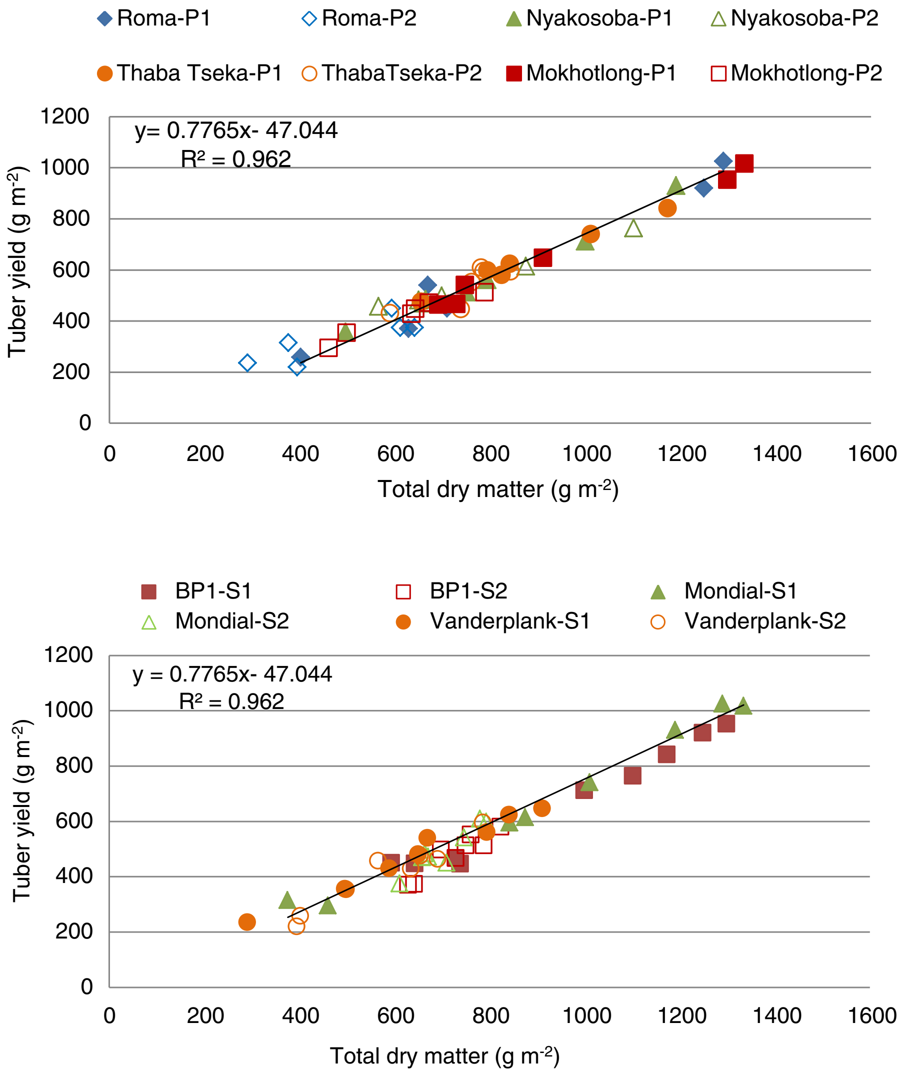

Fig. 5 Relationship between total dry matter and tuber dry matter yields for (**a**) the different planting date × site and (**b**) cultivar × season treatment combinations

Concluding Remarks and Relevance of the Findings for Potato Production

Potato production in sub-Saharan Africa has more than doubled since 1994 (FAOSTAT DATA 2010) but more so due to increased area than through increased yield and more farmers growing the crop. In Lesotho, the area increased from 500 ha in 1961 to 6,500 ha in 2009. In most African potato-producing countries, the output of potato increases faster than the population growth. Rwanda is another example: in 1980, the country produced 270,000 tons of potatoes on 45,000 ha (6 t ha^{-1}) and currently 2 million tons are produced on 150,000 ha (13 t ha^{-1}), a 7.4-fold increase, whereas the population increased about 2.5-fold. Yields on average may not have increased, which is mainly due to the fact that increasing the area necessarily means producing the crop on more

Table 5 Correlation diagram of ten crop observations

	Stem length	Tuber % dry matter	Foliar mass	Tuber yield	Total dry matter	Tuber number per plant	Average weight per tuber	Stem number	Harvest index	Radiation use efficiency
Stem length	1.0									
Tuber % dry matter	−0.261 ns	1.0								
	__−0.074 ns__									
Foliar mass	0.663**	−0.091 ns	1.0							
	__0.622**__	__−0.097 ns__								
Tuber yield	0.587**	0.005 ns	0.460**	1.0						
	__0.547**__	__0.091 ns__	__0.401**__							
Total dry matter	0.670**	−0.032 ns	0.669**	0.967**	1.0					
	__0.649**__	__0.036 ns__	__0.659**__	__0.953**__						
Tuber number per plant	0.568**	−0.318**	0.415**	0.565**	0.590**	1.0				
	__0.625**__	__−0.197**__	__0.414**__	__0.560**__	__0.596**__					
Average weight per tuber	0.115 ns	0.352**	0.123 ns	0.527**	0.476**	−0.338**	1.0			
	__−0.110 ns__	__0.322**__	__0.003 ns__	__0.468**__	__0.385**__	__−0.380**__				
Stem number	−0.078 ns	−0.117 ns	−0.065 ns	−0.075 ns	−0.075 ns	0.019 ns	−0.011 ns	1.0		
	__0.107 ns__	__−0.024 ns__	__0.002 ns__	__0.083 ns__	__0.071 ns__	__0.068 ns__	__0.001 ns__			
Harvest index	0.033 ns	0.168 ns	−0.374**	0.608**	0.402**	0.191 ns	0.455**	−0.021 ns	1.0	
	__−0.074 ns__	__0.210**__	__−0.463**__	__0.527**__	__0.280**__	__0.120 ns__	__0.479**__	__−0.002 ns__		
Radiation use efficiency	0.587**	−0.404**	0.386**	0.509**	0.537**	0.691**	−0.146 ns	0.165 ns	0.143 ns	1.0
	__0.169*__	__−0.281**__	__0.204**__	__0.298**__	__0.306**__	__0.380**__	__−0.035 ns__	__0.116 ns__	__0.053 ns__	

Regular figures are for BP1 only and bold for all cultivars in both seasons, both planting dates and all four sites

ns non-significant at $p\geq 0.05$

*$p\leq 0.05$ (significant); **$p\leq 0.01$ (highly significant)

marginal land for potato (lower altitudes). This brings down the average yields but there are also many examples of growers that strongly increase their yields by proper fertilisation and crop protection techniques. This, combined with the use of certified seed, will still increase yields further.

Potato is a knowledge-intensive crop and this study contributed to this knowledge. The situation described here for the conditions of Lesotho (summer rains, cold dry winters with too low temperatures for potato growth): high elevation with high solar radiation levels and large differences between daily maximum and minimum temperatures are typical for many other high altitude areas at latitudes between approximately 15° and 30° North and South of the equator. Such conditions are also encountered in, e.g., northern Ethiopia, some highlands in West Africa such as in Burkina Faso and Mali. In South America, such conditions prevail in Mexico (Toluca) and in southern Peru and Bolivia. Globally, subtropical summer highland crops approach an area of half a million hectare, thereby contributing substantially to food security. In the future, the crop will strongly benefit from the expected increase in CO_2 concentration of the air (Haverkort et al. 2013) in most of these areas and, with winters warming up a few degrees in the decennia to come, the longer growing seasons in these areas and growers adapting their cropping season (Franke et al. 2013) will further contribute to the success of the crop.

Our study revealed a number of findings of relevance for crop ecological science and for strategies of potato production in subtropical highlands in summer. The current actual yields in Lesotho are about 13 t ha^{-1}, while the average tuber yields in our field trials (first planting in the first season) were well above 7.5 t ha^{-1} dry matter or over 37.5 t ha^{-1} fresh yield. The strong variation among planting dates and seasons resulted in average fresh yields of about 23 t ha^{-1}, while the lowest yield obtained was 2.39 t ha^{-1} dry or 12 t ha^{-1} fresh tubers for cultivar Vanderplank in the 2011/2012 growing season at the Roma site. The calculated potential yields were between 9 and 14 t ha^{-1} tuber dry matter or between 45 and 70 t ha^{-1} fresh yields. The main abiotic factor limiting production proved to be a shortage of water supply, resulting primarily in lower radiation use efficiency and to a lesser degree a lower harvest index.

The study showed that there is a strong degree of variation in yields across sites, planting time and cultivar, which can be attributed to:

- *Site*: Roma lying lowest with the highest maximum temperatures and especially minimum temperatures and highest amount of long-term rainfall, but with great degree of erraticness of rainfall pattern had the lowest yields and tuber DM%, while Thaba Tseka, the highest and coolest site with adequate rainfall, had the highest yields.
- *Planting time*: The long-term weather averages show sufficient rain for crop growth ‘on average’ between October and March (Fig. 2). However, the rainfall distribution between seasons and within a season is very erratic (2010/2011 and 2011/2012), with excess rain on 1 day (with only part of the water infiltrating into the soil and the rest running off), followed by subsequent dry spells that can sometimes last for weeks (Fig. 3). This illustrates that it is opportune to plant early in summer to assure that enough soil water is collected and the growing season is long enough for optimal crop growth during the growing season.
- *Cultivar*: In some conditions, having an early cultivar can be a strategy to escape droughts that are more frequent towards the end of the growing season. This

> usually applies to winter and spring crops in Mediterranean climates. Our study showed that such a strategy is not opportune for rain-fed summer crops in subtropical highlands. The early cultivar Vanderplank performed poorly in conditions with transient dry periods. A late cultivar such as BP1 may shed some leaves when it is dry for a prolonged period but recuperate when it rains again.

It can hence be concluded that the lowest risk of low yields in rain-fed subtropical highlands is to plant late cultivars as soon as the weather permits it in the highest areas possible. If options for irrigation can be realised, actual yields of say 15 t ha^{-1} can be raised to yields of about 25 t ha^{-1} in dry seasons and well over 37 t ha^{-1} in seasons with adequate water supply from rainfall and irrigation, as was illustrated for experimental conditions in our trials.

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