Water stress responses of three potato cultivars

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Abstract

Potato are highly sensitive to water stress. It is unclear if cultivars have different physiological strategies to adapt to water stress. Understanding these responses could help to identify phenotypical traits of interest for breeding programmes. A field experiment was conducted in a rain-out shelter facility in Lincoln, New Zealand, growing three potato cultivars (‘Russet Burbank’, ‘Moonlight’ and ‘Karaka’) under full irrigation and severe drought conditions. Total dry biomass production, which ranged from 13.7 to 25.5 Mg DM/ha at final harvest, was significantly reduced by water stress with little differences between cultivars. Physiological parameters such as leaf area index (LAI), the proportion of solar radiation intercepted by the crop canopy (f), radiation interception (R_i), water use (WU), radiation and water use efficiencies (RUE and WUE) were also affected by water stress. All parameters were reduced under drought conditions, except for WUE which increased in dry plots. Similar yields (dry biomass) were achieved by cultivars using different strategies as illustrated by contrasting values of LAI, f, R_i and WU during growth. For instance, ‘Russet Burbank’ had a higher LAI than the other cultivars under full irrigation and until the onset of senescence, while ‘Karaka’ had the lowest LAI under drought conditions. Overall, ‘Moonlight’ intercepted more radiation than the other cultivars under both irrigation treatments by maintaining a higher green canopy along the growth cycle. These results showed that, while no cultivar presented a greater adaptation to drought, they displayed different strategies to reach similar amounts of dry biomass production under full irrigation or drought.

Additional keywords: *Solanum tuberosum* ‘Russet Burbank’, ‘Moonlight’, ‘Karaka’, irrigation, drought, water use efficiency, radiation use efficiency, crop physiology, abiotic stress.

Introduction

Farming is one of the key industries that underpins New Zealand’s export-led economy and potato is one of the main vegetable crops, with 10,591 hectares grown in New Zealand (PNZ 2019). Potato is a high value crop with over half of the production dedicated to the processed market and a quarter of the annual crop being exported. Canterbury is the largest growing region, with crops grown there usually requiring irrigation because rainfall is insufficient during the growing season to sustain economically viable yields.

With non-limiting conditions by water and nitrogen supply, plant biomass production (dry matter yield) is usually determined by the amount of radiation that is intercepted by the canopy and the efficiency by which the intercepted radiation is utilised to produce biomass through the process of photosynthesis (Monteith 1972; Russell *et al.* 1989). When water, an essential resource for the photosynthetic function of plants (Seiffert *et al.* 1995), is limited, plants become stressed, which reduces canopy expansion and radiation use efficiency (DallaCosta *et al.* 1997; Earl & Davis 2003; Abid *et al.* 2004). This is particularly important in areas where water is a limited resource, such as the Canterbury plains in New Zealand.

Using water resources more efficiently is key for New Zealand potato farming sustainability. Potato crops are known for their high water use efficiency (Shahnazari *et al.* 2007) when compared with other major crops such as cereals (FAO 2008). However, potato crops are also reported to be sensitive to drought (Vanloon 1981; Gregory & Simmonds 1992), although the response to water stress differs between cultivars (Obidiegwu *et al.* 2015; Aliche *et al.* 2018).

This study aimed to provide an understanding of how different potato cultivars differ in their response to water stress. The paper describes dry biomass production and key physiological parameters, including water use, in three potato cultivars under both unconstrained and constrained water supply. The findings aim to inform breeding efforts when screening genotypes for water-constrained environments.

Materials and Methods

Experimental details

The experiment was conducted at the New Zealand Institute for Plant and Food Research Limited (PFR) rain-out shelter facility, at Lincoln, Canterbury, New Zealand (43° 38’S, 172° 30’E). The facility allows the exclusion of rainfall from the experimental site (Martin *et al.* 1990). The site is located on a deep (>1.6 m in depth), well drained Templeton silt loam over sand (*Udic Ustochrep*, UDA Soil Taxonomy) (McLaren & Cameron 1996), with a plant available water-holding capacity of approximately 190 mm/m of depth (Jamieson *et al.* 1995). Physical characteristics of the soil have been described by Martin *et al.* (1992).

The site was under a mown perennial ryegrass (*Lolium perenne* L.) crop for the previous 3 years, and then oats for the 6 months prior to the establishment of the current experiment. The oat crop was grown to remove any excess nitrogen (N) from previous experimentation and to reduce the soil N concentrations variability over the experimental site. The oat crop was removed by mowing before preparing the experimental site for planting.

The experiment was setup as a randomised block design with four replicates and six factorial treatments of three potato cultivars and two irrigation regimes, giving a total of 24 plots. Plot size was 5.0 m long by 3.6 m wide, with a fallow buffer of approximately 0.4 m between plots. The three cultivars used were ‘Russet Burbank’, ‘Moonlight’ and ‘Karaka’. All three cultivars are suitable for medium to long season and the main end use is processing into French fries. However, some of their phenotypical characteristics differ, such as canopy architecture, stem thickness, tuber set number etc.

The irrigation was applied using a dripper irrigation system, with emitters spaced 150 x 150 mm apart in an offset arrangement. The irrigation regimes were:

i) drought, where irrigation was applied during N applications (fertigation) and on two occasions during mid- and late January to avoid the crop premature senescence;

ii) full irrigation, where crop water use was replaced weekly (calculated to 1800 mm depth using the methods described below).

Soil mineral N available to the crop at the start of the experiment, to 1500 mm depth, was measured at 97 kg N/ha across the experimental site. Average soil test results in MAF quick-test units (Mountier *et al.* 1966) were: pH 6.2, Olsen P 20, K 11, Ca 10, Mg 17, and Na 14. Base fertiliser was broadcast during site preparation and consisted of 700 kg/ha Diammonium phosphate (123.2 kg N/ha, 140 kg P/ha, 7 kg S/ha), 750 kg/ha Sulphate of Potash (315 kg K/ha, 127.5 kg S/ha), and 250 kg/ha Kieserite (50 kg S/ha, 37.5 kg Mg/ha). Side-dressings of N were applied three times during the growth of the crop:

i) 75 kg N/ha at 48 days after planting;

ii) 75 kg N/ha at 77 days after planting;

iii) 75 kg N/ha at 98 days after planting. All N was applied as dissolved urea (46% N) through the irrigation system (fertigation). Herbicide, fungicide and pesticide management was carried out to prevent yield limitation by pests and diseases.

The site was prepared by deep ploughing (200 mm), followed by one pass of a harrow and Cambridge roller, and power harrowing. After base fertiliser application, the site was maxi-tilled twice to incorporate the fertiliser.

The crop was planted by hand on 2 October 2018 in furrows 200 mm deep. Seed spacing was 0.25 m and row spacing was 0.72 m giving a total of 5 rows or 105 plants per plot. The first irrigation was applied to all treatments on 4 November 2018 (33 days after planting). Following that date, irrigation was applied according to treatments. Plots under drought irrigation regime received a total of 116 mm of water. Plots under full irrigation regime received a total of 580 mm of water. The last irrigation was applied in mid-February and following that the crop was left to naturally senesce (no chemical was used to desiccate the crop).

Measurements

Soil moisture

Reflectometers (Model CS650 Water Content Reflectometers, Campbell Scientific Inc., Utah, USA) were installed in each plot after emergence (33 days after planting) and used to measure soil volumetric water content (VWC) at the following depths:

0-150 mm (two reflectometers installed at this depth, within and between planted rows);

150-300 mm;

and then in 300 mm increments from 300 mm to 1800 mm depth (total of eight reflectometers per plot). Reflectometers were connected to a data logger (Model CR1000, Campbell Scientific Inc., Utah, USA) to record VWC at 15-min intervals.

Radiation interception

The proportion of global solar radiation intercepted by the crop canopy (*f*) was estimated from reflectance measurements taken every 5-10 days using a Trimble® GreenSeeker® crop sensing system (Trimble Agriculture Division, Colorado, USA). The GreenSeeker® is a handheld module that has a light source producing light in the visible red (660 nm) and near-infrared (NIR, 770 nm) wavelengths and a sensor recording the amount of reflectance of these wavelengths at the rate of 10 readings per second. These measurements were carried out on a 3-m transect following the rows in each plot and the sensor was positioned approximately 0.6 m above the crop canopy. Average reflectance values from the Greenseeker® were converted into a normalised difference vegetation index (NDVI), which has been previously used to approximate *f* (Carlson & Ripley 1997). As total reflectance values are influenced by the soil, bare soil readings were taken at each measurement date and used to scale NDVI values (Carlson & Ripley 1997):

$NDVI_{scaled}$ =

$(NDVI - NDVI_O) / (NDVI_S - NDVI_O)$, where $NDVI_O$ and $NDVI_S$ are the values of NDVI for bare soils and a surface with a fractional ground cover of ≥95% (full canopy cover), respectively.

Daily solar radiation (R_0) data was accessed from measurements at the Broadfields weather station (National Institute of Water and Atmospheric Research – NIWA 17603), which is located ~200 m away from the experimental site.

Biomass

A total of four sequential intermediate biomass harvests at 4-weekly intervals and a final tuber harvest at crop maturity were completed. Table 1 shows the dates of each harvest and the growth stage for the majority of the crop when the harvest was done. The final tuber harvest was carried out approximately 2 weeks after the crop had completely senesced, at 170 days after planting.

For each intermediate harvest, above and below ground fresh biomass for each plot was sampled from five plants of a row. Each sample was partitioned into: main stem from each plant (grouped together), remaining above ground biomass, and below ground biomass (below ground stems and tubers, excluding roots and rhizomes). Each sample of main stems was further partitioned into: leaf, stem, and dead material. Each partition was weighed fresh, and then again after drying at 60°C to constant weight. The main stem leaf area was measured using a leaf area meter (model LI-3100, LI-COR Inc., Nebraska, USA) and used to calculate

Table 1: Dates and indicative growth stage of the crop for each biomass harvest of ‘Karaka’, ‘Moonlight’ and ‘Russet Burbank’ potato grown under different irrigation regimes at Lincoln, Canterbury, New Zealand in 2018-19.

Harvest	Date (days after planting)	Growth stage
H1 – intermediate harvest 1	19 November 2018 (48)	Tuber initiation
H2 – intermediate harvest 2	18 December 2018 (77)	Row closure
H3 – intermediate harvest 3	14 January 2019 (104)	Full canopy
H4 – intermediate harvest 4	11 February 2019 (132)	Late canopy
H5 – final tuber harvest	8 April 2019	Fully senesced

leaf area index (LAI; m^2/m^2).

Each sample of remaining above ground biomass was weighed fresh. A 400-500 g subsample was then taken and used to measure dry matter content of the above ground biomass after drying at 60°C to constant weight.

Each sample of below ground biomass was washed free of soil and partitioned into below ground stems and tubers. Each partition was weighed fresh, then again after drying at 60°C to constant weight.

Final tuber harvest was carried out once the crop canopy was fully senesced. The sampling was taken from six plants of each of the three centre rows. Tubers were graded into reject (tubers less than 60 mm in length) and marketable commercial grades. Each grade was weighed fresh and a sub-sample from marketable tuber grades of ~500 g was used to measure tuber dry matter content after drying at 60°C to constant weight.

Calculations

Total biomass (Y_{DM}, Mg DM/ha) is reported as the sum of above and below ground dry matter biomass. For the final harvest, total biomass was represented by tuber dry biomass from both rejects and marketable grades, and above ground biomass was considered negligible. For consistency with previous literature, total biomass was converted to g DM/m^2 to calculate the efficiency of radiation utilisation.

Crop water use (WU, mm) for the season was calculated as the difference in soil water content from 0 to 1800 mm depth between when the automated reflectometers were installed (2 November 2018, crop emergence) and final harvest (ΔVWC), plus irrigation inputs during the growth of the crop (I): $WU = (\Delta VWC + I)$.

Water use efficiency (WUE, kg DM/ha/mm) was calculated as the quotient between Y_{DM} at final harvest and WU: $WUE = Y_{DM} / WU$.

Daily intercepted solar radiation through the growth of the crop (R_i, MJ/m^2) was calculated as the product of daily solar radiation and the proportion of intercepted photosynthetically active radiation (fractional): $R_i = R_0 \times f$.

Radiation use efficiency (RUE, g DM/MJ) was calculated as the quotient between Y_{DM} at final harvest and accumulated intercepted solar radiation: $RUE = Y_{DM} / R_i$.

Analysis

The analysis was carried out in R version 3.5.1 (R Core Team 2018). Each variable was analysed separately, and all variables except LAI were analysed using a linear mixed effect model (LMM) approach.

Total biomass was measured for the five sequential destructive sampling events. The fixed effects in the model were harvest time, cultivar, irrigation and all interactions. Plot and block were included as random effects to account for position in the trial and repeated measurements.

For LAI, random effects plot and block were estimated to have no effect and therefore were removed from the model. A linear model approach was carried out with fixed effects being harvest, cultivar and irrigation.

Crop canopy cover (NDVI) was recorded at 21 time-points. Fixed effects included in the model were date, cultivar, irrigation and all interactions. To account for repeated measurements a temporal (AR1) correlation was applied to plots.

Radiation use, water use and efficiencies (RUE and WUE) were measured at final harvest with the fixed effects in the models being cultivar, irrigation and its interaction. Block was included as a random effect to account for location of each plot.

For each of the variables, model assumptions were checked via standard residual plots and log transformations applied when needed. Post-hoc pairwise comparison p-values were adjusted using the false discovery rate (FDR) correction to account for multiple tests.

For ease of interpretation, where data were transformed to meet assumptions, the back-transformed means are presented in figures and tables. As such, these means do not have LSD associated with them. Trends are indicated in the text when $p<0.1$ (based on log transformed data where required) and an estimate of the variation associated with predicted means is provided by a 5% least significant difference ($LSD_{0.05}$) when applicable.

Results

Biomass

Total dry matter biomass ranged from 13.7 to 25.5 Mg DM/ha at final harvest, being affected by 2-way interactions between harvest time and irrigation ($p<0.001$), and harvest time and cultivar ($p<0.001$). There was no interaction between irrigation regime and cultivar ($p=0.382$). From H2 (row closure) onwards, water stress reduced Y_{DM} of the drought plots compared with the plots under full irrigation. The difference in Y_{DM} between fully irrigated and drought plots was more pronounced as the season progressed, with average differences across all cultivars of 3 and 10 Mg DM/ha measured at H2/H3, and H4/H5 respectively (Figure 1). The differences in Y_{DM} between cultivars at each harvest were negligible, except for H4 where 'Russet Burbank' yielded 3 Mg DM/ha lower than 'Moonlight' and 'Karaka' on average under both irrigation regimes. There was no difference in Y_{DM} between H4 and H5 under both irrigation regimes.

Leaf area index was affected by 2-way interactions between harvest time and irrigation ($p<0.001$), harvest time and cultivar ($p<0.001$), and irrigation and cultivar ($p=0.002$). Water stress resulted in a lower LAI for most of the growth of the crop compared with full irrigation (Figure 2). LAI increased to 5.3 and 3.1 at H2, for fully irrigated and drought treatments respectively, and then decreased progressively for the remainder of the season. 'Russet Burbank' and 'Karaka' reached peak LAI at H2: 3.7 and 3.0 under drought respectively, and 6.1 and 4.6 under full irrigation respectively. 'Moonlight' reached peak LAI at H3: 3.1 under drought and 5.6 under full irrigation. On average, 'Russet Burbank' produced the highest LAI under full irrigation, followed by "Moonlight' and then 'Karaka'. Under drought conditions, 'Russet Burbank' and 'Moonlight' produced similar LAI, while LAI for 'Karaka' was lower.

The proportion of intercepted solar radiation, *f*, was affected by 2-way interactions between sampling date and irrigation ($p<0.001$), and sampling date and cultivar ($p<0.001$). There was no interaction between irrigation and cultivar ($p=0.126$). There was no difference in *f* between drought and fully irrigated plots during the first part of the season (Figure 3).

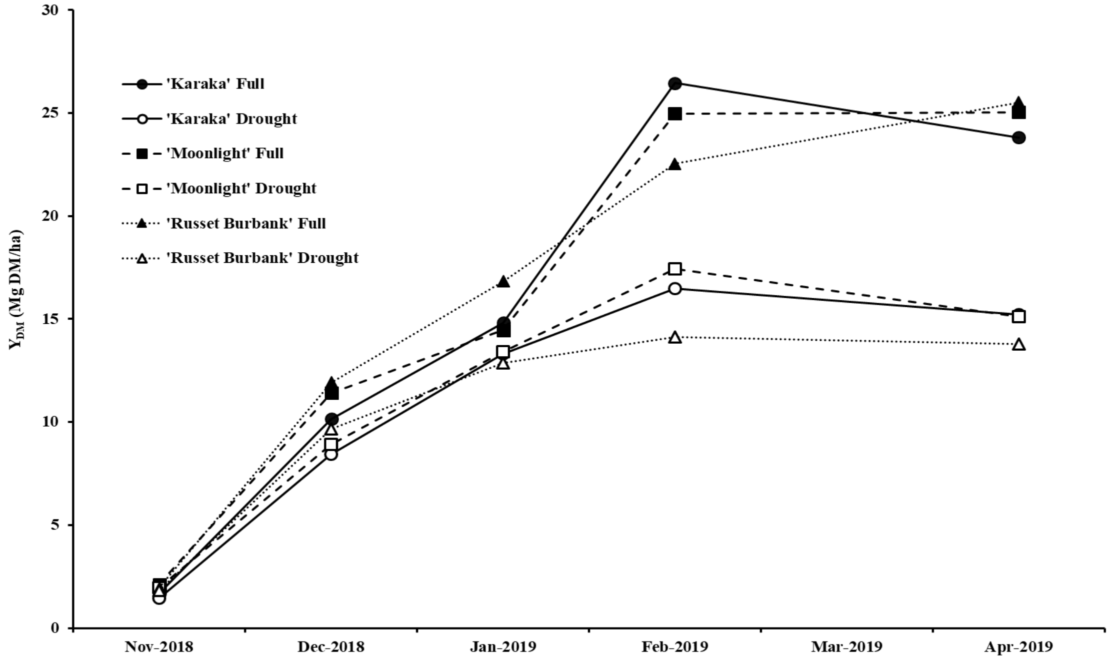

Figure 1: Total biomass (Y_{DM} Mg DM/ha) of 'Karaka' (○●), 'Moonlight' (□■) and 'Russet Burbank' (∆▲) potatoes grown under different irrigation regimes (Full irrigation = closed symbols, Drought = open symbols) at Lincoln, Canterbury, New Zealand in 2018-19.

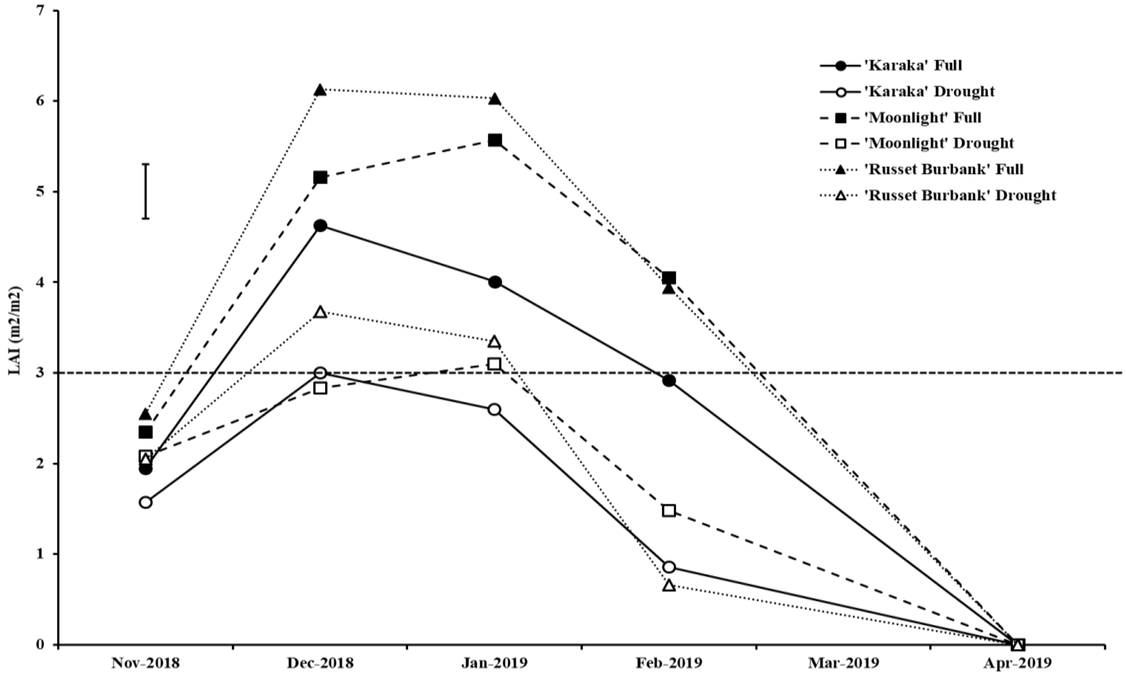

Figure 2: Leaf area index (LAI, m^2/m^2) of 'Karaka' (○●), 'Moonlight' (□■) and 'Russet Burbank' (∆▲) potato grown under different irrigation regimes (Full irrigation = closed symbols, Drought = open symbols) at Lincoln, Canterbury, New Zealand in 2018-19. The vertical bar represents the 5% least significant difference ($LSD_{0.05}$). The dotted line represents critical LAI of 3 m^2/m^2 which is associated with full ground cover (Haverkort *et al.*, 1991).

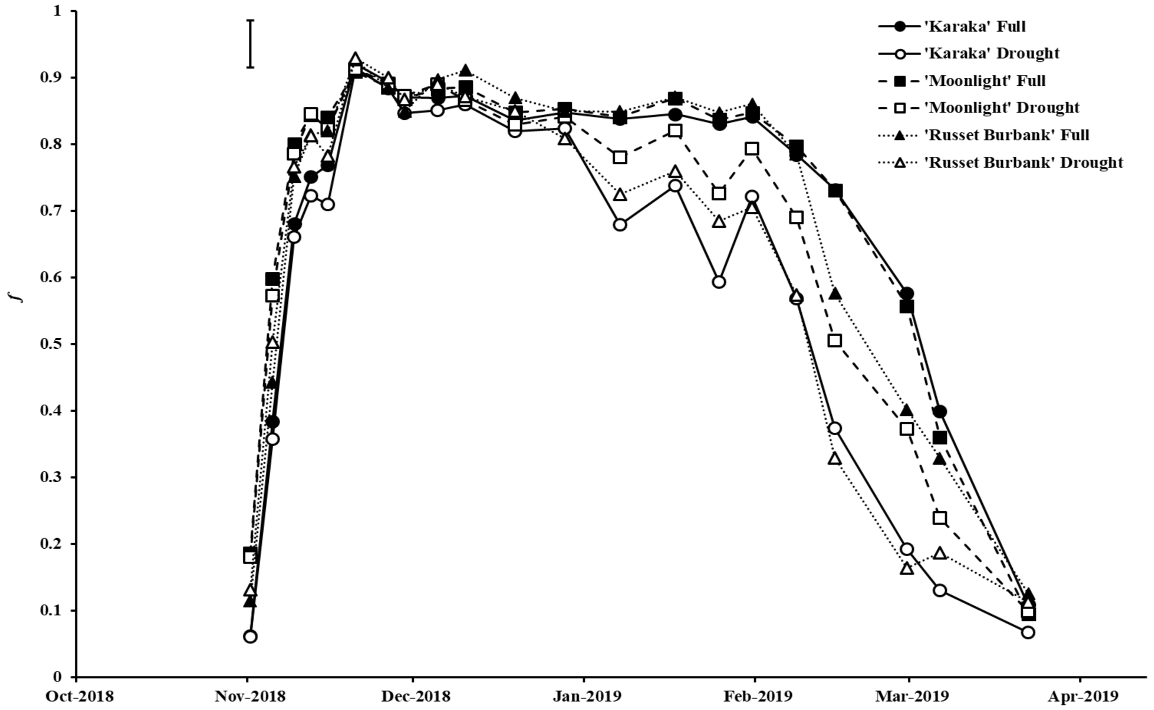

Figure 3: Proportion of intercepted solar radiation (*f*) by the canopy of 'Karaka' (○●), 'Moonlight' (□■) and 'Russet Burbank' (∆▲) potato grown under different irrigation regimes (Full irrigation = closed symbols, Drought = open symbols) at Lincoln, Canterbury, New Zealand in 2018-19. The vertical bar represents the 5% least significant difference ($LSD_{0.05}$).

All treatments reached their highest *f* (row closure) around the end of November (approx. 50 days after planting). Drought plots maintained closed canopy until early January, while the fully irrigated plots were able to maintain a closed canopy for longer, until February. At the beginning of the season, 'Karaka' had lower *f* compared with 'Moonlight'. While the crop was at full canopy, there was no difference in *f* between cultivars. From late January, when senescence had started for the fully irrigated plots and was well advanced for the drought plots (*f* dropped below 0.8), 'Moonlight' consistently intercepted more radiation than 'Russet Burbank' under both irrigation regimes.

Radiation interception and water use

Radiation interception was affected by irrigation regime ($p<0.001$) and cultivar ($p=0.008$), but there were no interactions between treatments ($p=0.122$). R_i was lower under drought conditions for all cultivars (Table 2) by an average of 300 MJ/m^2. Under both irrigation regimes, 'Moonlight' intercepted more radiation than 'Karaka' and 'Russet Burbank', with an average of 2241.1 MJ/m^2 intercepted against 2108.5 and 2077.7 MJ/m^2 for 'Russet Burbank' and 'Karaka', respectively.

There was an interaction between irrigation regime and cultivar for WU ($p<0.001$). Under full irrigation, all cultivars used similar amounts of water throughout the season averaging 627 mm (Table 2).

Water stress caused 'Russet Burbank' to use less water (227.8 mm) compared with 'Karaka' and 'Moonlight' (275.1 and 265.5 mm respectively).

There was moderate evidence to suggest an interaction between irrigation regime and cultivar on RUE (p=0.077). Water stress reduced RUE for all cultivars (Table 2). For 'Russet Burbank' and 'Moonlight', RUE was 1.13 and 1.06 g DM/MJ, respectively, under full irrigation, which was reduced to 0.70 g DM/MJ for both cultivars under drought. For 'Karaka', RUE was also reduced from 1.04 g DM/MJ, under full irrigation, to 0.81 g DM/MJ, under drought conditions.

WUE was affected by irrigation regime (p<0.001), but not by cultivar (p=0.338), and there was no interaction between the treatments (p=0.993). Water stress resulted in higher WUE for all cultivars (Table 2), with an average across cultivars of 57.3 and 39.3 kg DM/ha/mm for full irrigation and drought treatments, respectively.

Table 2: Radiation intercepted during growth (R_i), water use (WU), radiation use efficiency (RUE) and water use efficiency (WUE) of 'Karaka', 'Moonlight' and 'Russet Burbank' potato grown under different irrigation regimes (Full irrigation or Drought) at Lincoln, Canterbury, New Zealand in 2018-19. Note that WU, RUE and WUE data presented here were back-transformed from log transformation (required to meet assumptions) so no least significant difference is associated with these means.

Cultivar	Irrigation regime	R_i (MJ/m^2)	WU (mm)	RUE (g DM/MJ)	WUE (kg DM/ha/mm)
'Karaka'	Drought	1873.9	275.1	0.81	55.2
'Moonlight'	Drought	2144.0	265.5	0.70	56.7
'Russet Burbank'	Drought	1958.8	227.8	0.70	60.1
Average		1992.2	256.1	0.74	57.3
'Karaka'	Full	2281.4	625.6	1.04	37.9
'Moonlight'	Full	2338.3	642.3	1.06	38.7
'Russet Burbank'	Full	2258.1	614.2	1.13	41.5
Average		2292.6	627.4	1.08	39.4
$LSD_{0.05}$		145.4	n/a	n/a	n/a
Cultivar (p value)		0.008	<0.001	0.516	0.338
Irrigation regime (p value)		<0.001	<0.001	<0.001	<0.001
Cultivar x Irrigation regime (p value)		0.122	<0.001	0.077	0.993

Discussion

Water stress was a major factor affecting Y_{DM}, LAI, *f*, R_i, RUE, WU and WUE. All parameters were reduced by water stress, except for WUE which was higher under drought conditions. This is consistent with previously reported studies (Martin *et al.* 1990; Martin *et al.* 1992; DallaCosta *et al.* 1997; Obidiegwu *et al.* 2015; Camargo *et al.* 2016).

Although Y_{DM} was reduced by water stress, there were no major differences among cultivars under either irrigation regime. This implies that no cultivar displayed a greater adaptation to drought conditions. This could be explained by the timing of water stress, which likely occurred after tuber initiation due to the soil at the site being deep with a high water-holding capacity. An earlier water stress could have affected tuber set and produced yield differences among cultivars if phenotypical differences for this period had manifested. For instance, some cultivars have been reported to have greater sensitivity to water stress occurring before tuber initiation, while other cultivars are more affected by later drought conditions (Haverkort *et al.* 1990; Martin *et al.* 1990; Aliche *et al.* 2018). Interestingly, Y_{DM} did not change significantly between the late canopy and final harvest, which meant the effects of drought were prevalent during the earlier parts of the season but after tuber initiation.

There were differences in LAI between cultivars under both irrigation regimes. Under the full irrigation regime, LAI was equal to or exceeded 3 from late November to mid-February or early March depending on the cultivar. This has been previously reported as full ground cover by Haverkort *et al.* (1991) and could explain the lack of difference in Y_{DM} between the cultivars. The proportion of intercepted solar radiation, *f*, showed no differences among treatments in the first part of the growing season: all cultivars reached a similar peak of approximately 93% light interception by late November under both irrigation regimes. There were no differences in *f* among cultivars until senescence occurred, in January for the drought treatments and in February for the full irrigation treatments. It is possible that the differences in LAI could be explained by differences in canopy architecture among cultivars, which needs to be further investigated. Under drought conditions, all the cultivars still reached a LAI of around 3 in summer, and any existing difference might have been negligible to have a meaningful impact on Y_{DM}.

Radiation interception started to decline from early January for the drought treatments, while the fully irrigated crops were able to maintain maximum canopy cover for an additional month, capturing additional light for photosynthesis. The only cultivar effect was observed for 'Moonlight' having a higher fractional interception (*f*) than 'Russet Burbank' in the late season under both irrigation regimes. This did not result in significant differences in dry biomass production at the end of the crop growing season suggesting trade-offs with other physiological parameters.

For all cultivars, the differences in radiation interception were mainly caused by water stress, particularly through early senescence. The RUE was also reduced by water stress for all cultivars, illustrating a negative impact on photosynthetic capacity of dry crops. While all cultivars suffered from a reduction of RUE under drought, compared with full irrigation, 'Russet Burbank' and 'Moonlight' were more sensitive than 'Karaka'.

These results showed that, while there was no indication of a genotype more adapted to drought conditions, the cultivars displayed different strategies to produce similar yields under the same water supply. Similarly, cultivars used water at same amounts when fully irrigated but differed under drought conditions. 'Russet Burbank', which has previously been described as highly sensitive to water stress (Martin *et al.* 1990), had a lower WU compared with 'Moonlight' and 'Karaka'. A more in-depth look at the water extraction patterns is required to confirm these responses. The lack of difference in WUE between cultivars under water stress meant that none of them displayed a clear adaptation advantage to drought over the others.

Conclusion

Dry biomass production was similarly reduced by water stress in all three cultivars ('Russet Burbank', 'Moonlight' and 'Karaka'). However, genotypes showed differences in physiological traits (e.g. LAI, radiation interception and water use) suggesting different strategies to adapt to limiting conditions to reach similar biomass production. The similar responses among genotypes may be caused by the late timing of imposed drought in the experiment.

Future work might explore how genotypes respond to early drought before tuber formation.

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