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Radiation use efficiency and biomass partitioning to storage roots in fodder beet crops

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ABSTRACT

Intercepted photosynthetic active radiation (IPAR), radiation use efficiency (RUE) and partitioning of dry matter (DM) to storage roots (p_{root}, %) were quantified for fodder beet crops subjected to contrasting water (irrigated or rain-fed) and nitrogen (N; 0, 25, 50, 100 and 200 kg/ha) supply conditions in Canterbury, New Zealand. The objectives were to enhance the understanding of physiological processes controlling fodder beet response to abiotic stresses and also to estimate parameters for biophysical models that simulate crop growth. Data from three field experiments showed a wide range of fodder beet yield (14–29 t DM/ha) in response to water and N stress. These yield differences were mostly explained by the treatments effect on IPAR (650–1050 MJ PAR/ha), with relatively smaller responses in RUE and p_{root}. For unconstrained (fully irrigated; ≥100 kg N/ha) growth conditions, maximum values were 3.6 g DM/MJ PAR for RUE and 78% for p_{root} for total biomass at final harvest. The RUE for the rain-fed, 0 kg N/ha crops was reduced by up to 25%, while p_{root} was only marginally reduced (~3% in rain-fed crops) compared with crops under unconstrained growth conditions. While the RUE responded linearly to additional N supply in irrigated crops, rain-fed crops showed a more consistent decline in RUE across N fertiliser rates with 65–70% of unstressed values. High RUE values were observed across a wide range of crop N status (Nitrogen Nutrition Index [NNI] from 0.8 to 1.6) in irrigated crops. In contrast, RUE in rain-fed was low at high NNI estimates because of high N concentration in a smaller canopy area. The lower RUE in rain-fed crops was aligned with reduced leaf photosynthetic rates (Pn_{leaf}) although there was a high variability in Pn_{leaf} measurements. These results give a first quantification of IPAR, RUE, p_{root} and Pn_{leaf} in fodder beet. They provide insights on the relative sensitivity of fodder beet to water and N stresses. These results are valuable for the interpretation of crop responses and for setting parameters for biophysical models to simulate fodder beet growth.

1. Introduction

Crop physiological responses to water and nitrogen (N) supply can be represented by differences in intercepted photosynthetic active radiation (IPAR), radiation use efficiency (RUE) and partitioning of biomass to plant organs (Monteith, 1977; Sinclair and Muchow, 1999). This analysis framework also forms the basis of many process-based biophysical models used to assess crop yields (Holzworth et al., 2014). In the past decades, these physiological parameters have been assessed and represented in models for many crop species (Sinclair and Muchow, 1999). However, there is a pressing need to widen the range of crop systems represented in modelling frameworks used in future assessments (Ewert et al., 2015). Such effort is important to allow cropping systems with emerging social and economic importance to be assessed for both productivity and environmental outcomes. This is the case for fodder beet (*Beta vulgaris* subsp. *vulgaris* var. *alba* L.) use in winter-grazing for intensive dairy production in New Zealand. From 2013–2016, fodder beet planted area increased by up to 4-fold in New Zealand (Chakwizira et al., 2016a), with significant expansion trends also observed in Australia (Rawnsley et al., 2013) and Europe (Albayrak and Yuksel, 2010). This is explained by the combination of high (> 20 t DM/ha) DM yields and quality (Matthew et al., 2011; Chakwizira et al., 2014b, 2014c, 2016a), high (> 90%) grazing utilisation (Edwards et al., 2014a, 2014b) and perceived lower risks of N leaching losses in comparison with alternative winter-fed forages (Edwards et al., 2014a; Malcolm et al., 2016).

As a first step towards representing fodder beet physiology in models, it is necessary to quantitatively assess underlying processes that control crop growth (Chakwizira et al., 2016b, 2016c). To our knowledge, there are not yet any systematic investigation of RUE dynamics in

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fodder beet for optimal and constrained growth conditions. Published work on a closely related species, sugar beet (*Beta vulgaris* L. *ssp. vulgaris var. altissima* [Doell]), reported a wide range of RUE under unconstrained conditions from 3.0–4.0 g/MJ PAR (Milford et al., 1980; Damay and Le Gouis, 1993). Similarly, a wide variability of RUE has been reported in response to constrained water and nutrients with values ranging from 1.2 to 1.8 g/MJ PAR in sugar beet (Milford and Riley, 1980; Brown et al., 1987; Wright et al., 1997). Limited water and N were also shown to limit IPAR in sugar beet through reduced canopy expansion and increased senescence rates (Brown et al., 1987; Malnou et al., 2006). In fodder beet, canopy expansion was shown to be reduced by limited water and N (Chakwizira et al., 2014b, 2014c, 2016a) but it is unclear how stress responses affected IPAR, RUE and related physiological processes. These include processes such as the partitioning of biomass to storage roots (p_{root}; %) and leaf photosynthesis rates (Pn_{leaf}), which influence crop yield through assimilation and allocation of carbon in the plant.

In this study, we provide a first quantification of IPAR, RUE, Pn_{leaf} and p_{root} in fodder beet crops subjected to a wide range of water and N supply conditions in Canterbury, New Zealand. These results aim to enhance the physiological understanding of fodder beet responses to abiotic stresses and to provide parameters for biophysical models.

2. Materials and methods

2.1. Experimental design and site description

This paper reports on three separate experiments where N and/or water (W) limitation was imposed on fodder beet crops. The experiments were performed in the Canterbury region of New Zealand (43–44°S), during three consecutive spring-summer seasons from 2011 to 2014. Details of each study have been described in recent publications (Chakwizira et al., 2014b, 2014c, 2016a). These will be referred to as N-limited only (N-, 2011–2012), water limited only (W-, 2012–2013) and N and water co-limited (NW-, 2013–2014) experiments. In brief, Experiment (Exp.) N- and Exp. W- were carried out in adjacent sites at The New Zealand Institute for Plant & Food Research Farm (PFR), Lincoln, Canterbury (43°37′34.4″S, 172°28′13.4″E, 18 m a.s.l). The soils at both sites are a deep ($>$ 1.6 m) and well-drained Templeton silt loam [Immature Pallic soil (Hewitt, 2010); *Udic Ustochrept* (Soil Survey Staff, 1998)] with an available water-holding capacity (WHC) of ~190 mm/m of depth (Jamieson et al., 1995). Experiment NW- was carried out at the Lincoln University Ashley Dene Research and Development Station (43°38′45.5″S 172°20′34.4″E, 30 m a.s.l), located ~10 km from both Exp. N- and Exp. W- sites. Experiment NW- was on a shallow Balmoral/Lismore stony silt loam (Mottled Argillic Pallic Soil, *Udic Ustochrept*) (Webb and Bennett, 1986; Webb and Burgham, 1997), with shallow topsoil (0.2 m in depth) over gravel. The soil has a WHC of ~90 mm/m of depth estimated from Sim et al. (2012).

All three sites are subjected to similar climatic conditions; specifically, a cool temperate climate characterised by an average temperature of 12.0 °C (23 °C summer maximum and 1 °C winter minimum) and mean annual rainfall of ~600 mm evenly distributed throughout the year (Fig. 1).

2.1.1. Experimental design

All three experiments were set in a randomised complete block design. Experiment N- (Chakwizira et al., 2014b) had five rates of N (0, 25, 50, 100 and 200 kg/ha), replicated four times. Experiment NW- (Chakwizira et al., 2016a) consisted of a factorial combination of two rates of irrigation (rain-fed and 100% replacement of evapotranspiration [ET] twice weekly) and four rates of N (0, 50, 100 and 200 kg/ha), replicated three times. Finally, Exp. W- (Chakwizira et al., 2014c) had four water treatments (rain-fed and three frequencies of irrigation), replicated four times. There was no effect of irrigation frequency in the variables analysed for RUE and p_{root} calculations in this study, so results were pooled for irrigated and rain-fed crops. Details of agronomic management, total water deficit and irrigation calculations are given in the publications referenced above. Soil mineral N (nitrate and ammonium) tests were taken from individual plots, before the application of the N treatments and also at the end of the season to a depth of 1.0 m (or shallower at sites of limited soil depth, e.g. Exp. NW-; Chakwizira et al., 2016a). Crops were managed to minimise the risk of biotic stresses through the strategic use of agrichemicals. Soil fertility was monitored and managed to optimise concentrations of other macro- and micro-nutrients.

2.2. Measurements and calculations

Radiation use efficiency was estimated as the linear slope between accumulated total crop biomass (g DM/m^2; Section 2.2.1) and photosynthetic active radiation intercepted by the crop (MJ/m^2; Section 2.2.2). The p_{root} (fractional) was estimated as the quotient of storage roots biomass and total plant biomass.

2.2.1. Dry matter measurements

The DM measurements were taken once every 4–5 weeks for all experiments, starting at 8–12 weeks after sowing. Measured sequential harvests for all experiments were from 1 m^2 quadrats for the initial 1–3 harvests, and 2–6 m^2 quadrats for the subsequent harvests, including the final harvest. The quadrat size depended on time of harvest and hence crop size, smaller earlier in the season. The harvested area at the final harvests were within or close to the 4–5 m^2 range recommended from the study of Gibbs et al. (2015). Different areas of the plots were harvested each time. Detailed information is given in the relevant published papers (Chakwizira et al., 2014a, 2014b, 2016a). Plant density and total fresh mass per quadrat were measured in the field at each harvest and a representative 2-plant sub-sample was retained to determine total DM. Dry mass was determined after drying at 60 °C to constant mass. Each sub-sample was partitioned into leaf (combined petiole and lamina) and storage root components.

2.2.2. Solar radiation interception

Percentage radiation transmission through the canopy (τ) was measured at 7- to 28-day intervals using a Sunfleck ceptometer (Model SF-80; Decagon Devices, WA 99163, USA) for Exp. N-. For Exp. W- and NW-, a CropScan (MSR16R; Cropscan Inc. Rochester, MN, USA) and Trimble GreenSeeker® (Trimble Agriculture Division, CO, USA), respectively, were used to determine radiation interception (Hatfield, 2014; Chakwizira et al., 2015b). These authors showed that the overall radiation interception (R/R_o) between ceptometer and either a CropScan or GreenSeeker® was close and therefore instruments could be used interchangeably. For all experiments, radiation measurements were confined to around midday ($\pm$ 1 h) period, on sunny days only; hence the wide frequency variability from 7 to 28 days. The proportion of radiation captured by the crop (R/R_o) was calculated as in Eq. (1) (Gallagher and Biscoe, 1978):

$$\frac{R}{R_0} = 1 - \tau \tag{1}$$

Where R is the irradiance under the crop canopy and R_o is the irradiance above the crop canopy and τ is the mean transmittance of radiation into the crop canopy along all possible paths, weighted according to the geometric distribution of direct and diffuse radiation (Szeicz, 1974; Steven et al., 1986). Daily values of R/R_o were linearly interpolated from sequential measurements (Cirilo and Andrade, 1994).

Daily values of intercepted photosynthetic active radiation (IPAR, MJ PAR/m^2) for all experiments was calculated as the product of a daily estimate of R/R_o and daily PAR values estimated from total solar radiation measured at the Broadfields meteorological station (NIWA, 2016), which is located within 50 m of both Exp. N- and W-. Accumulated IPAR was calculated as the sum of daily IPAR estimates for the