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Research Article

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Significant Water Savings can be Made in Commercial Spinach Cropping without Adverse Impacts on Crop Yield or Shelf Life

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Abstract

Spinach (*Spinacia oleracea* L.) is grown extensively across the globe but requires irrigation to maintain both yield and leaf quality. Water resources are being put under increasing pressure as we endeavour to produce enough food, fuel and fibre for a growing human population. Thus, improving our water use efficiency is becoming ever more important. Here, we report the impacts of excess and deficit irrigation on spinach yield and quality. Mild deficit irrigation (-18% of commercial water application) had no significant impact on crop quality indicators or yield, with a trend for improved shelf life, when compared to the commercially irrigated crop. Alongside this, yield was only improved when water was applied in 40% above commercial levels. The yield and quality maintenance observed under mild water deficit was associated with a reduced stomatal index suggesting a useful trait for future breeding for drought tolerance. If this relationship is robust across environments and crop varieties, major water savings will be possible across the leafy salad agricultural sector, reducing the water footprint and improving the sustainability of crop production. Furthermore, this research has elucidated links between plant responses to irrigation modifications and the thermal spectra of the canopy, with the canopy range of temperature being the most sensitive indicator of soil moisture. There is potential for these relationships to be further developed across seasons and crops for use in future irrigation decision-making.

Keywords: Deficit irrigation; *Spinacia oleracea*; Stomatal index; Shelf life; Soil moisture; Infra-red; Thermal

Introduction

Since eighteen percent of the world's cropped land is irrigated and as this area produces 40-45% of food globally [1], limiting irrigation could have major impacts on food security. In order to ensure crop yields, irrigation is often applied in excess of crop requirements, meaning water is lost through evaporation, run-off or deep-percolation, with almost half of all abstracted water never reaching the crop [2]. Improving the efficiency of water use is therefore of critical importance in a future, water-limited environment, with an even greater demand for food.

Plants maintain their water status through physiological responses, which are especially important when water is limited. If a crop is growing under well-watered conditions, a balance is maintained between water uptake and transpiration, but when transpiration exceeds uptake in water-limited environments, plant water deficits develop and yield may be impacted. Plants can respond rapidly to limited soil water, through partial stomatal closure and reduced leaf expansion, decreasing water loss and enabling plant water potential to be maintained within a functional range [3]. In commercial agricultural systems, osmotic stress is likely to be mild allowing the crop to maintain its homeostatic water potential through reduced stomatal conductance and transpiration, thus avoiding severe dehydration [4]. Although decreased stomatal aperture and leaf area reduce transpiration under drought stress, they also limit biomass accumulation. Photosynthetic capacity is intrinsically limited when less CO_2 is able to enter the plant through the stomata and thus there is tension when breeding a high biomass crop, which is tolerant to drought stress.

To maximise yields and avoid problems associated with water deficits such as growth stunting, irrigation is necessary for many crops. Generally, crops are classified according to the way in which they are irrigated with four major categories: extensive; semi-intensive; intensive and saturated [5]. Moreover, the management of irrigation has been linked to both yield and crop quality in a number of crop types [6,7]. Leafy crops such as spinach fall into the third category along with other high value crops and these intensive crops must be irrigated at a relatively high level to attain both yield and quality [5]. When irrigation management practices have been compared with respect to leafy salad crops it has been shown that irrigation is often applied in excess to the crop's needs so as to prevent stress, or even death, of the crop [8]. Concurrently, it has been demonstrated that this excess-irrigation can be detrimental, because it generally results in shallow rooting, meaning the crop cannot forage for water if deficits arise. In fact, a mild water deficit in the early stages of establishment can be beneficial to the crop [8] as long as it is balanced by applying enough water to allow continued leaf expansion. It is therefore important that the optimal irrigation level for spinach is quantified, as is initiated in this study, so that irrigation can be targeted more precisely to attain sufficient yields of quality leaf.

Crop quality is of high importance when considering sustainability of production as crop wastage through insufficient shelf life is a global problem. Spinach has a relatively short shelf life (7-10 days) and, as with other leafy crops, this shelf life is determined by quality at harvest [9], as well as storage conditions [10]. There is some evidence to suggest that leaves made up of smaller cells, with a higher cell wall volume, are firmer and more able to resist the process of growing, harvest, transport and washing, which is necessary if the crop is to reach the consumer in

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optimal condition [9]. Furthermore, alongside the mechanical strength which high cell wall volumes give, decreased cell division/expansion may also lead to lowered stomatal numbers, which could act to limit transpiration and post-harvest wilting. Although it has previously been shown that lowered stomatal conductance through physiological changes can have this effect [11], altered cell patterning is less well understood. If leaf cell patterning can be manipulated through altered irrigation practices, which has the potential to give the joint benefit of reducing water inputs while improving crop quality and reducing downstream wastage.

The use of thermal imaging has shown potential as a tool for estimating plant water status through measuring plant temperature, which is an indicator of stomatal aperture [12]. Stomatal responses occur prior to any change in plant water status making stomatal conductance a sensitive pre-symptomatic indicator of soil water deficit [13,14] and non-transpiring plants can be up to 4°C hotter than their transpiring counterparts [15]. Although there has been a lot of work on the use of thermal imaging to identify water stress in a variety of crops [12,14], this technique has not, to our knowledge, been applied to leafy salad crops in the context of improving crop quality. The focus for this research is spinach, which has a large global market both as a salad and vegetable crop, with 867,728 Ha produced in 2011 [16]. This paper investigates the link between irrigation levels and spinach quality and yield, while considering the potential for using thermal images as a diagnostic tool for automated irrigation scheduling, with which to optimise crop yield and quality.

Materials and Methods

Plant material

Experimental work was carried out on a commercial farm in south-west Portugal at Azenha do Mar (latitude 37°28’24N, longitude 8°47’30W), where the soil type is organically-rich sand with a porosity of 45% and a density of 1.48 g cm^{-3}. A spinach crop was drilled on 21-22 March 2012 and was commercially maintained until 9 April 2012, when five irrigation treatments were implemented using micro-sprinkler irrigation. Deficit and excess irrigation treatments were applied through the use of different nozzles, which output water at distinct rates (Table 1). A randomised block design whereby treatment areas were arranged into three blocks, with one of each of the five treatments arranged randomly within each block (Table 1 and Supplementary Figure 1). T. Each block consisted of five beds, with five beds separating each block. Blocks were surrounded by at least two beds of commercially maintained spinach to minimise edge effects. Sprinklers were spaced approximately 8 m apart. Temperature sensors (Testo 174T, Testo, Alton, UK) were arranged across the field and logged the surface air temperature every 15 min throughout the experiment (Supplementary Figure 2). During the entire period of growth, air temperature ranged between 4.11-24.73°C, with an average of 13.77°C. Precipitation during this time was 65 mm, although only 2 mm was experienced during the experimental stage of the experiment where treatments were imposed and measurements made. Furthermore, the duration of irrigation, which was applied to establish the crop and supplement its growth, as determined by experienced growers, was recorded (Figure 1A). Irrigation was scheduled based on the experience of the growers at this commercial site and the micro-sprinkler nozzles used in the commercial treatment were unchanged from the standard commercial system for growing spinach in this area.

Irrigation treatment (Per cent of commercial)	Nozzle speed (L hr^{-1})	Irrigation water difference (Compared to commercial)
66	226	-34%
82	278	-18%
100	341	0%
118	401	+18%
142	485	+42%

Table 1: Description of irrigation treatments. Five irrigation levels were applied as detailed here.

Daily crop water relations

Measurements were taken over a 10 day period (15-24 April 2012) between 12:00 and 13:00 each day. These measurements consisted of six soil moisture and surface temperature point measurements each day in each study area using a Delta-T WET2 sensor connected to a HH2 moisture meter (Delta-T Devices, Cambridge, UK), with probe position being randomly selected. Furthermore, six infra-red images

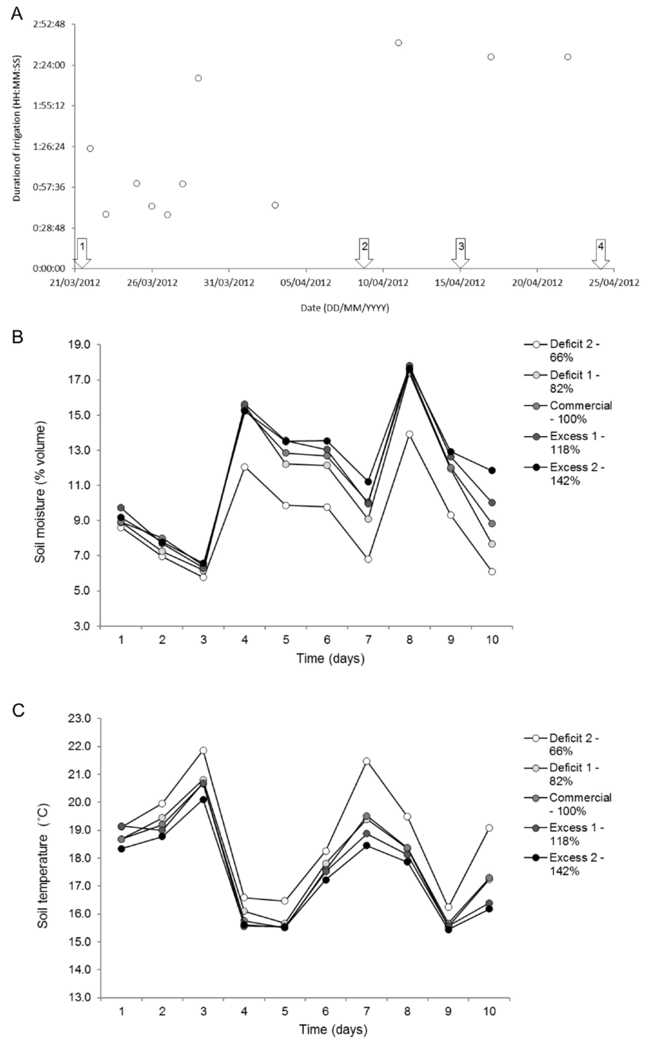

Figure 1: A. Calendar of irrigation for commercially-grown spinach under five irrigation treatments. Dates for drilling (1), treatment implementation (2), commencement of measurements (3) and harvest (4) are shown by arrows on the x axis. Spinach was grown in March–April 2012. B. Soil moisture (percent volume) and C. Soil temperature of commercially-grown spinach under five irrigation treatments. Treatments vary according to the percentage of commercial irrigation which they deliver and the speed at which they deliver it.

were taken of each study area on a daily basis using a TH9100WR thermal camera (NEC, Tokyo, Japan) from a distance of approximately 1 m above the crop. The camera operated in the region of 8-14 µm with 0.1°C thermal resolution and a spatial resolution of 320 (V) and 240 (H) pixels. Emissivity was set at 1.0 as it has been reported to induce errors of less than 1°C [17]. In order to account for environmental variation, reference surfaces were also employed for imaging purposes. A piece of wet filter paper was included in the image to mimic an optimally transpiring leaf, while a leaf orientated towards the sun was greased with petroleum jelly to simulate the condition of a non-transpiring leaf. These references were included in each image but were not included in the area analysed for canopy thermal properties. The exception to this was when the index of stomatal conductance (I_g) was calculated in order to evaluate crop water status without the need for ambient air temperature data [18]. I_g was determined using information from the 'wet' and 'dry' reference surfaces, using the equation below:

$$I_g = (T_{dry}-T_{leaf})/(T_{leaf}-T_{wet})$$

Where T_{dry} is the temperature of the dry reference surface, T_{wet} is the temperature of the wet reference surface and T_{leaf} is the leaf temperature.

Harvest measurements

On 24 April 2012, the day before commercial crop harvest, establishment was measured in each study area. The number of plants growing in a 20 cm^2 quadrat randomly placed five times in each study area was recorded. Furthermore six whole plants were sampled each for yield, epidermal imprints and shelf life. Samples were all transported immediately to a commercial cold chain where they were vacuum cooled (to 3°C) and transported back to the UK in crates (at 3°C) for processing and analysis. All processing was undertaken on 27 April 2012 at the University of Southampton.

Using six leaves per study area, leaf area was assessed by taking an image of a single leaf on a scaled background using a digital camera (Canon 350D, Canon Ltd., UK) and the images were imported into Image J (1.44°, National Institute of Health, USA) for analysis. Background was separated from the leaves automatically with some manual adjustment to calculate the leaf area in mm^2. Leaf fresh weight of the same leaves was recorded on a top pan balance (Scoutpro SPU402, O'Haus, USA) to an accuracy of 0.01 g and leaf dry weight measured after 48 h at 80°C.

The shelf life of baby salad leaves was used as a direct measurement of the processability of the samples [9]. Six plants were taken per study area and leaves were separated by excision from the roots, washed by hand and blot-dried before being placed into re-sealable polythene bags (25 × 15 cm). These samples were then stored in a cold room at 3°C ± 1°C. For the course of post-processing storage the bags were rotated daily and care was taken to avoid freeze damage. Individual bags of leaves were visually assessed on a daily basis at 15:00 for signs of breakdown due to damage caused by processing. When any bruising or decomposition was observed on the leaves the bag was rejected and removed from the trial as it was deemed to be at the end of its commercial shelf life.

Six leaves per study area were used to collect epidermal imprints. Imprints were taken from the abaxial surface of mature leaves to determine mean epidermal cell size and stomatal index (SI). Slides were kept in the dark at <4°C. Epidermal imprints were viewed on an Axioplan 2 microscope (Carl Zeiss, Oberkochen, Germany) and images were captured with a digital camera attached at x10 magnification. Images were imported for processing and analysis using Image J for windows (Image J. 1.44°, Wayne Rasband, USA). Cell size was calculated by tracing 10 epidermal cells, which did not border stomata, and the mean was taken. The number of epidermal cells and stomata in the field of view (FOV) were also counted so that SI could be determined using the following equation:

SI = Number of stomata / (Number of epidermal cells + Number of stomata) * 100

Statistical analyses

Results were tested statistically using SPSS 16.0.1 for Windows (SPSS, Illinois, USA). All thermal canopy and soil-based measurements were analysed using a Principal Component Analysis (PCA) and Pearson's correlations to determine links between soil moisture and a range of IR-based measures. Furthermore, 1-way ANOVAs were used to analyse each trait (establishment and post-harvest yield and quality traits – cell size, stomatal index and shelf life) individually using irrigation treatment as the factor. Where time was also a factor, a repeated measure ANOVA was employed using treatment and time as factors. All post-hoc testing consisted of Tukey's tests.

All thermal imagery was analysed using Image Processor Pro II software (Version 4.0, NEC, Tokyo, Japan). Estimates of canopy thermal properties such as the I_g and the minimum, maximum and range of temperatures per image, were based on the canopy so that multiple leaves were measured in order to reduce the error associated with varying leaf angles [14].

Results

Daily crop water relations

After installation of the different nozzle types, which controlled the rate of irrigation of each treatment area, soil moisture and temperature were monitored for a period of ten days (Figure 1B and 1C). Soil moisture was significantly affected, not only by treatment, with soil moisture increasing with irrigation rate ($F_{4,10}$=12.365, p<0.001), but also by time ($F_{9,90}$=191.020, p<0.0005), with interaction between the two factors ($F_{36,90}$=2.068, p<0.005). Maximal differences between the treatments were seen immediately subsequent to irrigation events, for example on days 6 and 10. It is worth noting that the soil on which the crop was grown was quick draining and it is likely that in the 12 h between irrigation events and soil moisture measurements, that the soil would have drained significantly, which may account for differences between treatments not being as large on some days. Soil temperature also varied between treatments ($F_{4,10}$=8.784, p<0.005) and over time ($F_{9,90}$=131.129, p<0.0005), however there was no interaction between these factors ($F_{36,90}$=1.095, p>0.5). Thermal imaging produced a large set of images from which a number of indicators were extracted for canopy thermal analysis, including minimum, maximum and mean temperature, temperature range as well as wet and dry reference surfaces (Figure 2A). Thermal canopy indicators were assessed as measures of soil moisture using PCA (Figure 2B, 2C and Table 2) and multiple Pearson's correlations (Supplementary Figure 3). Two components were extracted by PCA with the threshold for Eigenvalues set at 1, and these components explained 84% of variance cumulatively. The relationships contained within these components were explored in more detail to determine principal relationships (Figure 2C). The first component, which accounted for 68% of variance, measured soil moisture, soil temperature and all raw thermal traits. The second component described soil moisture and the index of stomatal conductance and explained 16% of the total variance. Raw thermal

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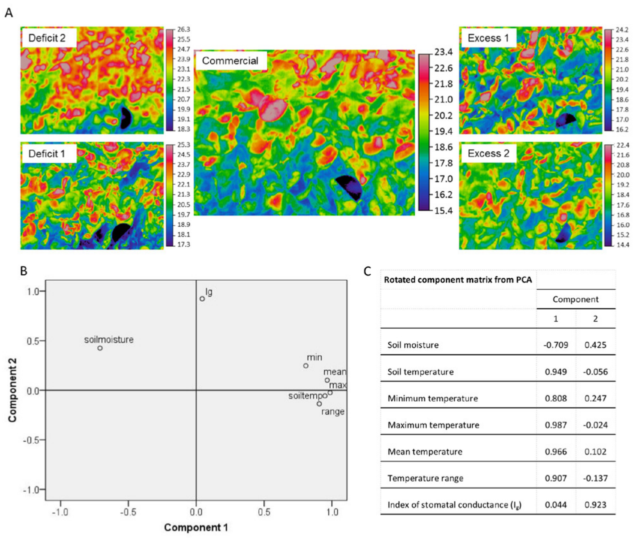
properties were more sensitive as indicators of water availability compared to water stress indices in this instance with the range of temperatures exhibited by the canopy most tightly correlated to the soil moisture (-0.72, $p<0.0001$) (Table 2 and Supplementary Figure 3).

Harvest measurements

Establishment did not vary between irrigation treatments ($F_{4,10}=0.078$, $p>0.05$, Figure 3A). Crop yield, as measured by fresh weight, increased as irrigation levels rose ($F_{4,10}=17.595$, $p<0.0005$), however it was unaffected by deficit 1 or excess 1, meaning the same yield was attained by irrigating in the range of 82–118% of commercial irrigation (Figure 3B). Additionally, although dry weight was affected by major irrigation changes (deficit 2 and excess 2) ($F_{4,10}=8.768$, $p<0.005$, Figure 3C), it was unaffected between 81.52–117.6% of commercial irrigation. Cell size was shown to increase between deficit and commercial irrigation levels, however there was no difference between commercial and excess irrigation ($F_{4,10}=18.158$, $p<0.0005$) (Figure 3D). SI was reduced by deficit irrigation, but was not increased when the crop was over-irrigated, compared to the SI of commercially irrigated crop ($F_{4,10}=14.223$, $p<0.0005$) (Figure 3E). The shelf life of the crop was improved by a slight deficit irrigation ($F_{4,10}=5.953$, $p<0.01$) but was not improved when the crop was over-, or under-irrigated to a more extreme extent (Figure 3F). This substantiated the cell size results, with commercial and over-irrigation showing no difference in cell size. However, there was a marked difference between the two under-irrigation treatments, despite their similarity in terms of cell size. This was likely due to the fact that despite the leaf being of a similar mechanical strength in the deficit 2 and deficit 1 treatments, the deficit 2 crop was severely water stressed and wilted (Supplementary Figure 2). In contrast, the deficit 1 crop had an increased cell wall volume to leaf area ratio without the negative effect on shelf life caused by decreased turgor pressure and wilting.



Rotated component matrix from PCA	Component	
	1	2
Soil moisture	-0.709	0.425
Soil temperature	0.949	-0.056
Minimum temperature	0.808	0.247
Maximum temperature	0.987	-0.024
Mean temperature	0.966	0.102
Temperature range	0.907	-0.137
Index of stomatal conductance (I_g)	0.044	0.923

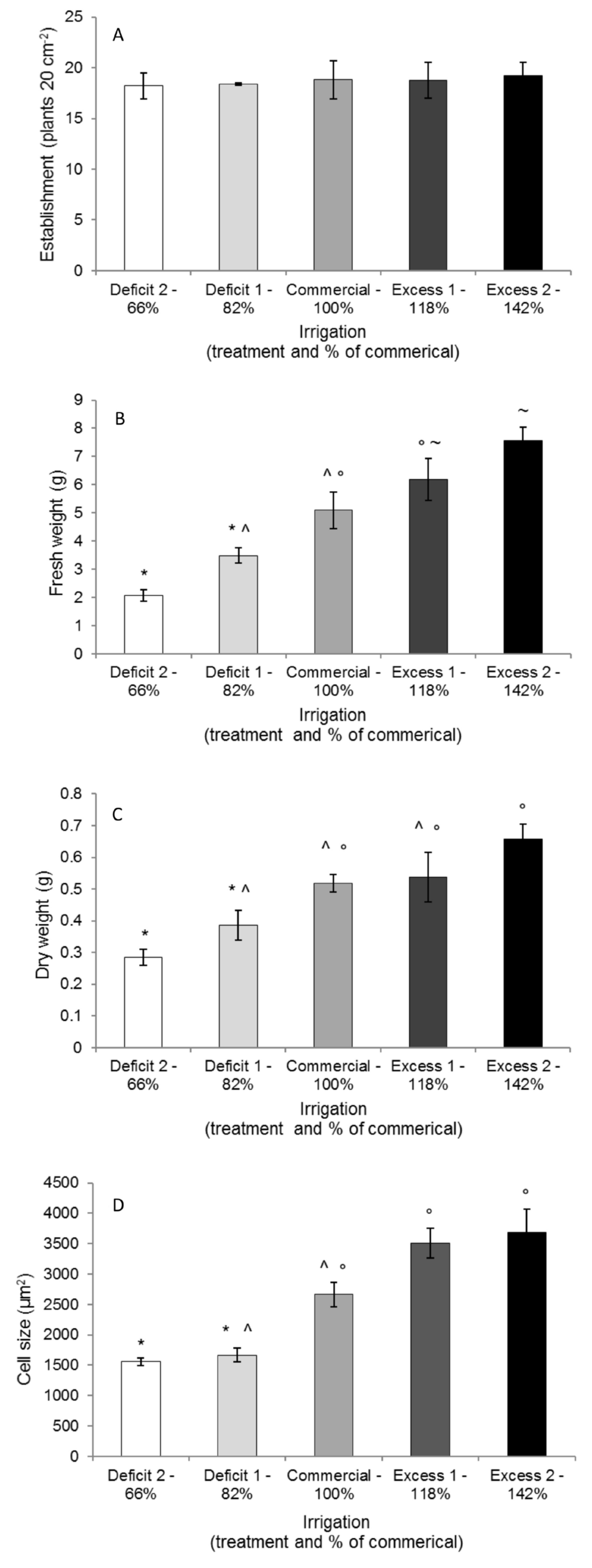
Figure 2: A. Example thermal images taken on Day 10 of the five treatments. Images were selected at random and each has an individual thermal scale. Deficit 2, 66%, 226 L hr^{-1}; Deficit 1, 82%, 278 L hr^{-1}; commercial, 100%, 341 L hr^{-1}; Excess 1, 118%, 401 L hr^{-1}; Excess 2, 142%, 485 L hr^{-1}. B. Component plot from Principle Component Analysis of thermal canopy properties and soil traits (moisture and temperature) when spinach was grown under five irrigation treatments at Azenha do mar, Portugal, in March–April 2012. C. Rotated component matrix from Principle Component Analysis. Soil moisture, soil temperature, minimum canopy temperature, maximum canopy temperature, mean canopy temperature, canopy temperature range and the index of stomatal conductance (I_g) were measured. Rotation converged in 3 iterations.

Discussion

Leafy salads and vegetables are nutritious crops of significant economic value, which are eaten globally [16]. However, the water which is necessary to produce them is limited in many regions. Here, we have illustrated the potential of deficit irrigation, showing that although there was a yield (fresh and dry weight) decrease when a spinach crop was severely under-irrigated, water savings of 18% were achieved with no impact on fresh or dry weight yield. Indeed, the shelf life of the crop following washing and processing was maintained, as quantified by ‘day to rejection’. Generally, deficit irrigation is used to stabilise yields, rather than improve them [19], given the intrinsic link between irrigation levels and biomass accumulation. It has been widely reported that the stomata respond rapidly to drought by reducing their aperture, thus restricting water loss as well as carbon assimilation [20]. Furthermore, this stomatal closure has been linked to decreased wilting and improved shelf life in a number of species [11]. However, a reduction in stomatal aperture is a relatively short-lived response and is often achieved using anti-transpirants, which are not suitable for leafy food crops. Another mechanism by which plants can restrict water use in response to environmental stress is through adjusting stomatal development in emerging leaves [21]. The capacity of plants to moderate stomatal differentiation is dependent on the ability of mature leaves to sense a water deficit and signal to emerging leaves, as well as the sensitivity of these expanding leaves to such signals. Thus we have elucidated a potential breeding target as stomatal index was reduced by deficit irrigation, and this, alongside lowered stomatal conductance acts to limit water loss. If stomatal index is restricted through deficit irrigation practices, with limited yield depression, shelf life could be improved. This extension of shelf life may be driven by a reduction in post-harvest wilting as well as through increased resistance to pathogen infection [22]. Although it has previously been reported that stomatal density can be manipulated in order to improve drought tolerance through reducing transpiration rates without affecting nutrient uptake

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings			Rotation Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	4.792	68.463	68.463	4.792	68.463	68.463	4.785	68.358	68.358
2	1.118	15.973	84.436	1.118	15.973	84.436	1.125	16.078	84.436
3	0.667	9.527	93.963	-	-	-	-	-	-
4	0.327	4.677	98.640	-	-	-	-	-	-
5	0.088	1.259	99.899	-	-	-	-	-	-
6	0.007	0.101	100.000	-	-	-	-	-	-
7	5.986E-16	8.551E-15	100.000	-	-	-	-	-	-

Table 2: Total variance explained by Principle Component Analysis. Measurements include: soil moisture, soil temperature, minimum canopy temperature, maximum canopy temperature, mean canopy temperature, canopy temperature range and the index of stomatal conductance (I_g).



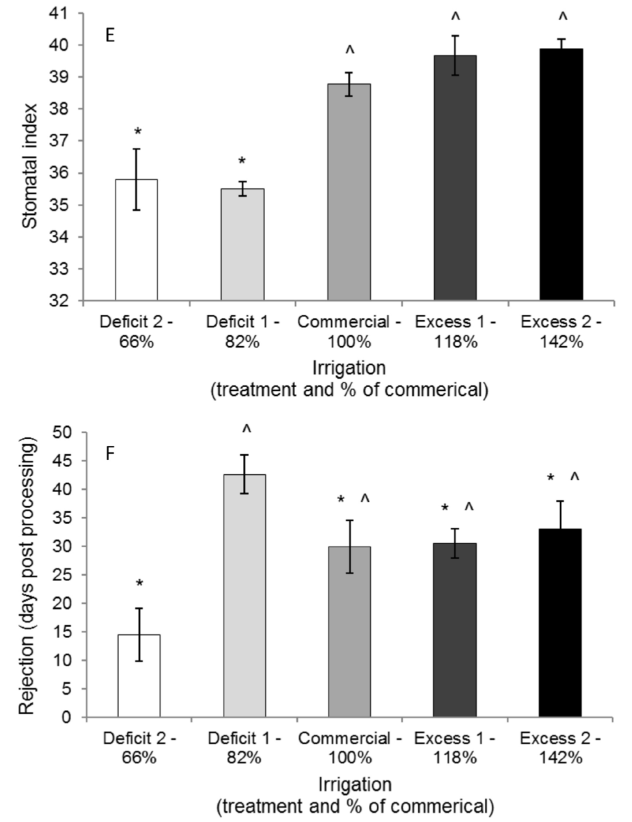


Figure 3: A. Crop establishment (measured immediately prior to harvest), B. fresh weight, C. dry weight, D. Cell size, E. Stomatal index and F. shelf life of commercially-grown spinach under five irrigation treatments. Each data bar represents the mean value of randomly selected points within treatment areas, ± SE, n=3. Tukey's homogeneous groups are marked with *^°~ (groups 1-4 respectively).

[23], the link to shelf life is less well understood. Taken together, stomatal development may be a potential breeding target if it is linked consistently with the ability to maintain shelf life.

Shelf life has been shown to be a critical indicator of salad leaf quality [9] and was maintained in this study even when water inputs were reduced by approximately 20%. In part, this is likely due to the lowered SI in plants grown with reduced water inputs, which minimises water loss and wilting. However, alongside this, deficit irrigation also triggered lower levels of cell expansion which led to the production of leaves made up of smaller cells. It has previously been demonstrated that leaves with many small cells are better able to withstand the processes of growth, harvesting and washing [9]. The proposed mechanism for this improvement in 'processability' was a firmer leaf due to an increased cell wall volume in leaves consisting of smaller cells, which can be seen in this research. However, our data showed that, although both water deficit treatments lowered cell expansion to a similar level, the wilting associated with the more extreme irrigation deficit overrode the potential benefit of the increased cell wall volume. Furthermore, there is a trade-off between improving shelf life and maximising yield accumulation, which is partly governed by leaf cell division. With a decreased level of cell production, water can be used more sparingly, yet this limits carbon assimilation through photosynthesis. We have shown here that yield can be maintained with an 18% irrigation reduction, indicating a possible improvement in water use efficiency.

Alongside the obvious economic benefits to lowering water inputs in agriculture, there are also major environmental and social benefits from a reduced water footprint and decreased crop wastage.

Additionally, we have also employed thermal imaging as an early diagnostic indicator of reduced transpiration. Rather than using individual leaf temperature, which does not consistently correlate with I_g, we measured whole canopy temperatures, which have previously been shown to allow for a more accurate detection of crop water stress, due to the averaging of multiple leaves [14]. It has been suggested that, given the canopy contains many leaves, this can counteract the effect of differing leaf angles and orientations [14]. This work has shown that the range of temperatures exhibited by the canopy is the most tightly correlated thermal trait to soil moisture. This is in line with previous work where it has been shown that water stress broadens the range of temperatures exhibited by the canopy [24]. The potential for this method to provide an accurate estimation of soil water content without the need to scale the temperatures to environmental fluxes through reference surfaces is important. It would significantly reduce the time and labour required to implement large-scale soil moisture assessments through thermal imaging, if reference surfaces did not need to be incorporated. However, in other cases it has been shown that I_g correlates well with stomatal conductance, as measured using porometry, in a number of crop types [14] and so this approach should not be discarded. It may be that in the instance of the research presented in this paper, environmental fluctuations were minimal and weather conditions ideal for imaging, meaning that reference surfaces were not necessary to account for ambient temperature changes.

Water is limited in many areas worldwide and limits crop production significantly [19]. Employing deficit irrigation strategies will enable a reduction in irrigation water which will, in turn, limit nutrient run-off and leaching from the root-zone, resulting in less pollution as well as a decreased requirement for fertiliser on the field [19]. Additionally, deficit irrigation strategies reduce air humidity around the crop and this reduces the risk of fungal diseases [25]. Furthermore, there are social benefits of deficit irrigation if it acts to stabilise yields as this would support economic planning. This research has shown that major water savings of almost 20% can be made without significant detrimental yield or quality effects in spinach and further work can now be undertaken in order to improve deficit irrigation strategies in spinach, as well as to transfer these findings to other crop types.

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