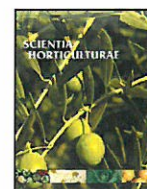




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Effects of drought stress during flowering of two pot-grown blackcurrant (*Ribes nigrum* L.) cultivars

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ABSTRACT

The drought stress tolerance of two blackcurrant cultivars (*Ribes nigrum* L., 'Narve Viking' and 'Ben Gairn') during the flowering period and their ability to recover following drought stress were studied by examining the effects of drought stress on growth and various physiological traits. The experiment was conducted under greenhouse conditions, and plants were either fully irrigated (FI), with a volume of water replacing the previous day's evapotranspiration, or non-irrigated (NI) for 12 days. Hereafter irrigation was continued (FI) or resumed (NI) to allow for 17 days of recovery.

Drought stress reduced the accumulated evapotranspiration of both cultivars mainly due to stomatal closure and a reduced leaf area. Stomata were more open in the morning than at midday, which could be attributed to an increase in vapour pressure deficit (VPD) at midday. Moreover, stomatal conductance (g_s) varied between days of treatment, possibly due to differences in air temperature and VPD. Drought stress reduced the leaf water potential (ψ_l), osmotic potential (ψ_π) and turgor potential (ψ_p) of both cultivars, but more so in 'Narve Viking' than in 'Ben Gairn', indicating that 'Narve Viking' was most affected by drought stress. In both cultivars osmotic adjustment only slightly contributed to turgor maintenance.

In both cultivars, the drought stress significantly reduced leaf and flower dry weight and there was no regrowth of flowers after 17 days of recovery. In 'Ben Gairn' the aerial biomass accumulation after 12 days of drought stress was less reduced and regrowth of roots during the recovery phase was faster than in 'Narve Viking'. This indicates that 'Ben Gairn' was more tolerant of drought stress and recovered better than 'Narve Viking' but may also to some extent reflect differences in plant size. However, a slow regrowth of roots and high N uptake activity of drought stressed 'Narve Viking' at the end of the recovery phase indicated that this cultivar was slowly recovering too.

The presented results stress the importance of installing irrigation systems in blackcurrant orchards during flowering and can assist the selection of drought stress tolerant cultivars in blackcurrant breeding programs.

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1. Introduction

Projections of future climate scenarios in Europe have concluded that annual precipitation is very likely to increase across most of Northern Europe (Parry et al., 2007), and the risk of summer drought is likely to increase in Central Europe (Rowell and Jones, 2006). In recent years, such as 2012, Northern Europe has experienced high overall rainfall, but there were nevertheless extended dry periods within the fruit growing season which are known to cause problems in blackcurrant cultivations (Kahu et al., 2009). Climate modeling studies by Schlyter et al. (2006) forecast that increases in the duration of summer drought are likely.

Periods of drought can seriously affect plant developmental processes if occurring at key stages during the growing season, and some woody species, especially those with superficial root systems, can be especially sensitive to drought or changes in soil water

Abbreviations: BG, 'Ben Gairn'; DW, dry weight; e_a , actual vapour pressure; e_s , saturated vapour pressure; ET_c , accumulated evapotranspiration; FI, fully irrigated; FW, fresh weight; g_s , stomatal conductance; LA, leaf area; NI, non-irrigated; NV, 'Narve Viking'; SE, standard errors of the means; VPD, vapour pressure deficit; ψ_l , leaf water potential; ψ_π , leaf osmotic potential; ψ_p , leaf turgor.

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regime. In blackcurrant, premature shedding of flowers and developing fruit was found by Kikas et al. (2011) to be considerably influenced by both genotype and weather parameters including temperature and precipitation. It is therefore important that suitably resilient germplasm of key crops, including blackcurrant, is identified and developed for production under future climatic challenges.

Limited water availability is one of the most important environmental factors influencing crop physiology, development and yield (Hsiao, 1973; Blum, 2011). Stomatal closure and reduced tissue water content are the most immediate responses to water stress (Chartzoulakis et al., 2002). Stomatal closure reduces water loss, and can be regarded as an avoidance mechanism reducing the rate at which water deficit develops (Chaves et al., 2003). Another effective component of drought resistance in plants is osmotic adjustment. Osmotic adjustment involves the net accumulation of solutes in a cell in response to a fall in water potential (ψ_1) of the cell environment, and is associated with a lowering of the osmotic potential (ψ_π) inside the cell. A lowering of the osmotic potential of the cell attracts water into the cell and helps to maintain turgor potential (ψ_p). Under drought conditions this could postpone dehydration and maybe benefit processes dependent on positive turgor such as cell elongation and stomatal opening (Sánchez et al., 1998). Continued drought stress typically results in developmental and morphological changes like reduced leaf area, plant height and dry mass production (Pagter et al., 2008; Álvarez et al., 2009). The consequences of drought stress on plant physiology and growth may vary depending on developmental stage. In some crops, soil water deficit has been shown to be crucial during key stages such as flowering, and small differences in water availability at these stages can result in large yield reductions (Álvarez et al., 2009; Ratnakumar and Vadez, 2011). In chickpea, drought stress during flowering and young pod development increased flower and pod abortion and reduced the final seed yield (Fang et al., 2009).

Roots play an important role in plant development and water status of the plant under different environmental conditions (Davies and Bacon, 2003; Maurel et al., 2010). Due to methodological difficulties the influence of drought stress on the belowground development and the ability of root systems to recover following drought have been less studied compared to aboveground plant growth and development (Franco et al., 2011). However, some studies found that the root to shoot ratio increased by drought stress due to reduced shoot growth (Blum, 1996; Niu and Rodriguez, 2008) whereas in oleander overall plant size, leaf area, root length and root weight were reduced by deficit irrigation (Bañón et al., 2006). The seasonal variation in growth of blackcurrant roots has been described by Atkinson (1972), but no information is available on blackcurrant root growth or uptake activity under limited water conditions and the ability of roots to recover following drought.

Current blackcurrant breeding programs are mostly based on the specific quality requirements from the industry and processing market and many of the main objectives are focused on yield and disease resistance (Brennan, 2008; Brennan and Graham, 2009). Given the expected increased frequency of severe drought episodes during summer (Sønsteby et al., 2012), it is important to grow plant material that has plastic or adaptive traits so that the plants can cope with extreme drought and the farmer can retain and maintain a commercial crop. There is significant potential to select blackcurrant cultivars with an increased phenotypic plasticity and ability to respond to and recover from stressful conditions (Hedley et al., 2010). Little is known about the ability of different blackcurrant cultivars to cope during and after drought (Wilson and Jones, 1980) and a better understanding of the influence of water stress on physiological and growth parameters for the most important North Sea region blackcurrant cultivars is needed. A study on one year old pot grown coffee trees showed that in more tolerant clones

Table 1

Morning and midday temperature and VPD at days of measurements during 12 days of drought stress in blackcurrant cultivars 'Ben Gairn' and 'Narve Viking'.

Day	Temperature (°C) Morning/midday	VPD (kPa) Morning/midday
0	–/21.8	–/1.49
2	–/21.1	–/1.33
5	23.0/28.0	1.36/2.85
7	18.0/18.7	0.78/0.78
9	26.5/26.4	2.39/2.79
12	26.4/27.1	2.12/2.79

negative effects of drought stress were postponed by partial closure of stomata, reduction in leaf area and turgor maintenance through osmotic adjustment (Pinheiro et al., 2005).

The overall aim of this study was to compare the effects of water stress during flowering in one Scandinavian ('Narve Viking') and one Scottish ('Ben Gairn') blackcurrant cultivar in order to identify physiological adaptations that may reduce water loss and retain productivity under drought conditions. We hypothesized that the two blackcurrant cultivars selected in different environments could differ in their ability to tolerate drought stress during flowering and their subsequent ability to recover. Therefore, the objectives of this study were: (i) to examine the relationship between evapotranspiration, stomatal conductance and plant water status during 12 days of drought stress starting at first open flower; (ii) to determine plant growth and dry matter distribution at the end of a 12-day drought period; and (iii) to determine dry matter distribution and root growth and activity during a 17-day recovery period following drought stress. Such knowledge can help in the adjustment of irrigation management practices to counteract negative effects of water stress caused by climatic changes on blackcurrant production, and would also assist the selection of drought stress tolerant cultivars in blackcurrant breeding programs.

2. Materials and methods

2.1. Plant material and growing conditions

A pot experiment was conducted under greenhouse conditions at Aarhus University, Aarslev, Denmark in April 2011 under natural light conditions and ambient photoperiod. The temperature set point was 18 °C day and night but the actual day temperature varied between 18 °C and 28 °C at midday (Table 1). The morning (9:00–10:00) and midday (12:30–13:30) vapour pressure deficits (VPD) were calculated from the air temperature (temp) and relative humidity (RH) that were measured every five minutes using PT1000 platinum resistors (Senmatic, Denmark), HMP 60 humidity probes (Vaisala, Finland) and a DataTaker 500 (Thermo Fisher, Australia). First the saturated vapour pressure (e_s) and actual vapour pressure (e_a) were calculated:

$$e_s = 0.61078 \times \frac{\exp(17.2693882 \times \text{temp})}{\text{temp} + 237.3} \quad (1)$$

$$e_a = \frac{RH \times e_s}{100} \quad (2)$$

and VPD expressed as:

$$VPD = e_s - e_a \quad (3)$$

One year old cold stored plants propagated from cuttings of blackcurrant cultivars 'Ben Gairn' and 'Narve Viking' were planted on 16 March in 3 L pots, 14.9 cm deep and 19 cm in diameter (Pöppelmann, VCD 19, Germany), in a sandy loam topsoil with 67% coarse sand, 16% fine sand, 15% clay, 2% silt containing 1.2% organic matter. From the day of potting, all plants were ebb/flood irrigated daily with a nutrient solution containing (in mg L⁻¹): 181 N, 30 P, 200 K, 32 Mg, 138 Ca, 18 Na, 41 Cl, 37 SO₄, 2 Fe, 1 Mn, 0.22 B, 0.1 Cu,

0.14 Zn and 0.08 Mo and with a pH of 6.0 and an EC of 1.99 dS m^{-1} . A total number of 60 plants per cultivar were used in the experiment; 44 plants were used for measurements during the drought treatment (4 plants on day 0 and 8 plants, 4 per irrigation treatment, on days 2, 5, 7, 9 and 12) and 8 plants for destructive analysis after 12 days of drought treatment. The remaining 8 plants per cultivar were used to study root activity during recovery and for destructive analysis at the end of the recovery phase.

2.2. Experimental design and treatments

The plants were placed on tables in a completely randomized layout. At the beginning of flowering (6 April) two different water availabilities were established: (1) fully irrigated (FI) and (2) non-irrigated (NI) for 12 days. Water loss (evapotranspiration) was recorded on a daily basis with an electronic scale, for each pot individually. The FI plants were given water individually every day in the late afternoon according to the weight loss since last irrigation, in order to obtain pot water holding capacity. For the plants that were exposed to drought (NI treatment), the water loss was recorded every day. After 12 days, NI plants were irrigated to pot holding capacity and during 17 days of recovery all plants were ebb/flood irrigated once a day to water holding capacity.

2.3. Plant water relations

Stomatal conductance (g_s) of four plants per treatment was measured on days 0, 2, 5, 7, 9 and 12 with a portable porometer (steady state porometer PMR-2, PP-Systems, UK). Three recordings were taken in the morning between 9:00 and 10:00 and at midday between 12:30 and 13:30 on one of the second youngest fully expanded upper canopy leaves.

Midday leaf water potential (ψ_l) and osmotic potential (ψ_π) were measured on the same leaf. Water potential was determined after stomatal conductance measurements using a pressure chamber (Plant Water Status Console 3000, Soil Moisture Equipment Co., Santa Barbara, CA, USA). After determination of ψ_l each leaf was immediately wrapped in aluminum foil, frozen in liquid nitrogen, and transferred to a -80°C freezer for subsequent leaf osmotic potential determination. Osmotic potential was measured using a dew point microvoltmeter (HR-33T, Wescor Inc., Logan, UT, USA). Turgor potential (ψ_p) was determined by the difference between osmotic potential (ψ_π) and leaf water potential (ψ_l):

$$\psi_p = \psi_\pi - \psi_l \quad (4)$$

2.4. Quantification of root growth

Root growth during recovery was quantified by repeated counting of roots at the vertical soil surface. At the beginning of the recovery phase a horizontal cut was made at the top of the pot and a flap pulled downwards without damaging the roots. A grid ($4 \text{ cm} \times 4 \text{ cm}$ cross) on a piece of transparent plastic was attached to cover the window, 4 cm from the base of the pot. Then roots intersecting with the horizontal and vertical lines of the grid were counted. At the opposite side of the pot a similar window was cut, a grid attached and root intersections counted. The average count per pot was used as a measure of root intensity. Grids were left on the pot and the flap and non-transparent tape used to cover the window until next counting. Counting was performed at the beginning of the recovery phase and after 7 and 14 days of recovery.

2.5. Root activity

In order to estimate the effect of NI and FI treatments on root activity, the root uptake of stable isotope ^{15}N was determined after

17 days of recovery. After 12 days of recovery, before supplying ^{15}N , plants were irrigated with water for two days instead of the nutrient solution to reduce the root-zone concentration of N. A solution of $198.6 \text{ mg Ca } (^{15}\text{NO}_3)_2$ enriched with 98% ^{15}N and dissolved in 150 mL demineralized water was used. Four injection holes distributed representatively over the soil surface were prepared and 2 mL of solution injected in each hole. In order to distribute the ^{15}N solution into the 10 cm deep soil profile it was injected with a syringe and needle that was slowly pulled from the hole while the solution was injected. After 72 h (exactly the same period for each pot), flowers, leaves and stems were harvested, dried at 80°C for 24 h, weighed and stored in plastic bags. In addition one non-enriched background sample per cultivar was taken. After biomass determination samples of flowers, leaves and stems were pooled and milled. A subsample was finely grinded ($<0.5 \text{ mm}$) and packed in tin capsules making two replicate samples per pot and sent for ^{15}N and total N analysis at the US Davis stable isotope analysis facility by an elemental analyzer PDZ Europa ANCA-GSL interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The ^{15}N abundance in excess of the natural abundance (0.367%) was calculated for the total aboveground biomass per pot as well as total N content.

2.6. Root length and diameter

After harvesting shoot samples in the ^{15}N experiment, the pots were stored cold at 4°C . Within few days, the roots from each pot were extracted by rinsing off soil and collecting all roots on a sieve with $250 \mu\text{m}$ mesh size. The root samples were stored cold in tap water, colored for 24 h in a 0.05% (w/v) aqueous solution of Neutral Red and analyzed for total root length and root length distribution in diameter classes by scanning in a flatbed scanner, followed by automated image analysis by use of the WinRHIZO 2002c software package (Regent Instruments Inc., Canada). The root samples were dried at 70°C for 48 h to constant weight and total root biomass determined.

2.7. Leaf area and plant biomass

The total leaf area (LA) was measured after 12 days of drought stress using a LI-COR 3100 leaf area meter (LI-COR Inc., Lincoln, NB). Plant biomass was determined after 12 days of drought stress and after 17 days of recovery. At sampling each plant was divided into flowers, leaves, stems and roots (the latter only following recovery), and fresh weight (FW) and dry weight (DW) was determined before and after drying in a ventilated oven at 70°C for 48 h to constant weight. The leaf water content was then determined.

2.8. Data analysis

Two-way analysis of variance by general linear models (Proc GLM in SAS 8.02 (Cary, NC, USA)) were used to examine the effects of cultivar and irrigation treatment on leaf area, leaf water content, specific leaf area, dry matter (flower, leaf, stem and root), shoot/root ratio, root length, length of main root, specific root length, diameter classes, root intensity, the ^{15}N excess and total shoot N. Mean values were compared by Tukey's Studentised Range Test at the 5% probability level.

Three-way GLM was used to examine the effects of cultivar, irrigation treatment and day of measurement on accumulated evapotranspiration, ψ_l , ψ_π , ψ_p and root recovery. Mean values were compared by Tukey's Studentised Range Test at the 5% probability level.

Four-way GLM was used to examine the effects of cultivar, irrigation treatment, day of measurement and time of measurement on g_s followed by a multiple comparison test using Bonferroni

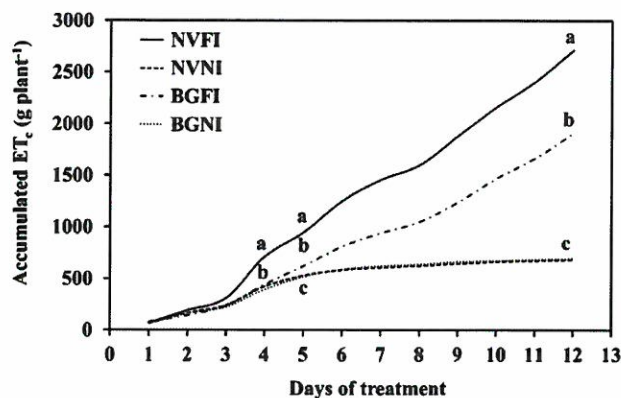


Fig. 1. Accumulated evapotranspiration (ET_c) of fully irrigated (FI) and non-irrigated (NI) blackcurrant cultivars 'Narve Viking' (NV) and 'Ben Gairn' (BG) over a 12-day period. Different small letters indicate significant differences ($P < 0.05$) at day 12 according to Tukey's test ($n = 4$).

correction. Prior to analysis g_s was \log_{10} -transformed to ascertain homogeneity of variance.

3. Results

During the first three days the accumulated evapotranspiration (ET_c) was similar for both cultivars and treatments (Fig. 1), but from day 4 onwards ET_c of FI 'Narve Viking' was significantly higher compared to FI 'Ben Gairn'. From day 5 of withholding irrigation, ET_c of NI plants were significantly decreased compared to FI plants of both cultivars. When grown at full irrigation, ET_c on day 12 was higher

for 'Narve Viking' than 'Ben Gairn' (Fig. 1), whereas ET_c did not differ between the two cultivars when plants were not irrigated.

For g_s a four way interaction between cultivar, time of day, irrigation treatment and day of measurement was seen (Fig. 2; Table 2). There was no significant effect of cultivar on g_s of FI plants, while there was a significant difference between cultivars when subjected to drought stress. Withholding irrigation significantly reduced g_s of 'Narve Viking' from day 5 onwards, both in the morning and midday, while 'Ben Gairn' showed reduced g_s from day 7 onwards in the morning and from day 5 onwards at midday. On some days g_s was higher in the morning than at midday. For FI plants of 'Narve Viking' the morning measurement was significantly higher than at midday on days 9 and 12, but for NI plants only on day 9. In FI plants of 'Ben Gairn' g_s in the morning was significantly higher than at midday on day 12 and in NI plants on day 5.

The leaf water potential and ψ_π decreased due to water stress, and more so in 'Narve Viking' than in 'Ben Gairn' (Table 2; Fig. 3). On days 0, 2, 5 and 9 no differences in ψ_l , ψ_π and ψ_p between FI and NI plants were found, but on days 7 and 12 ψ_l , ψ_π and ψ_p were lower in NI than in FI plants. The double interaction between cultivar and day showed that ψ_l was similar for the two cultivars except on day 7, where it was lower in 'Narve Viking' than in 'Ben Gairn'. The ψ_π and ψ_p never differed significantly between cultivars within days but on days 0 and 2 ψ_π was higher than on days 5, 7, 9 and 12. In 'Ben Gairn', ψ_p was higher on days 0, 2 and 7 than on days 5, 9 and 12, whereas in 'Narve Viking' ψ_p on day 0 did not differ from any of the other days.

The leaf area, leaf dry weight and leaf water content were lower in NI than in FI plants, whereas only the leaf area of FI plants differed significantly between cultivars after 12 days of treatment (Tables 3 and 4). The specific leaf area of FI plants was similar for the

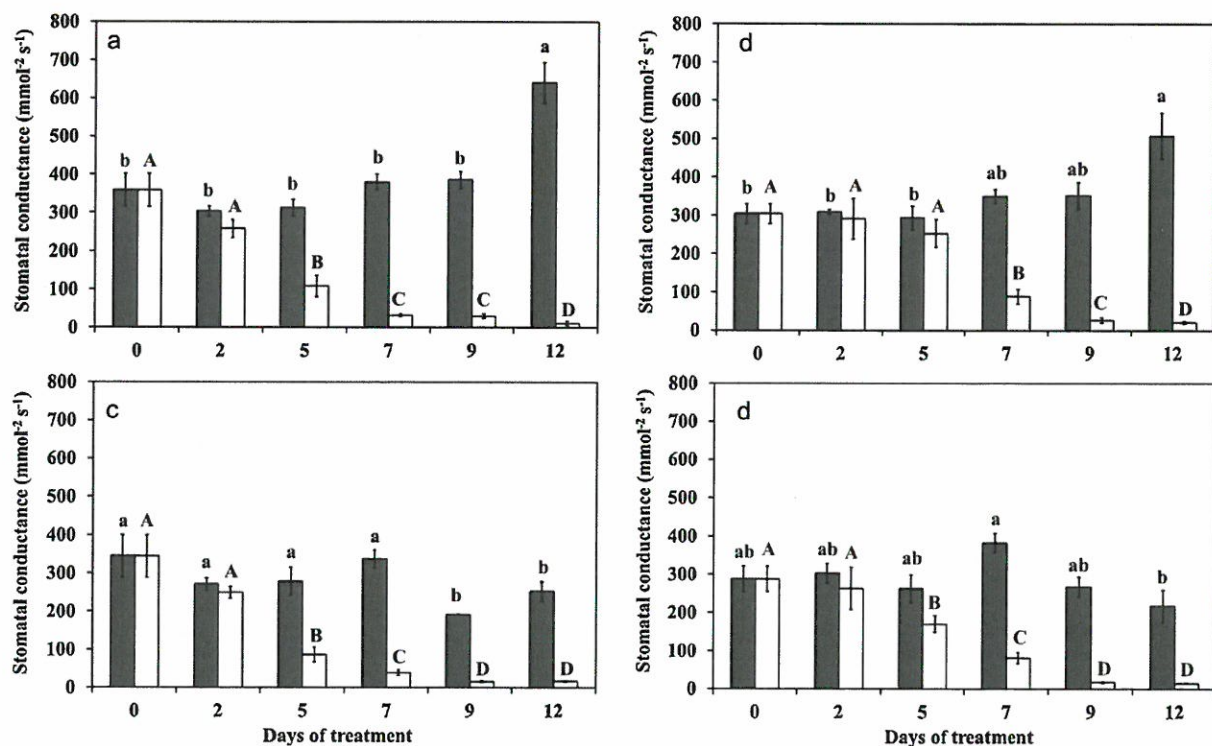


Fig. 2. Stomatal conductance (g_s) measured between 9:00 and 10:00 (a, b) and between 12:30 and 13:30 (c, d) for blackcurrant cultivars 'Narve Viking' (left) and 'Ben Gairn' (right) grown at full irrigation (black bars) or no irrigation (white bars). Different letters above bars indicate significant differences between days of treatment, within a cultivar, irrigation treatment and time of day at $P < 0.05$ according to Tukey's test. Small letters indicate full irrigation, capital letters no irrigation. Bars represent mean values \pm SE ($n = 4$).

Table 2

F values and significance of four-way analysis of variance of stomatal conductance (g_s) and three-way analysis of variance of leaf water potential (ψ_l), osmotic potential (ψ_π), turgor pressure (ψ_p) and root recovery data (Root_{rec}) for blackcurrant cultivars 'Ben Gairn' and 'Narve Viking'. Plants were fully irrigated or non-irrigated for 0, 2, 5, 7, 9 or 12 days (g_s , ψ_l , ψ_π , ψ_p) followed by 14 days of recovery (Root_{rec}).

Factor	g_s	ψ_l	ψ_π	ψ_p	Root_{rec}
Cultivar (cv)	34.07***	14.53***	0.10 ns	16.54**	0.55 ns
Days of treatment (day)	210.84***	184.56***	115.19***	41.11***	20.72***
Time	18.14***	–	–	–	–
Treatment (tm)	2047.55***	63.11***	67.06***	18.60***	94.81***
Cv \times day	7.08***	8.51***	5.65***	4.20**	0.77 ns
Cv \times time	5.50*	–	–	–	–
Cv \times tm	52.83***	8.97**	12.92***	4.51**	5.64*
Day \times time	2.50	–	–	–	–
Day \times tm	256.18***	18.96***	6.20***	8.56***	3.26*
Time \times tm	11.21***	–	–	–	–
Cv \times day \times time	5.48***	–	–	–	–
Cv \times day \times tm	6.90***	1.55 ns	2.08 ns	1.32 ns	1.24 ns
Cv \times time \times tm	13.71***	–	–	–	–
Day \times time \times tm	17.48***	–	–	–	–
Cv \times day \times time \times tm	5.58***	–	–	–	–

ns: no significant difference.

* Significant difference at $P < 0.5$.

** Significant difference at $P < 0.01$.

*** Significant difference at $P < 0.001$.

Table 3

Effects of full irrigation (FI) or no irrigation (NI) on total leaf area, leaf water content and specific leaf area in blackcurrant cultivars 'Ben Gairn' (BG) and 'Narve Viking' (NV) after 12 days of treatment. Values with the same letters within a column are not significantly different at $P < 0.05$ according to Tukey's test (mean \pm SE, $n = 4$).

Cultivar/treatment	Total leaf area (cm^2)	Leaf water content (g g^{-1} DW)	Specific leaf area ($\text{cm}^2 \text{g}^{-1}$ DW)
BGFI	1385 \pm 74 b	3.06 \pm 0.05 a	225.57 \pm 3.08 ab
BGNI	624 \pm 33 c	2.41 \pm 0.18 b	216.66 \pm 6.81 ab
NVFI	1834 \pm 82 a	3.45 \pm 0.05 a	256.51 \pm 8.87 a
NVNI	576 \pm 40 c	2.04 \pm 0.15 b	191.36 \pm 6.96 b

two cultivars, whereas withholding water decreased specific leaf area of 'Narve Viking'. The stem dry matter did not differ between FI and NI plants within cultivars. The flower dry matter of NI plants was reduced compared with FI plants in both cultivars after 12 days of treatment (Table 4).

After 12 days of drought stress the root intensity was higher for FI plants than for NI plants and the root intensity was similar in the two cultivars (Fig. 4).

When 12 days of NI was followed by 17 days of recovery, 'Ben Gairn' showed better leaf regrowth and relatively better stem regrowth than 'Narve Viking' (Table 4). Hence, following recovery the leaf and stem biomasses of NI 'Ben Gairn' were 134% and 58% greater than following drought stress, while in 'Narve Viking' the corresponding numbers were 20% and 0.8%. In FI plants, the leaf and stem biomasses of 'Ben Gairn' were 62% and 15% greater after recovery than before recovery, while the corresponding numbers in

FI 'Narve Viking' were 113% and 43%, respectively. While FI plants of both cultivars increased their flower biomass by ca. 300% during the recovery phase, no regrowth of flowers of NI plants was observed in any of the cultivars. In NI 'Narve Viking' the flower biomass even decreased further (by –79%) during recovery.

After 12 days of NI and 17 days of recovery, the root dry weight, root length and root intensity were significantly higher for FI than NI plants of 'Narve Viking' (Tables 4 and 5, Fig. 4), whereas in 'Ben Gairn' there were no differences between FI and NI plants. This is supported by root window observations of root intensity during the recovery period (Fig. 4), where NI plants of 'Ben Gairn' showed a faster increase in root intensity compared to NI plants of 'Narve Viking'.

After recovery, the root systems were divided into the main root and fine roots. The main root was longer in FI than in NI plants of both cultivars. Fine roots were divided into five diameter classes,

Table 4

Dry matter distribution between different organs of blackcurrant cultivars 'Ben Gairn' (BG) and 'Narve Viking' (NV) after 12 days of no irrigation (NI) or full irrigation (FI) and after 17 days of recovery at FI, as well as the shoot to root ratio after recovery. Different letters within columns indicate significant differences according to Tukey's Test at $P < 0.05$ (mean \pm SE, $n = 4$).

Cultivar/treatment	Day 12, dry matter (g plant ⁻¹)					
	Flowers	Leaves	Stems		Shoot	
BGFI	0.33 ± 0.04 a	6.1 ± 0.3 a	9.6 ± 0.8 ab		16.1 ± 0.8 ab	
BGNI	0.09 ± 0.01 b	2.9 ± 0.2 b	6.2 ± 0.9 b		9.2 ± 1.1 b	
NVFI	0.56 ± 0.12 a	6.8 ± 0.8 a	15.3 ± 2.5 a		22.6 ± 3.4 a	
NVNI	0.14 ± 0.05 b	3.0 ± 0.3 b	12.0 ± 2.1 ab		15.2 ± 2.8 a	
Cultivar/treatment	12 days of drought stress or full irrigation + 17 days of recovery at full irrigation, dry matter (g plant ⁻¹)					
	Flowers	Leaves	Stems	Shoot	Root	Shoot/Root ratio
BGFI	1.35 ± 0.12 a	9.9 ± 1.5 ab	11.0 ± 0.9 b	22.3 ± 2.3 b	11.9 ± 1.1 b	1.9 ± 0.2 ns
BGNI	0.10 ± 0.05 b	6.8 ± 0.2 bc	9.8 ± 1.0 b	16.7 ± 1.1 b	9.6 ± 0.7 b	1.7 ± 0.1 ns
NVFI	2.23 ± 0.54 a	14.5 ± 1.3 a	21.9 ± 2.2 a	38.6 ± 3.4 a	19.3 ± 2.7 a	2.0 ± 0.3 ns
NVNI	0.03 ± 0.02 b	3.6 ± 0.9 c	12.1 ± 0.6 b	15.8 ± 1.1 b	10.5 ± 1.6 b	1.5 ± 0.2 ns

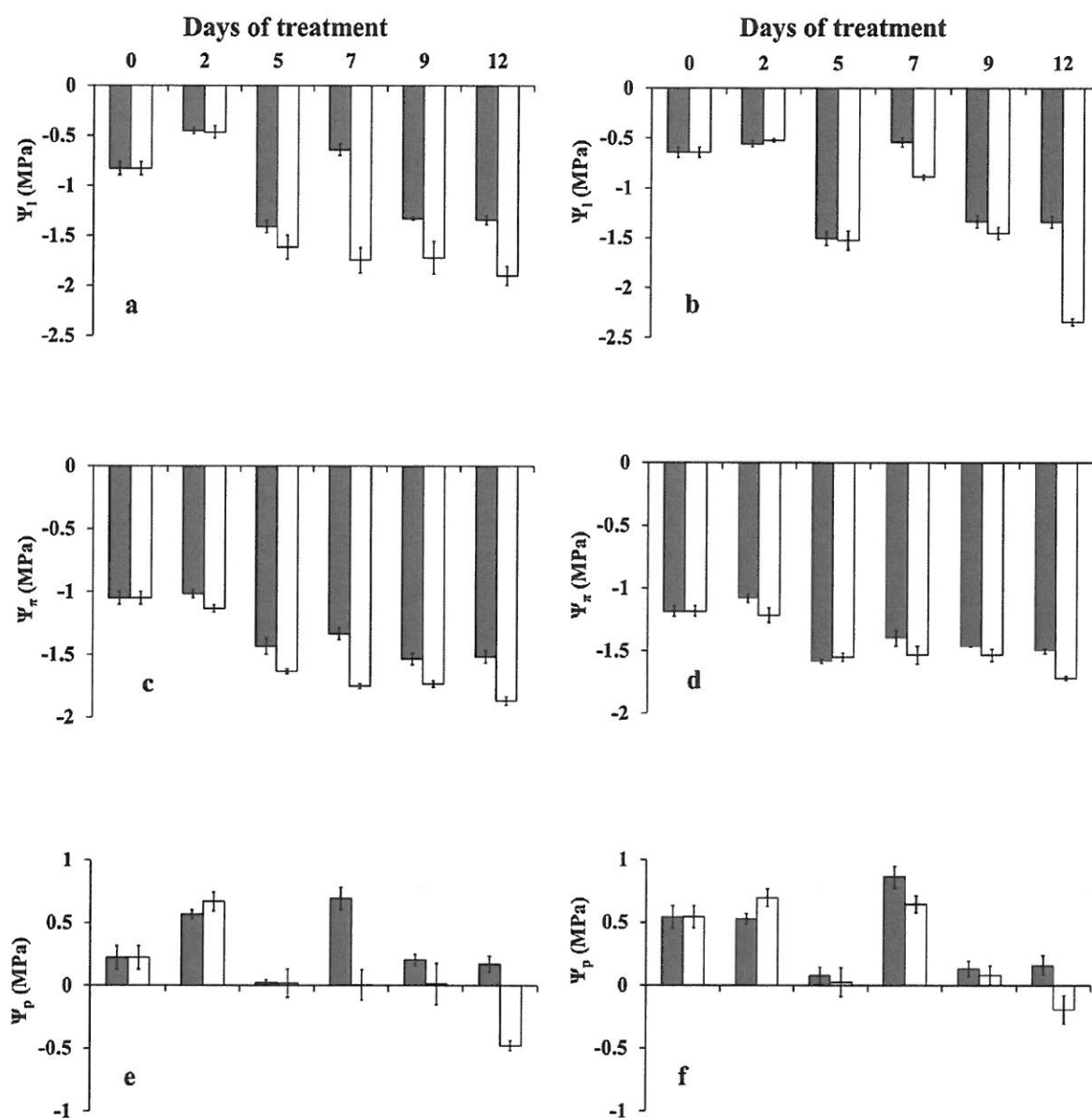


Fig. 3. Leaf water potential (ψ_l), osmotic potential (ψ_π) and turgor potential (ψ_p) of fully irrigated (black bars) and non-irrigated (white bars) blackcurrant cultivars 'Narve Viking' (a, c, e) and 'Ben Gairn' (b, d, f) over a 12-day period. Bars represent mean values \pm SE ($n=4$).

Table 5

Effects of full irrigation (FI) and no irrigation (NI) followed by 17 days recovery on root length, root diameter classes, length of main root and specific root length in blackcurrant cultivars 'Ben Gairn' (BG) and 'Narve Viking' (NV) grown under greenhouse conditions. Different letters within columns indicate significant differences according to Tukey's Test at $P < 0.05$ (mean \pm SE, $n=4$).

Cultivar/treatment	Root length (m)	Length of main root (m)	Specific root length (m g ⁻¹)
BGFI	7.1 ± 0.4 b	0.18 ± 0.002 a	8.55 ± 1.48 ns
BGNI	5.7 ± 0.7 b	0.11 ± 0.009 b	5.93 ± 0.37 ns
NVFI	12.7 ± 0.8 a	0.18 ± 0.010 a	7.23 ± 1.70 ns
NVNI	6.3 ± 0.2 b	0.13 ± 0.004 b	5.47 ± 0.52 ns

Cultivar/treatment	Diameter classes of root length in mm				
	0.0–0.2	0.2–0.5	0.5–1.0	1.0–3.0	>3.0
BGFI	1040 ± 203 a	3812 ± 245 b	1601 ± 61 b	607 ± 85 b	80.1 ± 21 b
BGNI	907 ± 158 b	2858 ± 303 b	1429 ± 197 b	473 ± 10 b	79.9 ± 13 b
NVFI	1496 ± 86 a	6837 ± 480 a	3031 ± 291 a	1187 ± 109 a	132.4 ± 13 a
NVNI	953 ± 91 b	3451 ± 113 b	1292 ± 67 b	465 ± 10 b	100.6 ± 32 b

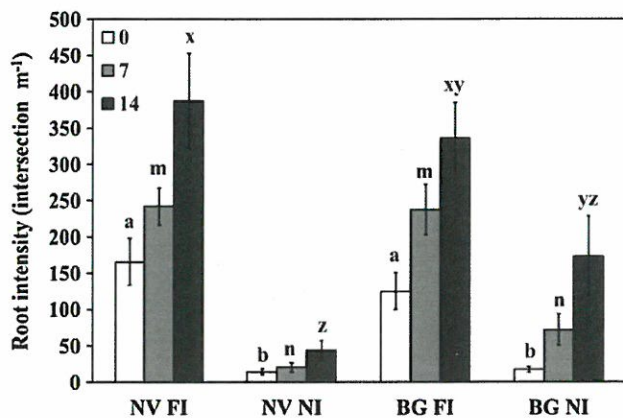


Fig. 4. Root intensity at the vertical pot soil surface after 12 days of no irrigation (NI) or full irrigation (FI) followed by 0, 7 and 14 days of recovery in blackcurrant cultivars 'Narve Viking' (NV) and 'Ben Gairn' (BG). Different small letters indicate significant differences between cultivar and irrigation treatment within days ($P < 0.05$). Bars represent mean values \pm SE ($n = 4$).

and the FI plants of 'Narve Viking' had higher root length than NI plants in all classes. In 'Ben Gairn' only the root length in diameter class 0–0.2 mm was significantly higher in FI than in NI plants (Table 5). The shoot to root ratio and specific root length were not significantly different between cultivars and treatments after the recovery phase (Tables 4 and 5), but tended to decrease for NI plants ($P = 0.08$).

After recovery a significantly higher ^{15}N excess was seen in 'Narve Viking' than in 'Ben Gairn' (Fig. 5a), whereas the ^{15}N excess was similar for FI and NI plants in both cultivars. A similar amount of total shoot N was found in all treatments except for the FI treatment of 'Narve Viking', which was three times greater than NI 'Narve Viking' and two times greater than FI and NI plants of 'Ben Gairn' (Fig. 5b).

4. Discussion

Water withholding induced a significant reduction in ET_c of 'Narve Viking' and 'Ben Gairn' from day 5 onwards. Simultaneously, g_s measured at midday decreased significantly, indicating that the decrease in ET_c was at least partly due to stomatal closure. Stomatal closure under drought conditions shows the ability of blackcurrant to control transpiration from the already existing leaf area and reduce water loss. The closure of stomata is, together with growth inhibition of developing leaves, among the earliest responses to drought stress (Chartzoulakis et al., 2002; Guerfel et al., 2009). In our study a significant reduction in g_s was observed at day 5 in the morning in 'Narve Viking' but not in 'Ben Gairn' until day 7, indicating that 'Narve Viking' responded slightly faster to the drought treatment.

Stomata of blackcurrants were more open in the morning than at midday. This was probably due to factors that increase leaf temperature and transpiration, such as the higher air temperature and VPD at midday (Cuevas et al., 2006; Yu et al., 2009). A two year study of grapevine subjected to different soil water availabilities (Centeno et al., 2010) showed that g_s was a good indicator of drought stress, but that g_s showed greater variability than ψ_1 , possibly due to differences in light exposure of the leaf and VPD. Similarly, in both FI and NI plants midday differences in g_s between days of measurement varied along with differences in VPD. On warm days with high VPD, g_s was generally lower than on cooler days with lower VPD. It has previously been reported that evapotranspiration and g_s decreases with increasing VPD (Rosati et al., 2006).

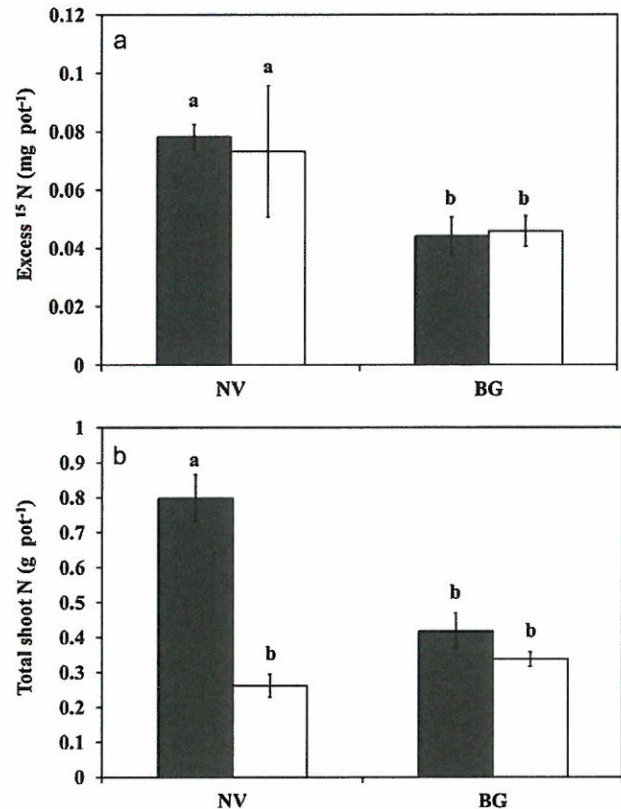


Fig. 5. The ^{15}N excess of natural abundance in the aboveground biomass (a) and total shoot N (b) of fully irrigated (black) and non-irrigated (white) blackcurrant cultivars 'Narve Viking' (NV) and 'Ben Gairn' (BG) after 17 days of recovery. Different letters above bars indicate significant differences according to Tukey's test at $P < 0.05$. Bars represent mean values \pm SE ($n = 4$).

The leaf water potential decreased due to drought stress in both cultivars. The significantly greater reduction in ψ_1 of 'Narve Viking' than 'Ben Gairn' on day 7 could partly be explained by differences in drought stress level due to plant size, as a difference in accumulated evapotranspiration between FI and NI plants was seen from day 4 in 'Narve Viking' but not until day 5 in 'Ben Gairn'. A relatively smaller reduction in leaf area and leaf water content of NI 'Ben Gairn' compared to NI 'Narve Viking' indicate that 'Ben Gairn' was less drought stressed than 'Narve Viking'. On the warmest days (days 5, 9 and 12), all plants, including FI plants, lost turgor, indicating that blackcurrants are generally sensitive to high temperature. The reduction in ψ_1 and ψ_π of NI plants on days 7 and 12 was probably due to tissue dehydration, since ψ_p also decreased. This indicates that blackcurrant lacks or has limited capacity to adjust osmotically. Alternatively, the apparent lack of osmotic adjustment may be ascribed to fast stress development. Osmotic adjustment is normally a slow process (Chaves et al., 2003), and fast droughting might not result in osmotic adjustment as previously observed in Mediterranean buckthorn and hummingbird fuchsia (Bañon et al., 2003; Pagter et al., 2008). Negative ψ_p probably appeared due to methodological differences and inaccurate measurements of ψ_1 and ψ_π from wilted leaves (Blum, 2011).

A reduction in plant biomass due to drought stress has been previously shown in several plant species (e.g. Petropoulos et al., 2008; Sankar et al., 2008; Álvarez et al., 2011). This was confirmed in our study, with NI plants having a reduced total leaf area and leaf dry matter accumulation. A decrease in specific leaf area of NI 'Narve Viking' plants could be related to a decrease in leaf area, higher solute accumulation and increased leaf thickness. In olive trees,

leaf structural changes depended on water availability, where specific leaf area decreased under limited water conditions (Guerfel et al., 2009). A reduction in plant biomass may to some extent be the result of declining photosynthesis, since stomatal closure not only limits water loss but also restricts CO₂ entry into leaves (Panković et al., 1999; Pagter et al., 2005). Reduction in leaf area could also be due to loss of turgor and hence reduced expansion growth (Chartzoulakis et al., 2002). The large reduction of above-ground biomass after 12 days of drought treatment could also result from changed biomass partitioning between leaves and roots. By increasing the proportion of water-absorbing root biomass relatively to the water-losing leaf biomass, the plant can exploit the limiting water resource in a more efficient way (Rodrigues et al., 1995). However, the reduction in root intensity after 12 days of treatment indicated that the allocation of dry matter to roots was also reduced.

The observed reduction in biomass allocated to flowers of NI plants of both blackcurrant cultivars showed that flowers are very sensitive to drought stress. This is in accordance with earlier studies on reduced flower dry weight due to limited water availability (Razmjoo et al., 2008; Álvarez et al., 2009; Asrar et al., 2012). The reduced flower biomass was not only due to reduced flower development and growth but also flower abortion (visual observation). The sensitivity of blackcurrant flowers to drought stress may become of increasing importance in the future, since in parts of Europe, including the UK, there has been reduced rainfall around the flowering period in recent years (Anon., 2011, 2013).

Leaf, stem and root growth of 'Ben Gairn' recovered after drought stress whereas flower growth did not, showing that flowers were more sensitive to drought stress than other plant organs. In 'Narve Viking' no organs showed significant regrowth following 17 days of recovery, and the flower abortion continued resulting in a further reduction in flower biomass. This indicates, that 'Narve Viking' was more stressed after 12 days of NI, and can therefore be considered less drought tolerant, or to have a lower ability to recover than 'Ben Gairn'. This was supported by the much reduced leaf area, leaf water content and specific leaf area in this cultivar. Moreover, the relatively small increase in stem dry matter accumulation following recovery indicated that drought stress continued to inhibit growth of 'Narve Viking' in the recovery phase. In a study of ten sugarcane cultivars, 10 days of drought stress caused a significant reduction in biomass and stalk diameter, and 10 days of recovery was not sufficient for full recovery (Jangpromma et al., 2012).

The shoot to root ratio of blackcurrant after the recovery phase was not significantly different between treatments. However, the shoot to root ratio tended to decrease in NI plants ($P=0.08$), indicating that shoots were more affected by water stress than roots (Franco et al., 2011). However, the reduction of leaf area may reduce root growth, as it depends on supply of carbohydrates from the shoot (Li et al., 2009).

Root growth results obtained by different methods confirmed that 'Ben Gairn' had a better root recovery than 'Narve Viking'. In NI plants, the length and biomass of roots after 12 days of drought followed by recovery was only 50% in 'Narve Viking' compared with ca. 80% in 'Ben Gairn'. Moreover, faster root growth was observed in 'Ben Gairn' compared to 'Narve Viking' at the vertical soil surface during recovery, and 'Narve Viking' was affected by drought in all diameter classes of roots, whereas in 'Ben Gairn' only roots with the smallest diameter were affected. In a study on sugarcane, a significant reduction in root length and root dry weight was observed after 10 days of drought stress, but the root system recovered within 10 days of re-watering (Jangpromma et al., 2012). This indicates that the ability of roots to recover after drought stress depends on the severity of stress, recovery period and plant species.

The cultivar 'Narve Viking' was found to have higher root N uptake activity based on ¹⁵N results compared to 'Ben Gairn'. Even

after a severe reduction in the aboveground biomass and inhibition of root growth, NI plants of 'Narve Viking' were able to assimilate ¹⁵N, indicating that roots were active. This was also supported by the small but significant regrowth of roots during the recovery phase, even though the plants hardly showed any aboveground growth. The root activity was similar in NI and FI plants, showing the ability of both cultivars to regain nitrogen uptake after a recovery phase. A similar finding of regained N uptake activity after drought was found in Mediterranean acacias, but the response differed between species (Werner et al., 2010).

5. Conclusion

The blackcurrant cultivars 'Ben Gairn' and 'Narve Viking' partially closed stomata in response to drought stress. However, g_s of both FI and NI plants were affected by VPD and air temperature, showing that the two blackcurrant cultivars are sensitive to high temperature and VPD. Except for flowers, growth of aboveground parts of 'Ben Gairn' recovered following drought stress, whereas growth of 'Narve Viking' did not recover during 17 days of recovery. Similarly, 'Ben Gairn' had a better root recovery than 'Narve Viking'. However, 'Narve Viking' had a small regrowth of roots and N uptake activity, indicating that the cultivar was slowly recovering from the drought treatment. Drought stress during flowering severely reduced flower biomass and flower abortion was observed. Drought stress during flowering therefore reduces the potential for commercial yields at harvest, but to which level depends on the cultivar and its ability to cope with unfavorable conditions. Our results suggest that the two important North Sea region cultivars clearly differed in drought response, with 'Narve Viking' being less drought tolerant than 'Ben Gairn' although the difference may in part be due to differences in plant size. Further studies are underway to examine the genetic basis of these differences, so that they can be exploited in future blackcurrant breeding programs to develop new cultivars that are resilient to unpredictable and changing environmental conditions.

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