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Cite As: Simpson, KLS, Jackson, G & Grace, J 2012, 'The response of aphids to plant water stress - the case of Myzus persicae and Brassica oleracea var. capitata' *Entomologia experimentalis et applicata*, vol 142, no. 3, pp. 191-202.

DOI: 10.1111/j.1570-7458.2011.01216.x

The Effect of Interaction Between Infestation by the Aphid *Myzus Persicae* and Water Stress on the Physiology of Cabbage (*Brassica Oleraceae Var Capitata*)

Authors: K.L.S Simpson and G.E Jackson

Address for correspondence:

Dr Gail E. Jackson
School of Geosciences,
The King's Buildings
The University of Edinburgh,
West Mains Road,
Edinburgh EH9 3JN

THE EFFECT OF INTERACTION BETWEEN INFESTATION BY THE APHID *MYZUS PERSICAE* AND WATER STRESS ON THE PHYSIOLOGY OF CABBAGE (*BRASSICA OLERACEAE VAR CAPITATA*)

K.L.S. SIMPSON AND G.E. JACKSON

Abstract. Cabbage (*Brassica oleraceae var capitata*) plants grown under controlled conditions and two levels of water stress were infested with *Myzus persicae* in a factorial experiment. Two experiments studied the potential interaction of stresses, one focussed on plant physiology and the other on aphid development. In the first case maximum photosynthetic rate (A_{max}), stomatal conductance (g_s), leaf fluorescence yield, leaf SPAD estimation of chlorophyll and final mass were measured. In the second case water potential components, total aphid population, aphid intrinsic rate of increase (r_m) and fecundity were measured. In both cases, leaf temperature and soil moisture were measured.

Under aphid stress, cabbage plants of both water stress treatments show reduced A_{max}, lower SPAD values, higher osmotic potential and reduced final biomass compared to control plants, all at $p<0.01$. Aphid infestation also led to higher leaf water potentials, at $p<0.05$.

Water stressed plants showed reduced A_{max}, lower SPAD values, reduced leaf water potential, lower turgor and reduced final biomass compared to control plants, all at $p<0.01$. Osmotic potential was significantly lower, at $p<0.02$.

Plants under combined aphid and water stress showed significantly reduced SPAD and final biomass, with comparatively higher leaf water potentials.

The size of the *M. persicae* population was reduced on droughted plants at $p<0.01$, significantly covarying with soil moisture and leaf temperature. Aphids on droughted plants had lower r_m at $p<0.03$ and lower fecundity per aphid at $p<0.01$. Aphid numbers were correlated positively with soil moisture and negatively with leaf temperature.

On the basis of this research it can be deduced that aphid infestation prevents solute accumulation in the vacuole of a drought stressed cabbage. This may be an attempt to increase local turgor or prevent too great a difference in osmotic potential between themselves and the host. At the same time changes in the host akin to drought stress take place. These are of benefit to *M. persicae* on otherwise healthy, well watered plants. On cabbage plants already suffering water shortage no counteracting force is enough to overcome the host's reduced physiological health.

1. Introduction

The hypothesis where plant stress can lead to increased nitrogen availability for phytophagous insects, resulting in greater reproduction and survival has been considered since originally put forward by White (1969). The suggestion is that as the stress on a plant increases, the value as an insect food source increases to a maximum point before falling off as the plant begins to senesce.

Some of the physiological responses to water stress may indeed lead to conditions that benefit *Myzus persicae* Sulz (Wearing and van Emden, 1967; Wearing, 1972). Plants are adapted to coping with short periods of stress using osmotic adjustment to accumulate solutes and maintain cell turgor, enlargement and growth during times of water shortage (Hsiao, 1973; Taiz and Zeiger, 2006). Stress metabolites, osmolytes, soluble nitrogen and sugars, secondary compounds, abscisic acid (ABA), and protein hydrolysis increase with water stress (English-Loeb et al., 1997; Meyer et al., 2006; Kitao et al., 2007). Since phloem is typically too low in nitrogen quality, with poor essential amino acid availability, and too high in simple sugar concentration (Douglas, 2006), an increase in the availability of scarcer nitrogen and protein rich compounds would give a potentially richer diet for feeding insects. For example, higher essential amino acid levels in the phloem leads to higher survival rates, shorter development times and increased rates of increase and overall fecundity in *M. persicae* (Karley et al., 2002).

These barriers to a phloem-feeder's success are overcome in some aphids with symbiotic gut bacteria and specific enzymes. An aphid's life is dependent on the balance of osmotic pressure between its body and the phloem. The phloem is already far more 'concentrated' than the aphid – *"phloem-feeding insects are expected to shrivel as they feed"* – a fate counteracted by converting simple sugars to complex

ones (Douglas, 2006). With the typically increased concentration of sap resulting from drought stress, this may be too strong a change for the aphids to cope with.

As yet, the idea of a 'plant-stress hypothesis' where increased insect populations are seen in some years of drought is more climatical observation than proven in experiment. It may be relevant to insects other than phloem-feeders or to stresses other than drought. In aphids, the response hangs balanced in the phloem between improved nitrogen availability and excess sugar concentration.

Early work on drought and aphids, (Kennedy et al., 1958; Wearing, 1972) found that aphids responded negatively to sudden and sustained water stress, but suggested that where the host had opportunity to recover some turgor, aphid responses were likely to be more positive. *M. persicae* was found to have improved fecundity and survival on older intermittently stressed leaves and young droughted leaves, with poorest performance on well-watered mature leaves (Wearing, 1972). Research *Sitobion avenae* by Fereres et al. (1988) found severe water stress to be significantly linked to increased density of aphid populations. The combination of aphids and water shortage caused losses of over a third to crop yields.

Cabrera et al. (1995) found aphid growth and development rates decreased on water stressed plants. Pons and Tatchell (1995) found reduced fecundity and reproductive rates in aphids on drought stressed hosts. Hale (2002) found generally reduced rates of population increase under mild drought conditions of -0.5 MPa.

Drawing this past work together, Huberty and Denno (2004) found concurring evidence in their meta-analysis that *prolonged and severe* water stress led to significant negative effects on phloem-feeding insects, most likely caused by reduced leaf turgor and water content that countered the increased nitrogen levels. They proposed a 'pulse stress hypothesis' where periods of stress and recovery allowed the insects to benefit from stress-induced nitrogen increases without losing the ability to take up phloem through the stylet.

In this research, the potential interaction between the aphid, *M. persicae* and water stress in cabbage (*Brassica oleraceae var capitata*) is investigated. *M. persicae* is a generalist feeder with multiple suitable hosts. It has been found to settle and migrate on a host plant based on the gradual senescence of leaves, starting infestation at the base and moving upwards as new growth emerges and old leaves begin to die (Harrington and Taylor, 1990). Outwith the physiological changes already discussed, water stress, leading to premature senescence may accelerate the rate at which an infestation develops, with aphids moving more quickly up the plant and eventually stunting new growth at the centre of the cabbage as the remaining dying leaves are less suitable.

This paper will examine both aphid and plant populations in a factorial design. Gas exchange measurements of maximum photosynthetic rate (A_{max}) and stomatal conductance (g_s) enable an assessment of drought impact. These values are expected to decrease with water stress and with aphid infestation. The chlorophyll fluorescence yield parameters Δ F/Fm and Fv/Fm measured here, are parameters defined by Genty et al. (1989) to investigate the yield of electron transport in photosystem II, which in turn affects the efficiency of CO_2 uptake. This can be one of the first areas to be affected by plant stress (Maxwell and Johnson, 2000) and may show responses where photosynthetic readings do not. Estimation of leaf chlorophyll with a SPAD meter will be rapid and allow large sample sizes. Several studies show that leaf chlorophyll content shows a strong correlation with leaf nitrogen content (van den Berg and Perkins, 2004). Host plant final biomass readings will show any impact of drought and aphids on plant growth. Soil moisture will monitor the progress of the water stress treatment and also indicate level of water use by the plant, depending on how rapidly the readings vary. Increasing leaf temperature should correlate with closing stomata. Total leaf water potential gives an immediate reading for water stress, osmotic potential gives the level of concentration for vacuole and phloem constituents, and turgor pressure is expected to have a strong relationship to aphid performance.

The aphid population was monitored through photographic record to show trend over time. The intrinsic rate of increase (r_m) and fecundity as defined by Wyatt and White (1977) were measured to determine the effect of host quality. Previous research by Mittler (1967); Wyatt and Brown (1977) found increasing daylight length and air temperature positively affected *M. persicae* population characteristics. As the leaf stomata close in response to water stress, the leaf temperature is predicted to rise, this may

lead to increased rates of increase and fecundity irrespective of the expected response to changing diet quality.

The suite of measurements taken should give a picture of the plant-aphid interaction under water stress at a whole plant and insect level.

2. Method

Experimental Design. All work used *Brassica oleraceae var capitata*, 'Greyhound' variety. All work was conducted in the same controlled environment room at the King's Buildings Campus, Edinburgh University. The regulated conditions were: ambient temperature at 21°C ± 0.2, photosynthetically active radiation (PAR) levels at 100 μmol $m^{-2}s^{-1}$, and a 16 hour photoperiod. The average humidity was 50%, giving an approximate vapour pressure deficit (VPD) of 1.24 KPa.

The dates for work carried out were: Experiment A in November to December 2009 and Experiment B in February to March 2010. Plants were grown identically in 130 mm cubed pots for five weeks, prior to the start of treatments. At five weeks, plants were randomly assigned to one of four treatments in a full factorial design, twice weekly watered (W), once weekly watered (D), aphid infested (A) and no aphids (N). This description of treatments introduces the abbreviations used throughout. Each plant was watered by a saucer at the base, 'D' plants received 125 ml on watering days, 'W' plants were watered *ad libitum* and could receive up to 500 ml on watering days. The *M. persicae* strain used was descended from an insecticide-susceptible colony, provided by the Scottish Crop Research Institute (Dundee, UK).

Experiment I used 24 cabbages for plant physiological work took place in November to December 2009 and Experiment II for aphid population work on 40 cabbages through February to March 2010.

Plant Measurements.

Soil Moisture (A & B). The soil moisture values were measured with a Delta-T Theta Probe ML2 (Delta-T Devices Ltd, Cambridge, UK) connected to a Delta-T HH2 Moisture Meter. Measurements were made on a 24 plant sample in weeks 1 and 5 of Experiment I. For Experiment II, measurements were taken in weeks 2 to 5, n = 19–40.

Leaf Temperature (A & B). Individual leaf temperature was taken with a Fluke Infra-Red Thermometer, positioned 20 mm from the youngest fully expanded leaf's surface to minimise the area of the sensor. In Experiment I, n = 20–24, readings in weeks 2, 3 and 5. For Experiment II, n = 19–40 with data from weeks 2 to 5.

Gas Exchange Measurements (A). All measurements were made between 1000 and 1300 using a LI6400 Photosynthesis System (LI-COR Biosciences Inc. Nebraska, USA). An initial light response curve was generated in the first week to determine a suitable chamber PAR level, allowing comparison of the maximum photosynthetic ability between stressed and unstressed plants, The chosen light level was 1200 μmol m^{-2} s^{-1}, this was the point where gas exchange levelled in respect to PAR. Temperature was controlled at 21°C, CO_2 was controlled at 370 μmol CO_2 mol^{-1} and flow rate to the sample cell was set to 500 μmol s^{-1}.

The youngest fully expanded leaf at week five was tagged and followed through readings taken in weeks 1 to 3; n = 9–23

Fluorescence Measurements (A). All measurements were made between 1000 and 1300 using a Walz MiniPAM system (Heinz-Walz GmbH, Effeltrich, Germany) on the same leaves sampled for gas exchange, in weeks 1 to 4; n = 9–23.

The suite of measurements were conducted on both light and dark adapted leaves. 'In the light' measures gave the Yield-parameter (based on the Genty parameter $\Delta F/Fm$). 'Dark adapted' measures gave Fv/Fm (at least 30 minutes dark adapt time). The system was operated on 'Burst-mode' for measurements and all other settings were as default. The leaf-clip was used for light adapted measures

and the proprietary leaf-clips were used for dark adapted measures. Background elements of the fluorescence signal were eliminated with the 'Auto-Zero' function before readings were taken.

Leaf Chlorophyll Estimation (A). An estimation of chlorophyll content in the same leaves sampled for gas exchange and fluorescence was made with a Minolta SPAD meter (Konica Minolta Sensing Inc.). Each leaf was sampled three times and the mean found in weeks 1, 3 and 4; n = 10–20.

Biomass (A). Plants were harvested at the end of experiment 'A' and dry weight was measured, n = 24.

Water Potential Components (B). The plant water potential in cabbage was described with Equation (1).

$$\textit{water potential } (\Psi) = \textit{turgor pressure } (\Psi_p) + \textit{osmotic potential } (\Psi_s) \quad (1)$$

Total leaf water potential, Ψ was measured weekly for 35 days with a Scholander-type Plant Moisture System (Skye Instruments Ltd., Powys, UK) between the hours of 1000 and 1300. Fully expanded leaves were excised and immediately transferred to the chamber, readings were taken in weeks 1 to 5, n = 6–21.

The leaf was then removed from the chamber, sealed in a 10 ml plastic syringe and immediately snap-frozen in liquid nitrogen. Leaves were stored in liquid nitrogen and defrosted for 30 minutes. At least 10 μl of cellular sap was expressed by depressing the syringe plunger. Sap was collected in a small dish and immediately sampled with a 10 μl pipette, transferred to a filter paper disc and analysed with a Wescor Vapro5520 Vapour Pressure Osmometer (Wescor Inc., Utah, USA).

The error component from dilution of syplasmic water by apoplasmic water is acknowledged from Callister et al. (2006), but not corrected for.

Turgor pressure was then calculated from Equation (1).

Aphid Population.

Population size (B). Five aphids were placed on each plant by day 7. Aphids were counted on 20 plants in weeks 3 to 5, using multiple photographs taken with a digital camera of 6.0 megapixel resolution saved in high quality resolution JPEG format. Pictures of the upper and lower surface of each leaf were taken, as well as the congested young leaves at the cabbage center. Aphids were counted in Adobe Photoshop Elements. Individuals were marked on the photograph as they were counted to ensure no accidental repetition.

Intrinsic Rate of Increase (B). Clip cages were used in the population study. Two adult colony nymphs were caged separately on each experimental plant at the beginning of the water or drought treatment, one day later the adult was removed and one of the known 1 day old nymphs produced was left in the cage. Afterwards the cages were checked daily, with progeny removed if produced. 23 cages were studied through to completion.

All aphids were followed to the end of their life–beyond the period required for intrinsic rate of increase calculation–to allow measurement of total fecundity as well.

Intrinsic rate of increase (r_m) was calculated using the method of Wyatt and White (1977), laid out in Equation (2)

$$r_m = 0.738(log_e M_d/d) \quad (2)$$

Where d is the pre-reproductive period and M_d is the number of progeny produced in a period equal to d.

Data Analysis. All analyses and figures are generated using Minitab 15 Statistical Software (Minitab Ltd., Coventry, UK). Analyses of variance (ANOVA) were performed on gas exchange, water potential and SPAD data, all tested for normal distribution and equal variance. Aphid photographic count data was log10 transformed to normalise distribution and form paired covariate data with the normally distributed soil moisture and leaf temperature in ANOVA. This count data was also left untransformed and analysed in its original poisson distribution with the appropriate t-test. The fecundity data was also poisson distributed, and was t-test analysed with this distribution. r_m and nymph per adult per day data was analysed with ANOVA since they were normally distributed with equal variance.

3. Results

Water stress treatment led to significantly drier soil for the 'D' treatment in both Experiments, at $p<0.01$, see Figure 1 for details.

Water stress treatment led to significantly warmer leaves in the 'D' treatment in both Experiments, at $p<0.01$, see Figure 2.

There was a significant effect of aphid infestation ($F_{1,39} = 19.81$, $p<0.01$), water stress ($F_{1,39} = 7.5$, $p<0.01$) on photosynthetic rate, with a weak trend towards interaction at $p<0.08$. Figure 3 shows the spread and trend of data over the experiment period, as, over time the drought treatments both decline ($F_{2,39} = 18.75$, $p<0.01$), but aphid infestation in combination with drought leads to poorest rates of A_{max}.

Stomatal conductance, shown in Figure 4, was significantly affected by water stress ($F_{1,36} = 5.72$, $p<0.03$). The trend over time is toward a decrease conductance ($F_{2,36} = 5.08$, $p<0.02$). Water shortage leads to the poorest g_s values.

Figure 5 shows the spread and trend of fluorescence yield in the light over the experiment period, and the trend is that both water stress and aphid infestation cause a reduction in light adapted chlorophyll fluorescence yield. The fluorescence yield of a watered but aphid infested plant appears similar to the droughted plants. Contrary to expectations, the data was not normally distributed, so a non-parametric Kruskal-Wallis test was carried out. No significant difference was found except between the two most extreme values ('WN' day 7 against 'DN' day 28)

There was no significant effect of either treatment on Fv/Fm ratio.

SPAD estimation of leaf chlorophyll was affected by water stress ($F_{1,43} = 12.32$, $p<0.01$), aphid stress ($F_{1,43} = 7.85$, $p<0.01$) with a significant interaction ($F_{1,43} = 8.28$, $p<0.01$). Combined aphid and water stress leads to lower SPAD readings.

Both water stress ($F_{1,20}=51.21$, $p<0.01$) and aphid infestation ($F_{1,20}=40.8$, $p<0.01$) led to a significant decrease in dry weight of plants, with a significant interaction ($F_{1,20}=5.38$, $p<0.05$). The aphid infestation leads to a decrease in mass for watered plants equivalent to water stress alone. Figure 7 shows the data.

The water potential components are illustrated in Figure 8.

In leaf water potential, Figure 8a, there is a significant negative effect of drought treatment ($F_{1,65}=34.73$, $p<0.01$), a comparatively positive, weaker response to aphid infestation ($F_{1,65}=4.21$, $p<0.05$). There is a significant interaction effect ($F_{1,65}=7.12$, $p<0.01$). Time was also a factor, $F_{4,65}=6.86$, $p<0.01$).

Osmotic regulation, Figure 8b, shows a significant decrease with drought treatment ($F_{1,63}=6.00$ $p<0.02$), aphid treatment ($F_{1,63}=23.6$ $p<0.01$) and a weak trend towards interaction at $p<0.08$.

Turgor, Figure 8c, was significantly higher in the watered treatment, ($F_{1,52}=17.21$ $p<0.01$) with time also a factor, $F_{4,52}=6.25$, $p<0.01$).

Analysis of variance of the total aphid population is shown in Table 1. Since matching measurements of leaf temperature and soil moisture could be included in the analysis with aphid counts, the data could be correlated (Figure 9). Aphid numbers were negatively correlated with leaf temperature (Pearson value = -0.271, $p<0.05$) and positively correlated with soil moisture (Pearson value = 0.387, $p<0.01$).

Poisson analysis of the raw count data showed significantly more aphids on watered plants (Z = -76.17 at p<0.01), Figure 10a,

TABLE 1. ANOVA Repeated measures Summary Table for aphid counts per plant, with covariate volumetric soil water content and leaf temperature

	Aphid counts per plant			
Factor	df	F	P	
Moisture	1	18.47	0.000	p<0.01
Temperature	1	7.87	0.008	p<0.01
Day	2	1.70	0.195	ns
Water	1	60.37	0.000	p<0.01
Error	43			

The water stress treatment reduced aphid population r_m ($F_{1,21}$ = 6.05, p<0.03), see Figure 10b, total fecundity per aphid (Z = -2.80, p<0.01), shown in Figure 10c, and fecundity per adult per day ($F_{1,21}$ = 6.59, p<0.02), as illustrated in Figure 10d.

4. Discussion

The significant aphid effects found here present a fast acting stress that is similar in magnitude and style to water shortage. Despite receiving more than double the water ration of a droughted plant, watered cabbages infested with aphids showed significant reductions in photosynthetic rate and final weight with significantly less negative osmotic potential. These are the same patterns shown here in droughted cabbages infested with aphids, with reduced photosynthetic rate and final weight and a significantly less negative osmotic potential compared to solely water stressed plants. Previous research has found similar trends (Riedell, 1989; Cabrera et al., 1994; Burd and Elliot, 1996; Macedo et al., 2003).

A significant reduction in photosynthesis and trends toward lower fluorescence yield presented here imply damage to the efficiency of photosystem II electron transport, similar to results found with Russian wheat aphid (*Diuraphis noxia*) by Burd and Elliot (1996) and Macedo et al. (2003). It was expected that measurements of dark-adapted Fv/Fm would have shown clear reductions under aphid stress, as found in Blanco et al. (2007), where the method is suggested as a rapid identifier of aphid stress, however no significant effect was found in this research.

Loss of turgor pressure in response to aphid stress seems typical in past research (Burd and Burton, 1992; Cabrera et al., 1994), but no significant effect was found here.

Typical early drought responses include reduced cell growth, wall synthesis and protein synthesis (Hsiao, 1973). Reduction in biomass with aphid infestation, found here, was similar to the reduction in biomass caused by drought alone. There are similarities between water and aphid stress as types of stress effect, as found by Warrington and Whittaker (1990) on Sitka spruce with green spruce aphid (*Elatobium abietinum*). Riedell (1989) also found that droughted barley (*Hordeum vulgare*) infested with aphids for seven days showed reduced increases in dry weight upon removal of the stresses. In addition, it was concluded that the aphids had induced drought-like symptoms in well watered, but infested plants with reduced stomatal conductance, relative water content, more negative leaf water potential and lower chlorophyll levels. Cabrera et al. (1995) similarly found lower sucrose, soluble sugar and total chlorophyll levels and photosynthetic rates in well watered but aphid infested barley seedlings.

The first drought responses are followed more slowly by reduced stomatal opening and CO_2 assimilation in combination with proline and sugar accumulation, as a process of osmotic regulation decreases the vacuole osmotic potential (Hsiao, 1973). The maintenance of osmotic potential in droughted, aphid infested plants, shown here, could be due to prevention of the typical drought response to accumulate proline and other amino acids, which in turn lowers omostic potential, a possibility suggested by Riedell (1989) with *Diuraphis noxia*. Similarly, Cabrera et al. (1994), found a rise in proline accumulation in droughted and aphid infested plants, but this was lower than the rise in solely droughted plants. They

concluded that aphids induced a water-stress-like response in plants but in addition could have made an impact on local turgor pressure. With the addition of the results from this work, it is reasonable to say that although some aphids cause drought-like symptoms in their host, the attractive feature is not the increasing osmotic potentials in the phloem, which are a negative factor for aphids.

What other dietary changes do happen when aphids attack a host? Divol et al. (2005) found that *M. persicae* infestation on celery (*Apium graveolens*) led to a number of changes in genetic regulation of processes. Genes induced after aphid stress included those affecting photosynthesis, which were up-regulated within 3 days of infestation, although this did not translate into direct photosynthesis measurements in their work. Genes relating to a plant's response to oxidative stress were significantly up-regulated and a number of other genes associated with phloem-specific responses as well, including enzymes for amino acid biosynthesis. Effects were also found on the genes associated with cell wall modification and water entering the phloem, suggesting some control on turgor pressure.

The mean r_m in this study for watered plants was approx. 0.25, which compares with the Wyatt and White (1977) re-analysis based on the Wyatt and Brown (1977) study of *M. persicae* on chrysanthemum, which found rates of 0.211 - 0.393 at temperatures of 18°C and 24°C respectively. Fecundity per adult per day on watered cabbage plants was 8.55 ± 1.1, which compares with other studies (Wearing, 1972; Karley et al., 2002). This allows us to draw reasonable conclusions based on differences from these 'control' values. All the measures of aphid population performance showed a significant negative impact of water stress, with lower total numbers, r_m and fecundity. Aphid numbers were significantly correlated to soil moisture and leaf temperature. Although rises in ambient temperature seem to favour *M. persicae* populations (Wyatt and Brown, 1977), a local change at leaf level, in probable response to closing stomata, provided no additional benefits.

There is an additional. significant time-effect in most of the results, which shows that short-term experiments could easily miss some of the stress responses. Many studies only cover periods of infestation of about seven days (e.g, (Riedell, 1989; Cabrera et al., 1995; Divol et al., 2005)) and could miss some of the effects seen in this study.

The original 'plant stress hypothesis' does not seem to be relevant to phloem-feeding insects, such as aphids. The nature of their adaptations to phloem as a food source are robust enough to buffer some changes in diet composition (Douglas, 2006), but long term drought, even with 'pulses' of watering does not provide a direct benefit to the aphid population. In theory the 'pulse-stress' hypothesis, where bouts of dry and wetter conditions overall balance out the drought responses, would answer the question of why aphids sometimes appear to multiply on stressed hosts. This may be because the early reduction in protein synthesis leaves spare amino acids ready to be converted by aphid gut symbionts, whilst the sap remains dilute enough (in comparison to severe drought) for the aphid enzymes to cope. However, the level of experimentation required to find the exact suitable pattern which leads to aphid success would be unlimited. It seems more reasonable to conclude that, in general, aphids prefer the security of diet provided by a well watered host. Although the host is negatively affected with reduced physiological efficiency and growth, the supply of food will last longer and more predictably than a stressed plant would.

The relationship between aphid and water stress is complex, but interlinked. This research confirms that aphid stress causes 'drought-like' symptoms in otherwise healthy plants, that aphid stress prevents a plant's typical survival responses when already under drought stress and that the combination of stresses is doubly damaging to plant health and performance. It suggests that aphids prevent osmotic regulation in both droughted and well-watered plants leading to a beneficial maintenance of the normal concentration of nutrients in the vacuole.

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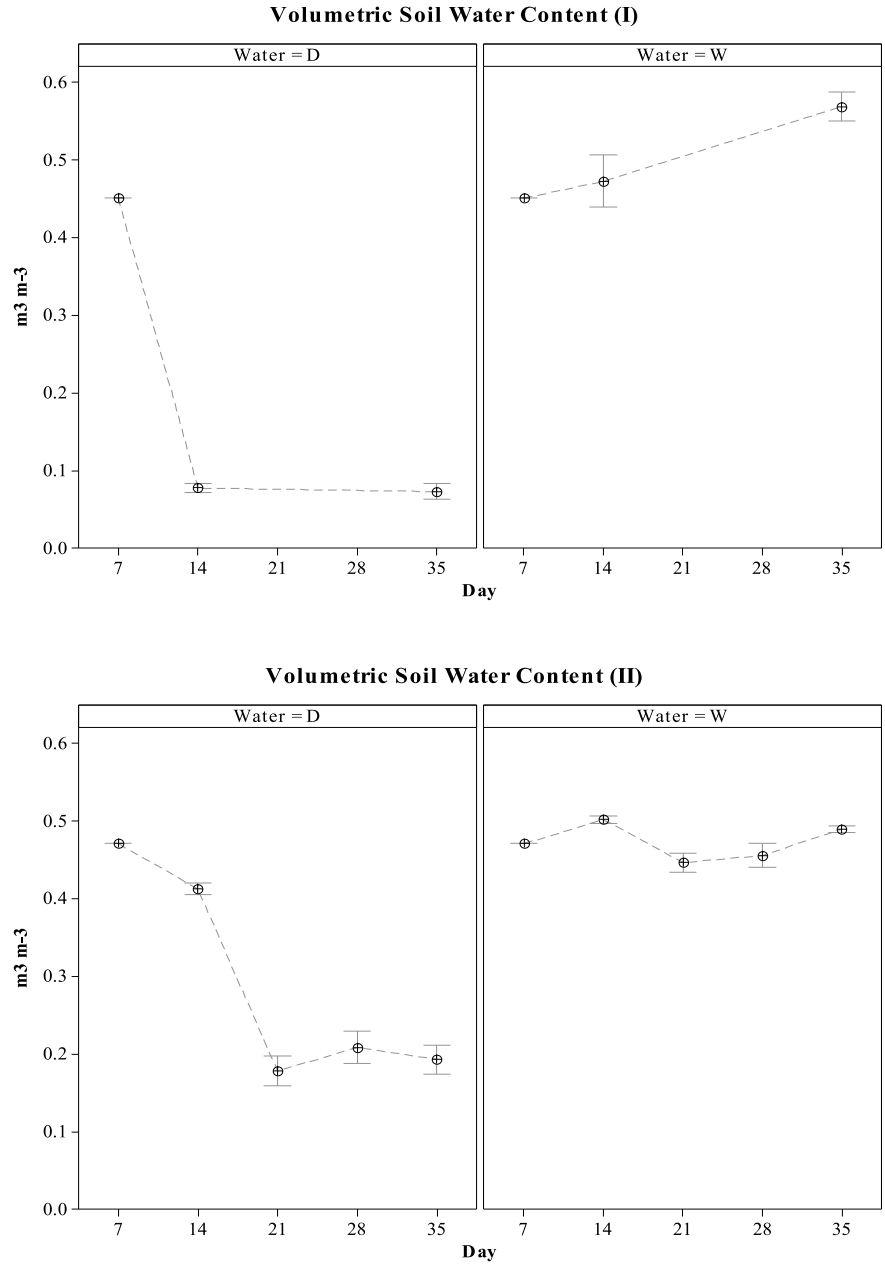


FIGURE 1. Volumetric soil water content. Panel variables are 'drought' (D) and 'watering' (W) treatment. Error bars are one standard error from the mean

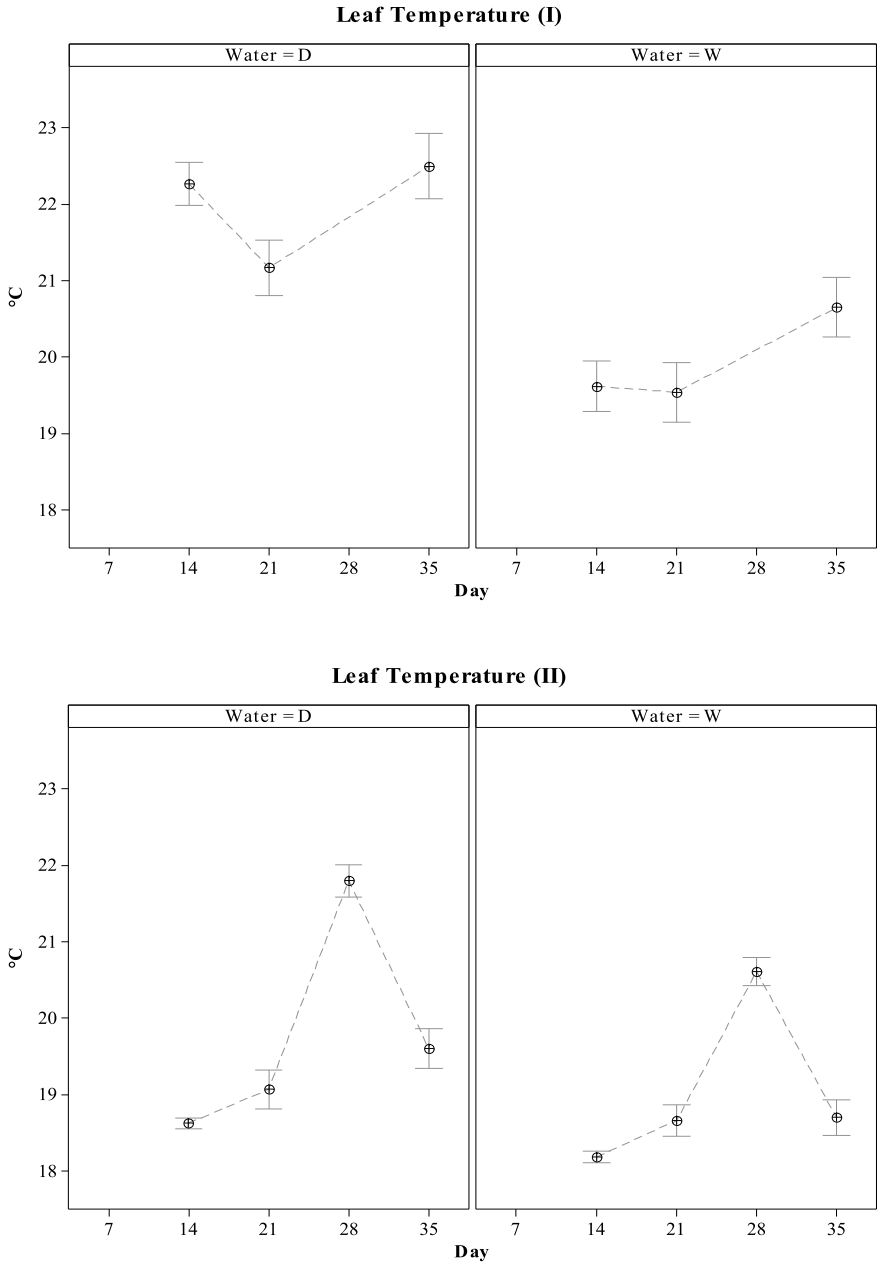


FIGURE 2. Leaf temperatures. Panel variables are 'drought' (D) and 'watering' (W) treatment. Error bars are one standard error from the mean

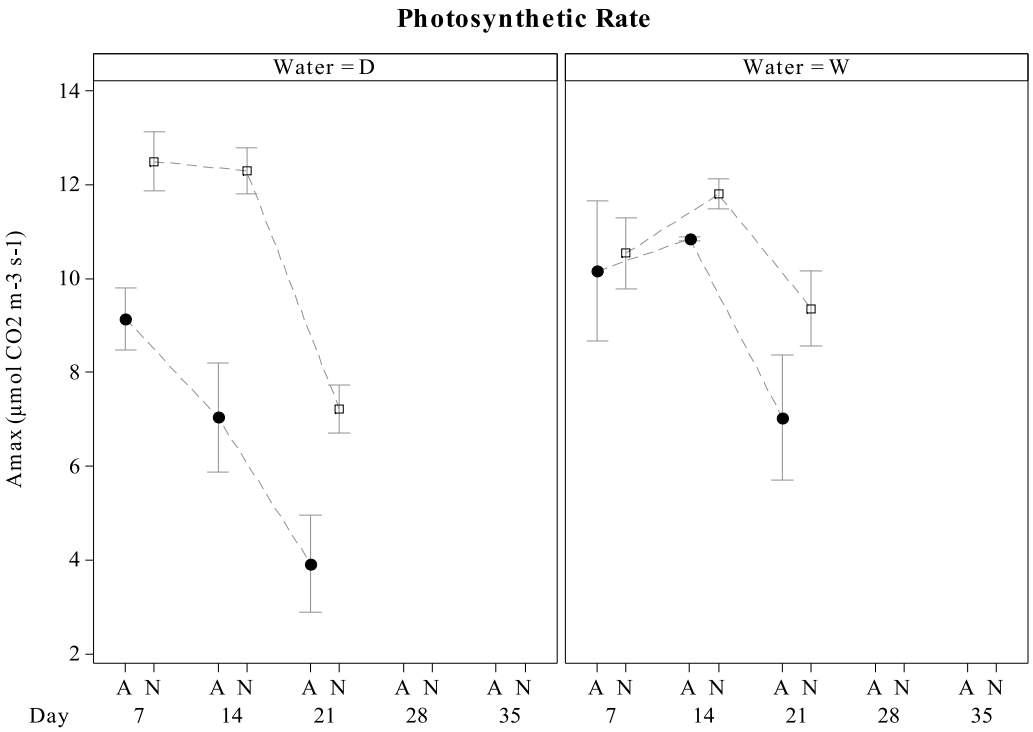


FIGURE 3. Maximum photosynthetic rate. Panel variables are 'drought' (D) and 'watering' (W) treatment. Closed circles • are 'aphid' (A) and open squares □ are 'no aphid' (N) treatments. Error bars are one standard error from the mean

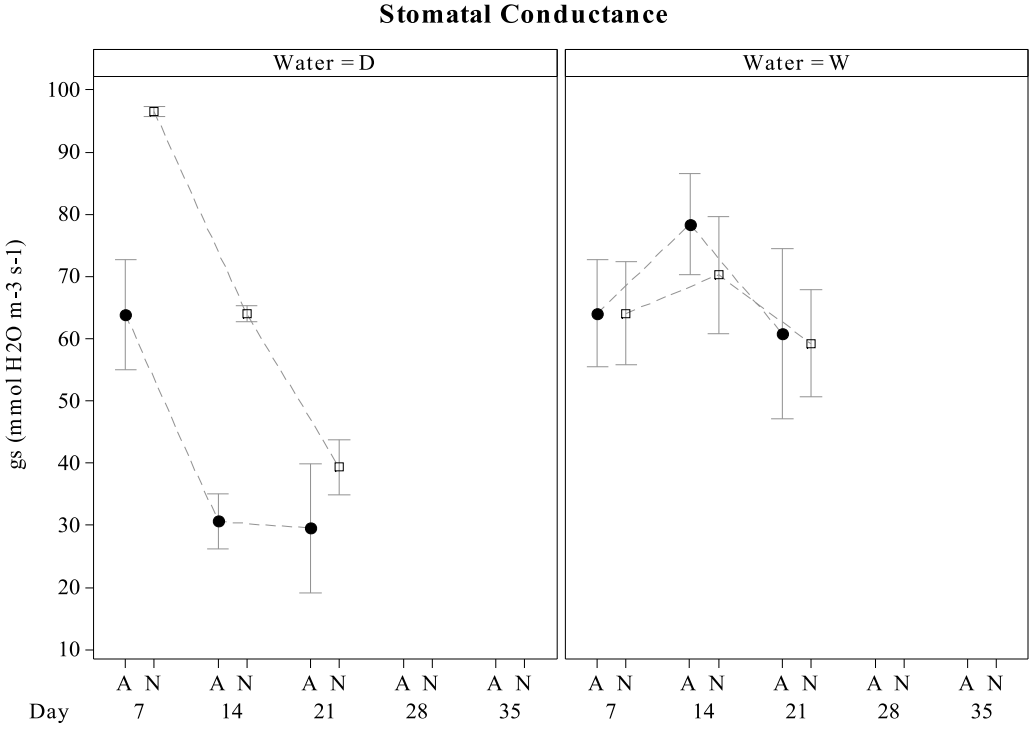


FIGURE 4. Stomatal conductance rates. Panel variables are 'drought' (D) and 'watering' (W) treatment. Closed circles • are 'aphid' (A) and open squares □ are 'no aphid' (N) treatments. Error bars are one standard error from the mean

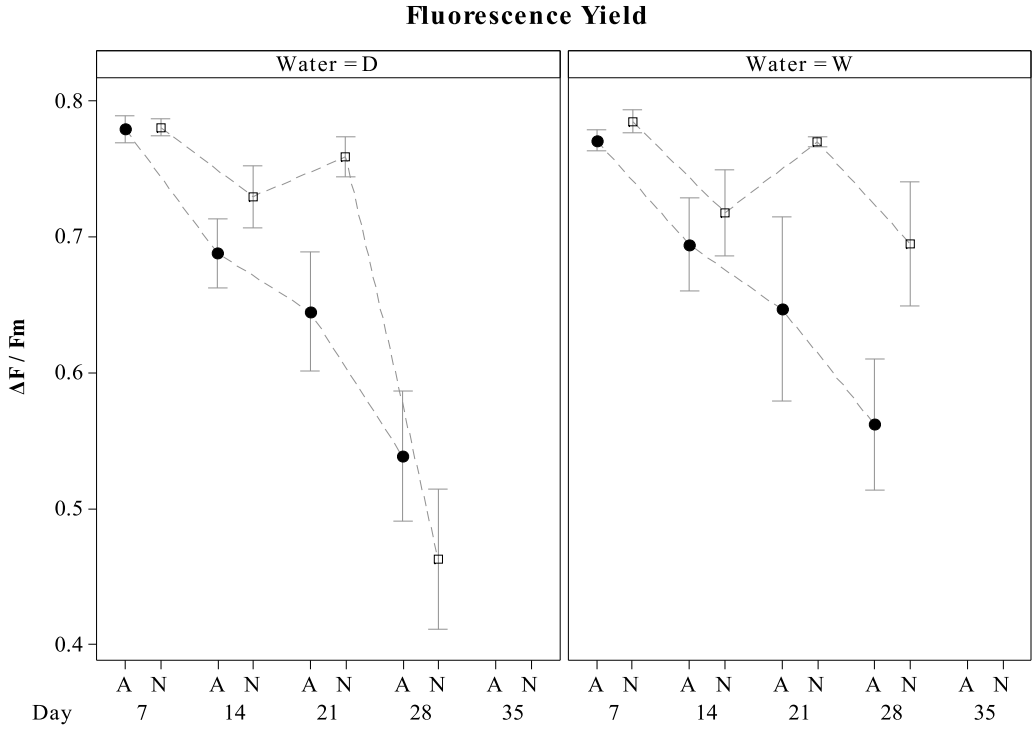


FIGURE 5. Chlorophyll fluorescence data. Panel variables are 'drought' (D) and 'watering' (W) treatment. Closed circles • are 'aphid' (A) and open squares □ are 'no aphid' (N) treatments. Error bars are one standard error from the mean.

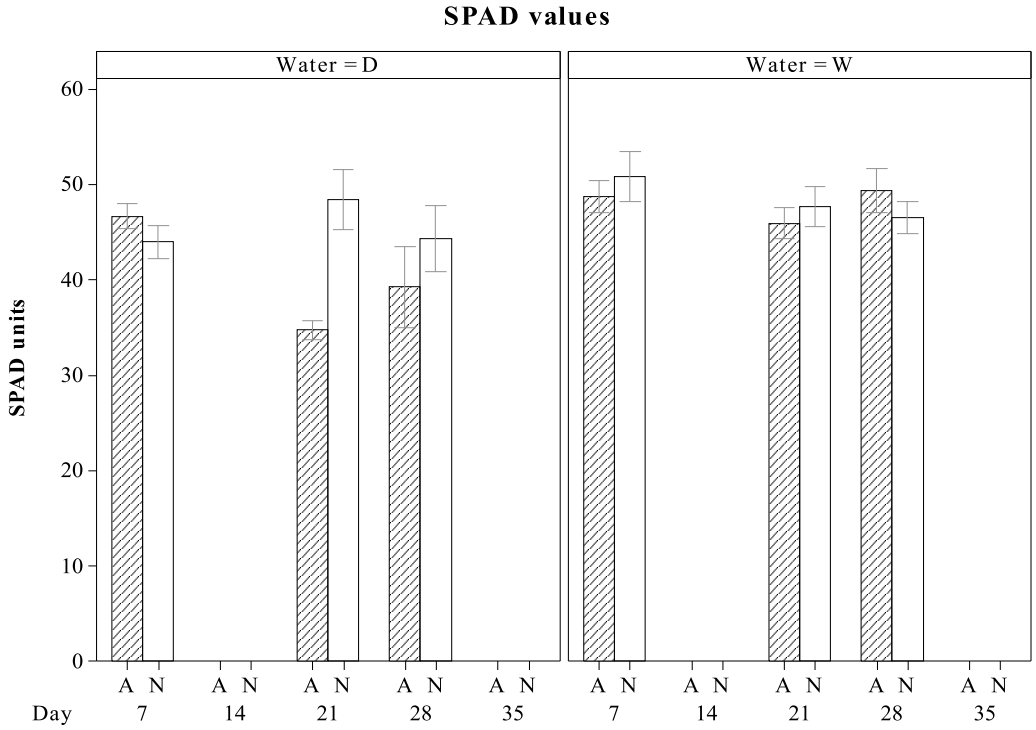


FIGURE 6. SPAD values. Bars are 'drought' (D) and 'watering' (W) treatment. Error bars are one standard error from the mean

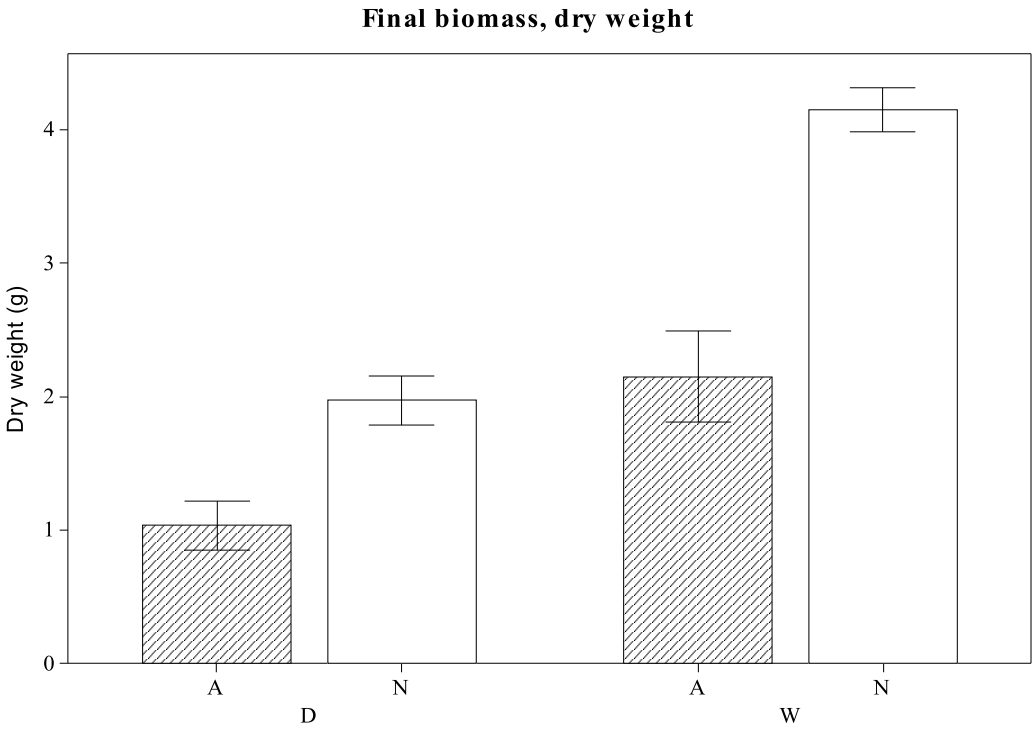
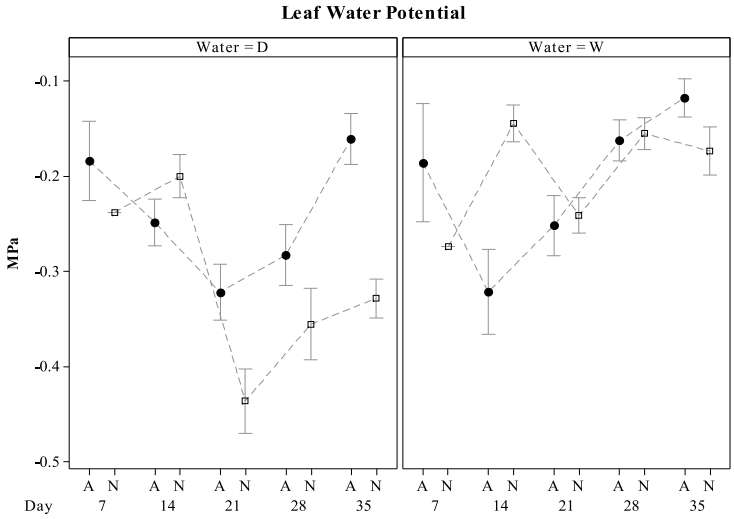
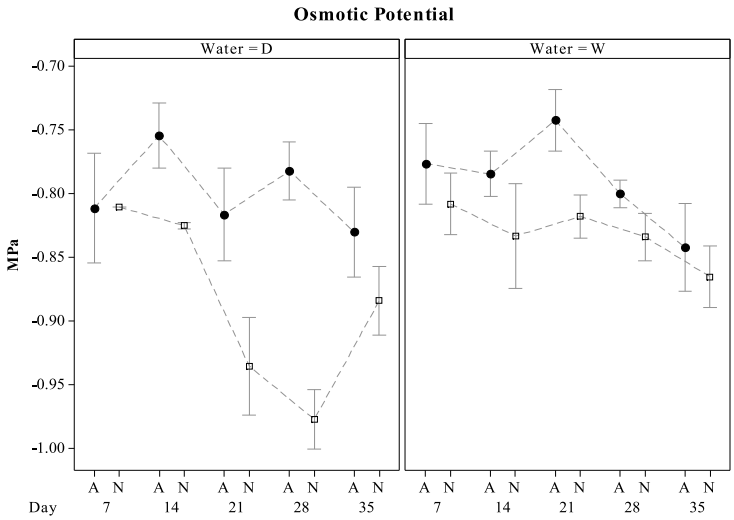


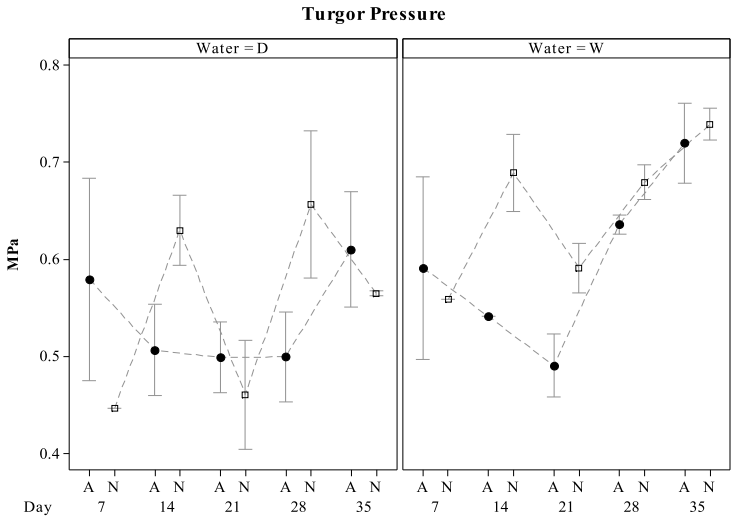
FIGURE 7. Dry weight values. Bars are 'drought' (D) and 'watering' (W) treatment. Error bars are one standard error from the mean



(A) Leaf water potential

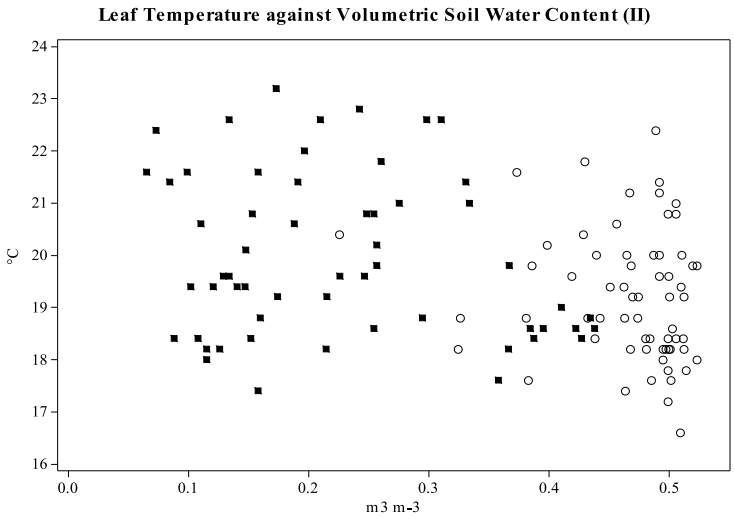


(B) Osmotic potential

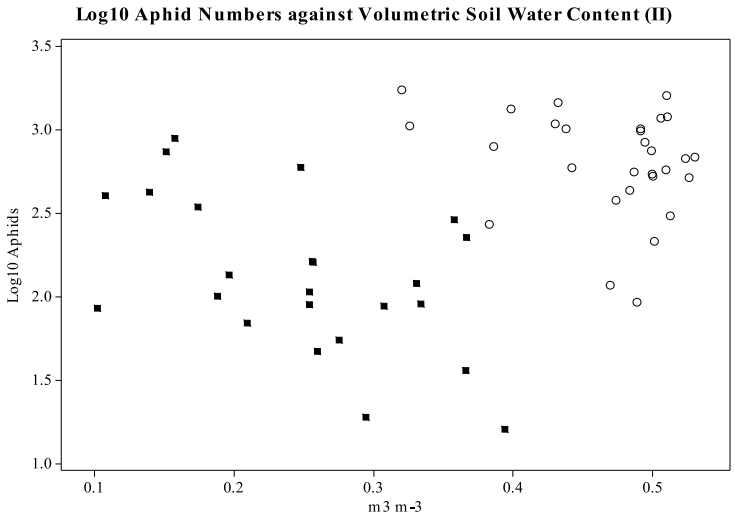


(C) Turgor pressure

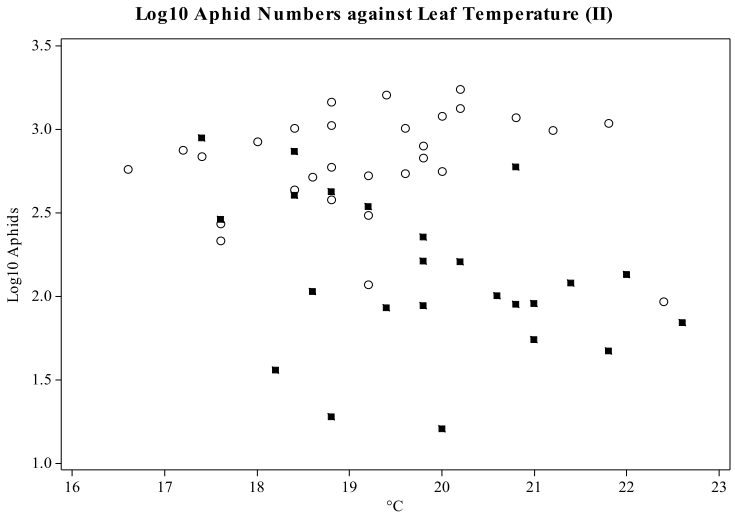
FIGURE 8. Measured potentials over time. Panel variables are 'drought' (D) and 'watering' (W) treatment. Closed circles • are 'aphid' (A) and open squares □ are 'no aphid' (N) treatments. Error bars are one standard error from the mean



(A) Leaf Temperature & Soil Moisture

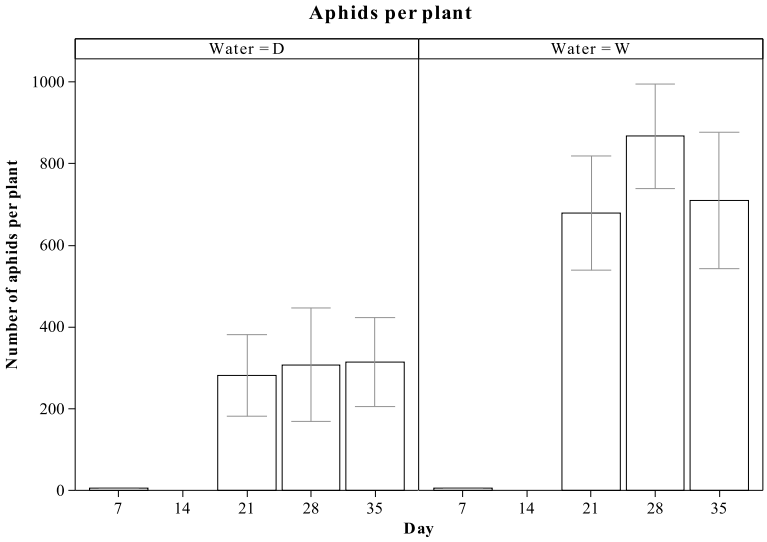


(B) Aphids & Soil Moisture

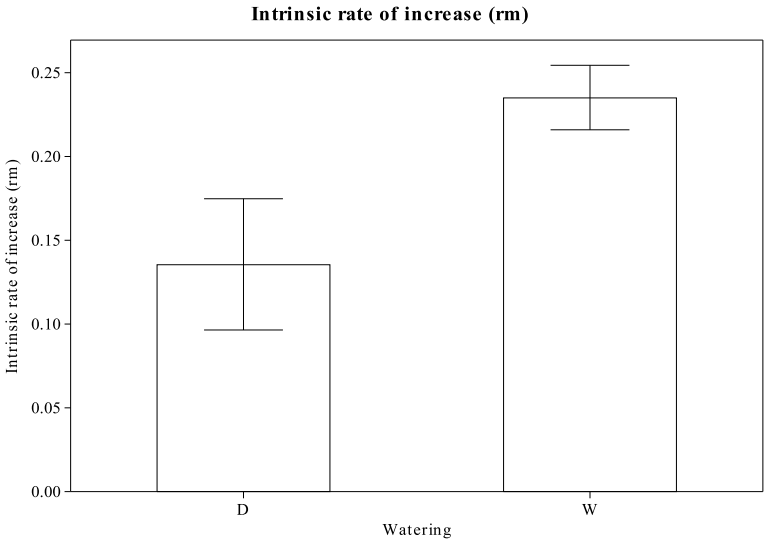


(C) Aphids & Leaf Temperature

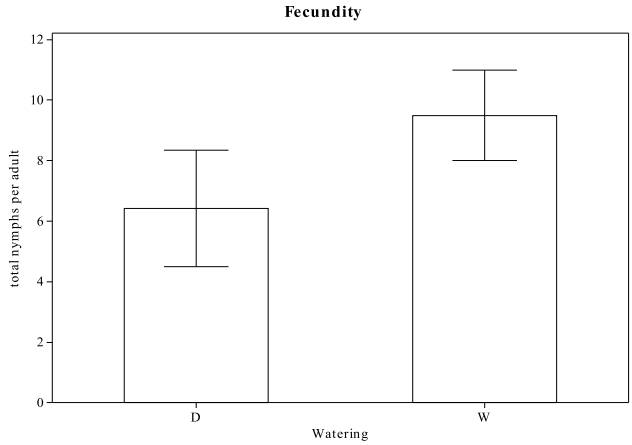
FIGURE 9. Correlation of aphid counts with soil moisture and leaf temperature. Open circles ○ are 'watered' treatment, closed squares ■ are 'droughted' treatment. The following are Pearson correlation with p-values (a) -0.32, $p<0.01$ (b) 0.387, $p<0.01$ (c) -0.271, $p<0.05$



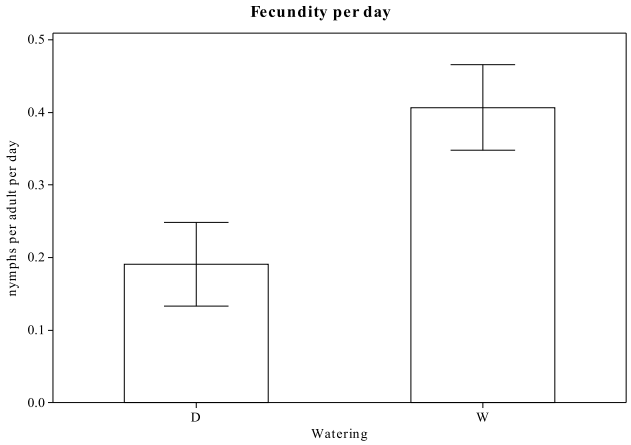
(A) Total aphids per plant



(B) r_m by treatment



(C) Fecundity per adult aphid



(D) Fecundity per adult aphid per day

FIGURE 10. Aphid population data