《生物科学杂志(ISSN 2958-4035)》
Journal of Biological Sciences (ISSN 2958-4035)

ChengZhu Science™

Serial in November, 2022

ChengZhu Science Research Center Limited

(Hong Kong Registration NO. 80561228)

Journal article DOI is registered via JiangXi Province ChengZhu Environmental Engineering Company Ltd, with Crossref membership (DOI prefix 10.58473)

出版人： 刘焕 香江出版社有限公司

Publisher: Liu Huan, Xiangjiang Publishing Company Ltd.

ISSN 2958-4035



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Article2: Inter-specific and intra-specific comparison in the responses to UV-B radiation and to water deficit in Trifolium (Leguminosae)/三叶草属（Trifolium）植物种间和种内对 UV-B 辐射和干旱等逆境生理的比较性研究

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DOI: https://doi.org/10.58473/JBS0004

Formally published on 30/11/2022; Latest revised on 23/04/2026.

Abstract:

This research tested the impacts of drought stress and UV-B stress on the physiology of Caucasian clover (*Trifolium ambiguum M. Bieb.*) and two populations of white clover (*Trifolium repens L.*). Physiological adjustment pathways under each environmental stress and under mixture stress conditions were compared, with substantial discussion on the basis of experimental results simulated in Lab.

Key Words: Caucasian clover, White clover, UV-B Radiation, Drought Stress, Physiological adjustment pathway

Key features of science finding:

Caucasian clover (*Trifolium ambiguum M. Bieb.*) and two populations of white clover (*Trifolium repens L.*) were grown for 9 weeks with supplemental application of UV-B radiation at a rate of approximately 13 kJ m^{-2} day^{-1}. Parameters of total aerial biomass, net photosynthesis, conductance, transpiration, water use efficiency, relative chlorophyll content, water solute potential ΨW, canopy temperature were tested in this research. Drought stress was also simulated during the last four weeks. Compared with the control, the total aerial (Dry Matter) DM production across clovers decreased by 81% under drought condition. However, Caucasian and Tienshan clover showed higher drought tolerance in terms of osmotic adjustment. Under well-water condition, the total aerial biomass yield of Tienshan clover was not significantly affected by UV- B, while Kopu II was sensitive to UV-B. By the intra-specific comparison within white clover species, Tienshan clover, which showed less UV-B sensitivity and higher tolerance to drought, was less productive and had a

original habit with multiple forms of stress. Further more, drought stress reduced UV-B sensitivity in both clover species. On the other hand, UV-B treatment also improved water-deficit tolerance across clovers by 43% under drought. In comparison, for Caucasian clover, UV-B increased the total aerial biomass yield by 84% under drought conditions. This indicated that UV- B might lead to a higher improvement of drought tolerance in Caucasian clover than in white clover. However, results also indicated that the pathways of physiological adjustments would differ between UV-B radiation and drought stress conditions.

关键知识点译文：

一个高加索三叶草 (Trifolium ambiguum M. Bieb.) 的种群和两个白三叶草 (Trifolium repens L.) 的不同种群在 UV-B 辐射和干旱的模拟实验室条件中栽培了 9 个星期。总体生物量干重，初级光合作用，大气传导率，蒸腾量，水利用效率，树冠温度，叶绿素相对含量、溶质势能等参数在实验室条件下进行了测试。与适宜生长条件相比，所有三叶草植物在干旱逆境中生长的总体干重平均降低了81%。然而，高加索三叶草和天山白三叶草以渗透调节的方式显示出了更高的抗旱性。在水分充足的条件下，天山白三叶草生长的总体干重并无显著地受到 UV-B 辐射的影响，然而 Kopu II 白三叶草品种却对 UV-B 辐射很敏感，说明天山白三叶草显示出了对 UV-B 辐射和干旱的较强抗逆性。此外，天山白三叶草起源于一个充满各种逆境生理条件的生境中，并且生产力较低。干旱条件降低了三叶草植被对 UV-B 辐射的敏感性。同样的，UV-B 辐射增强了三叶草植被对干旱的抗逆性。比较而言，UV-B 辐射对高加索三叶草在抗旱性的提高更为显著。然而，实验结果表明了三叶草属植物分别在UV-B辐射和缺水等不同逆境条件下的生理调节机制和路径应该有所不同。

关键词：高加索三叶草，白三叶草，UV-B 辐射，干旱逆境，生理调节路径

1.Introduction

The increasing level of ultraviolet (UV)-B radiation, as a result of ozone depletion, has been recognized. The enhanced UV-B radiation may lead to large effects on the productivity of plant (Lindroth et al., 2000). Because the UV-B level in New Zealand is significantly higher than that at comparable latitudes in the northern hemisphere, these consequences caused by increasing UV-B radiation have been paid more attention in NZ (Lindroth et al., 2000).

White clover (*Trifolium repens L.*), as the most important legume species in NZ, effectively contributes to the soil nitrogen content for pasture growth due to its ability of atmospheric N fixation. It also has a high nutritious value for grazing ruminants. However, the taproot of white clover usually goes to senescence within two years and its persistence in pasture ecosystem mainly relies on the adventitious roots (Black et al., 2006). Consequently, white clover is relatively sensitive to water stress, which has become one of the main limitations to the productivity of pastures based on the white

clover in many areas of NZ (Barbour et al., 1999). There were two white clover populations used in this experiment. Kopu II, which has notable characteristics of high stolon density, long persistence under grazing, high yielding, and large leaf size, is a NZ cultivar for rotational grazing (Kopu II White Clover, 2006); Tienshan, originated from China, evolved under high level of UV-B irradiance with low annual rainfall (Hofmann et al., 2000).

Compared with white clover, Caucasian clover (*Trifolium ambiguum M. Bieb.*), which produces rhizomes rather than stolons and has a persistent deep taproot, has a longer persistence and higher drought tolerance in temperate pasture ecosystems, although it is less competitive in the establishment, mainly because it allocates more dry matter to the root system, which leads to a reduction of radiation interception by the shoot (Black et al., 2006).

Previous studies on white clover showed the interaction between drought and UV-B. It was suggested that populations evolved under higher natural level of UV-B irradiance were more tolerant to UV-B (Hofmann et al., 2001). Populations, which had well adaptation to drought stress but lower productivity, also had higher UV-B tolerance (Hofmann et al., 2003b). UV-B sensitivity, which was measured mainly by plant growth attributes, decreased with longer duration of drought stress and increasing exposure to UV-B radiation (Hofmann et al., 2003a). UV-B radiation increased levels of UV-B absorbing compounds and flavonol glycosides, which could also be enhanced by water stress. Both drought and UV-B radiation were able to cause accumulation of osmoregulator proline and lead to reduction of osmotic (solute) potential in leaf cells. Further more, leaf water potential under drought stress could be improved by UV-B radiation (Hofmann et al., 2003b).

However, there were still fewer studies on the inter-specific comparison in the responses to UV-B irradiance and to water stress (Hofmann et al., 2001). We hypothesized that clovers (both within and between species) adapted to drought stress might have higher UV-B tolerance. Further more, a combination of drought and UV-B stress might decrease the sensitivity to each of these environmental stresses.

2.Materials and methods

There were two populations of white clover (*Trifolium repens L.*) used in this experiment: cultivar Kopu II and ecotype Tienshan. Caucasian clover (*Trifolium ambiguum M. Bieb.*) cultivar Endura was also compared. Plants were established as 4-6 months old seedlings. In the controlled environment, the ratio of day length to night length was 14h:10h at a temperature of 20ºC and 15ºC, respectively. The light level was set to be approximate 400 μmol m^{-2} sec^{-1}. The RH was approximately 50%. Clovers were planted in the 1:1 mixture of Wakanui silt loam and pumice. The top 2 cm layer of the pots, each of which was 8.5 L, contained a 4:1 mixture of composted bark:pumice, adding to small amounts of lime, Hydraflo wetting agent, and Osmocote

slow-release fertilizer.

There were four treatments in this experiment. Well-water (WW): Plants were watered at a daily rate of 5% below field capacity of the soil; Drought (DR): Plants were watered when 2% above permanent point wilting occurred; UV+: Plants were exposed to UV-B radiation at a rate of approximate 13 kJ m^{-2} day^{-1} from 12 Philips UV lamps; UV-: The UV- room contained a dummy rig with un-energised lamps. The duration of UV+ treatment was 9 weeks, while drought treatment started from the beginning of the 6th week after establishment. Each UV treatment (UV+ or UV-) was divided into 4 blocks. Each block was subdivided into 2 water treatments (well-watered and drought). Data was analyzed using the GENSTAT General Analysis of Variance Procedure.

2.1.Total aerial biomass yield (DM production)

Consistently large and green leaves, some inflorescence (flower cluster) and peduncle (inflorescence stalk) materials, and some stolon materials (in white clover) were harvested using scissors. Then they were dried out in oven at a temperature of 80ºC for 48 hours.

2.2.Gas exchange

LICOR 6400 Gas Exchange System was applied to test the gas exchange parameters in a young, fully unfolded leaf per pot. There were four parameters determined: Net photosynthesis (A or Pn) (μmol CO_2 $m^{-2}sec^{-1}$); Conductance (g) (mol H_2O $m^{-2}sec^{-1}$); Transpiration (E) (mmol H_2O $m^{-2}sec^{-1}$); Water use efficiency (WUE) (mmol CO_2/mol H_2O).

2.3.Relative chlorophyll content

Relative chlorophyll content was tested in three randomly-chosen leaves per pot using SPAD chlorophyll meter.

2.4.Canopy temperature (ºC)

Canopy leaf temperature per pot was determined using Infrared thermometer.

2.5.Water potential ΨW (MPa)

Water potential ΨW in a young and fully unfolded leaf per pot was determined by pressure bomb.

2.6.Corrected osmotic potential ΨS and osmotic adjustment(MPa)

Osmotic adjustment (OA), which is defined as the difference in corrected osmotic potential S(100) between control and stressed plants, was calculated by the formula:

$$S\,(100) = \frac{S\,(RWC - RWCa)}{1 - RWCa}$$

Where RWCa is the correction factor for dilution by apoplastic water, which is an estimated value. It is estimated to be approximately 0.1 for most plants in most situations. The osmotic (solute) potential was tested using by osmometer.

2.7.Time to reach drought (Day)

The time to reach drought was counted from the well-watered stage to the 2% above permanent point wilting stage.

2.8.Other morphological factors

The inflorescence DM, petiole length, leaf appearance rate, stolon elongation rate, specific leaf mass, % leaf dry mass, leaf damage, leaf senescence, leaf lamina size, and leaf lamina dry mass were also measured in this experiment.

3.Results

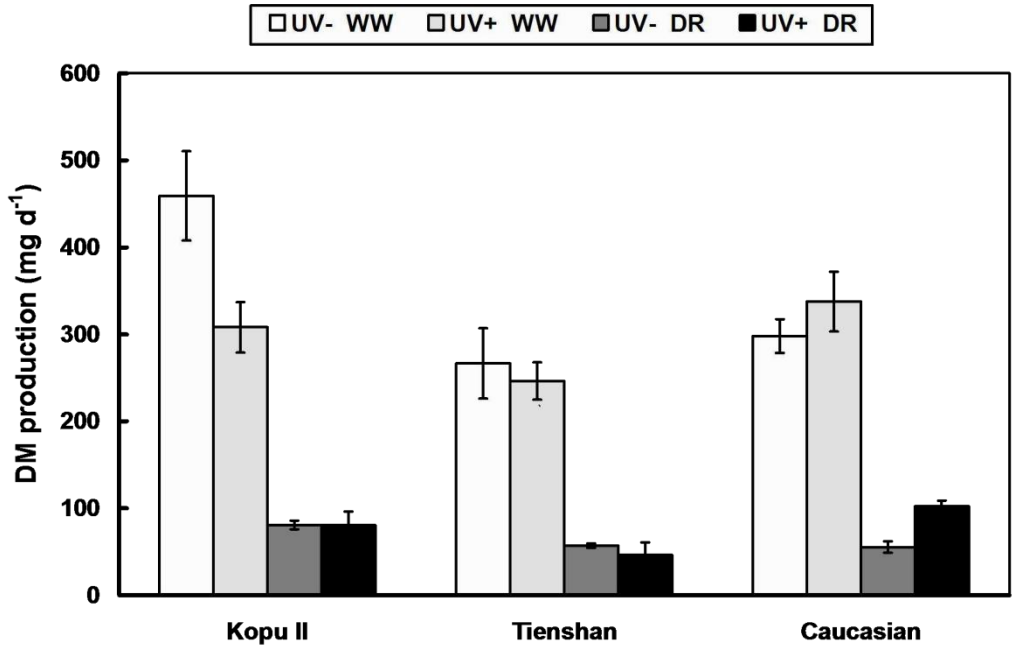


Figure 1. Total aerial biomass yield of Kopu II, Tienshan, and Caucasian clover, grown with (UV+) and without (UV-) supplementation of approx. 13 kJ m^{-2} day^{-1} UV-B, under well-water (WW) or drought (DR) conditions. Error bars are SE.

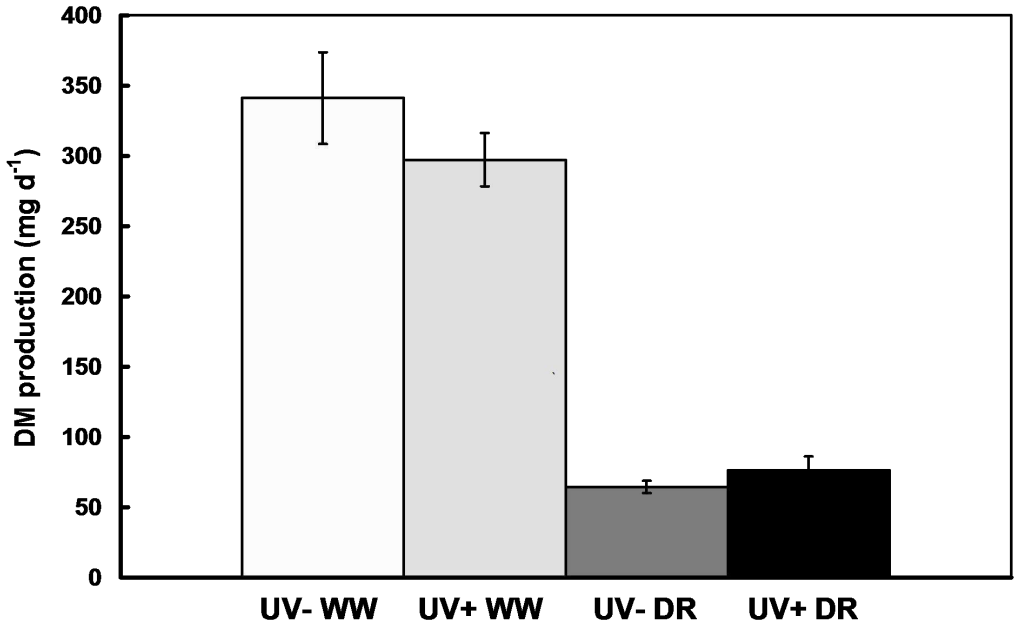


Figure 2. Total aerial biomass yield across clovers grown with (UV+) and without (UV-) supplementation of approx. 13 kJ m^{-2} day^{-1} UV-B, under well-water (WW) or drought (DR) conditions. Error bars are SE.

3.1.Total aerial biomass yield

The total aerial biomass yield across clovers was significantly ($P<0.001$) decreased by drought (Fig 2). Compared with the control, the total aerial DM production across clovers decreased by 81% under drought condition (UV-DR). In addition, in the control conditions, the total aerial biomass yield of Kopu II was higher than Tienshan clover.

The total aerial biomass yield was significantly ($P<0.01$) affected by the interaction between UV-B and populations. However, clovers responded to UV-B variously (Fig 1). Under well-water treatment, the total aerial biomass yield of Kopu II decreased by 33% as UV-B was applied. However, under drought condition, Kopu II did not show significant response to UV-B. For Tienshan clover and Caucasian clover, there was no significant UV-B-induced difference in the total aerial biomass yield, under well-water conditions. However, for Caucasian clover under drought conditions, UV-B increased the total aerial biomass yield by 84%.

3.2.Photosynthesis and transpiration

Drought significantly ($P<0.001$) affected the net photosynthesis (A), conductance (g), transpiration (E), water use efficiency (WUE) and canopy temperature (Table 1). Compared with the control, the net photosynthesis (A), conductance (g), and transpiration (E) across clovers decreased by an average of 45%, 75%, and 65%,

respectively, under drought treatment (UV-DR). Correspondingly, the water use efficiency (WUE) and canopy temperature across clovers under drought treatment (UV-DR) increased by an average of 67% and 12%, respectively, compared with the control (Table 1).

Net photosynthesis (A) was also significantly ($P<0.05$) decreased by UV-B (Table 1). Under well-water condition, a decrease of 23% across clovers was caused by UV-B. Further more, under well-water treatment, UV-B significantly ($P<0.05$) decreased the conductance and transpiration across clovers by 40% and 33%, respectively. However, there was no significant effect of UV-B on the relative chlorophyll content.

Table 1. Biological responses across clovers, grown with (UV+) and without (UV-) supplementation of approx. 13 kJ $m^{-2}day^{-1}$ UV-B, under well-water (WW) or drought (DR) conditions. (SE)

Attribute	**UV- WW**	**UV+WW**	**UV- DR**	**UV+ DR**
Net photosynthesis (A)	18.4	14.20917	10.1	7.868333
	(1.378405)	(0.849452)	(0.909657)	(0.722696)
Conductance	0.410333	0.244833	0.1046	0.102392
	(0.053581)	(0.024324)	(0.014434)	(0.013456)
Transpiration	4.247778	2.8475	1.47375	1.445083
	(0.387179)	(0.240628)	(0.186697)	(0.169303)
Water use efficiency	4.411081	5.15228	7.355093	5.788899
	(0.197779)	(0.215182)	(0.575411)	(0.397018)
Canopy temperature	20.93333	20.73333	23.39167	22.45833
	(0.154887)	(0.16299)	(0.233049)	(0.382864)
Chlorophyll content	49.41667	46.93333	50.45833	50.36667
	(1.25691)	(1.583692)	(1.277335)	(1.932589)

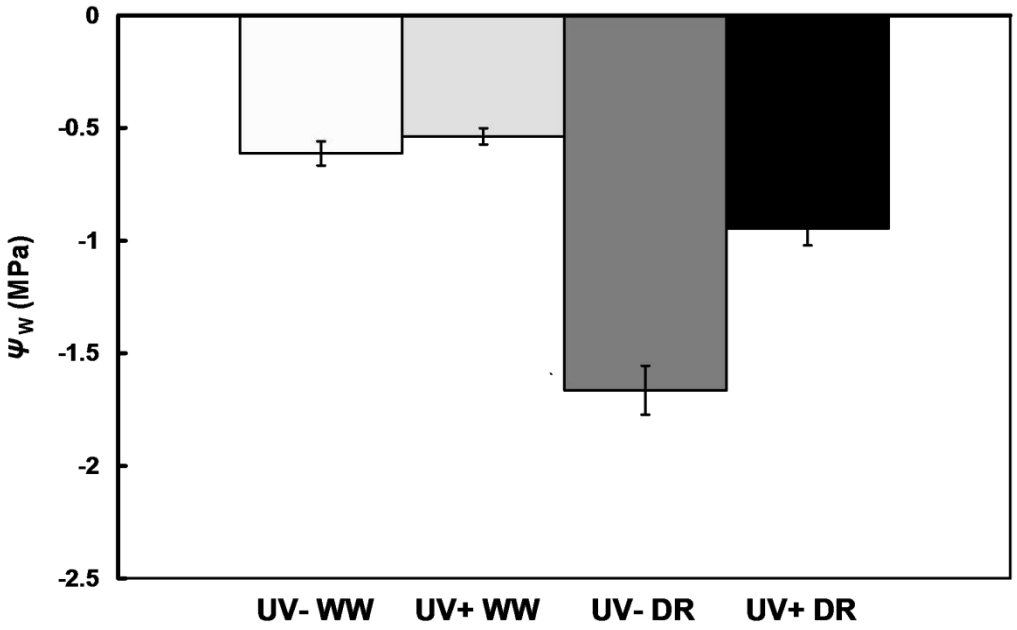


Figure 3. Leaf water potential across clovers grown with (UV+) and without (UV-) supplementation of approx. 13 kJ $m^{-2}day^{-1}$ UV-B, under well-water (WW) or drought (DR) conditions. Error bars are SE.

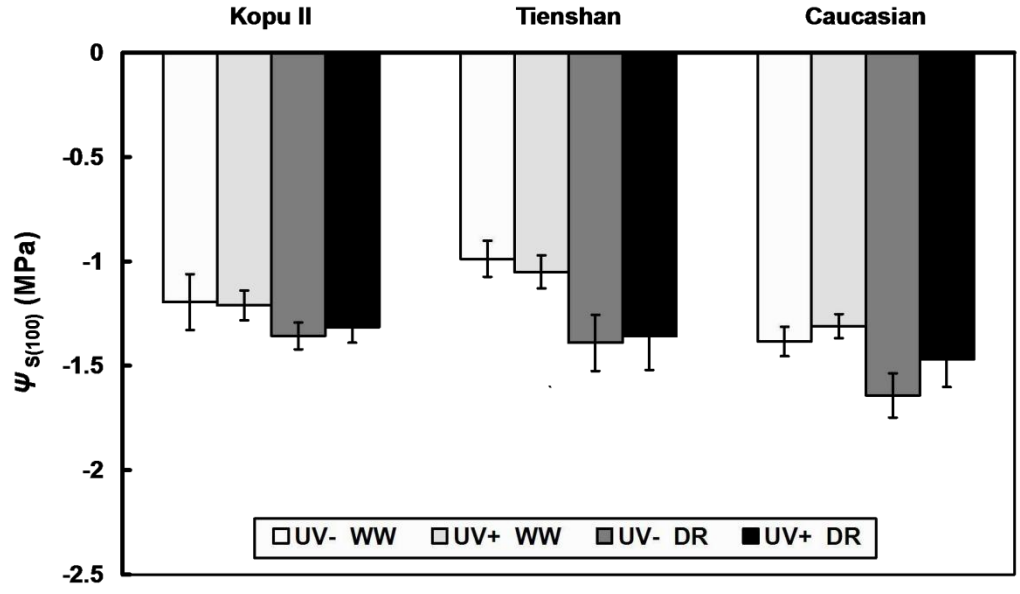


Figure 4. Leaf osmotic (solute) potential of Kopu II, Tienshan, and Caucasian clover grown with (UV+) and without (UV-) supplementation of approx. 13 kJ $m^{-2}day^{-1}$ UV-B, under well-water (WW) or drought (DR) conditions. Error bars are SE.

3.3.Water relations and Osmotic adjustment (OA)

Water potential was significantly (P<0.001) affected by UV-B and drought, and their interaction (Fig 3). In comparison with the control, water potential across clovers was decreased by an average of 172% by drought (UV-DR). However, under drought treatment, UV-B increased water potential across clovers by 43%. Further more, UV-B significantly (P<0.05) increased the time to reach drought across clovers by 36% (Fig 5). Especially, for Tienshan clover under well-water condition, UV-B increased water potential by 27% (not list).

Osmotic (solute) potential (OA) was significantly (P<0.05) decreased by drought (Fig 4). Compared with the control, a decrease of 19% and 41% in the osmotic potential (OA) was caused by the drought (UV-DR) in the Caucasian clover and Tienshan clover, respectively. However, clover Kopu II did not show significant osmotic adjustment response to drought.

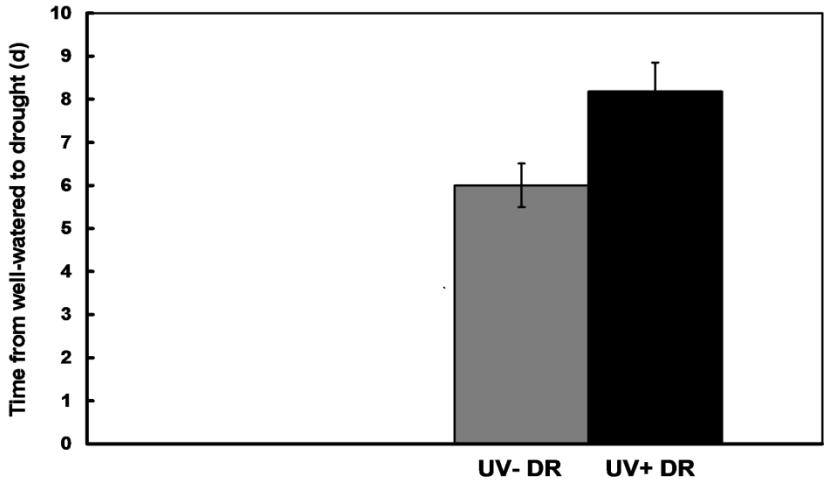


Figure 5. Time to reach drought across clovers grown with (UV+) and without (UV-) supplementation of approx. 13 kJ m-2 day-1 UV-B, under well-water (WW) or drought (DR) conditions. Error bars are SE.

3.4.Plant morphology

The inflorescence DM, petiole length, leaf appearance rate and stolon elongation rate were significantly (P<0.001) reduced by drought (Table 2), as well as leaf lamina size (P<0.01) and leaf lamina dry mass (P<0.05). Especially, under drought condition, Tienshan clover had higher leaf appearance rate than Kopu II (not list).

Both specific leaf mass and % leaf dry mass were significantly (P<0.001) increased by drought (Table 2). However, UV-B tended to reduce specific leaf mass and leaf dry mass. Leaf damage and leaf senescence across clovers were significantly (P<0.001) increased by both UV-B and drought. However, for the Caucasian clover under drought condition, UV-B led to less leaf damage, and leaf senescence did not show

significant response to UV-B.

Table 2. Significance of morphology changes across clovers affected by UV-B and Drought. ns, P≥0.1; *** P< 0.001; ** P< 0.01; * P< 0.05; + P< 0.1; ↑ increase; ↓ decrease.

Attribute	UV-B	Drought
Inflorescence DM production	ns	***↓
Leaf damage	***↑	***↑
Leaf senescence	***↑	***↑
Leaf lamina size	ns	**↓
Leaf lamina dry mass	ns	*↓
Specific leaf mass	*↓	***↑
% leaf dry mass	+↓	***↑
Petiole length	ns	***↓
Leaf appearance rate	ns	***↓
Stolon elongation rate	ns	***↓

4.Discussion

Drought significantly decreased the total aerial biomass yield across clovers (Fig 2). Water deficit reduced water uptake from soil, and hence decreased water potential in leaves (Fig 3), which eliminated cell turgor. This reduction in growth under drought conditions could also be supported by the reduction of net photosynthesis rate (A) (Table 1), which was mainly due to a decrease of carbon dioxide assimilation caused by the reduced stomata conductance. Stomata closure, which was one of the main mechanisms involving in the drought acclimatization in plants, could prevent water vapour loss from transpiration. Consequently, the increase of canopy temperature was caused by the reduction of transpiration (Table 1), which adjusted energy balance in leaves (Taiz & Zeiger, 2006). However, stomata closure led to a higher reduction rate in transpiration than in carbon dioxide assimilation, which caused the increase of water use efficiency (WUE). Barbour et al., (1999) also reported the increased water use efficiency in white clovers by drought stress.

Net photosynthesis (A) was significantly reduced by UV-B (Table 1). This was mainly due to the reduction of stomata conductance caused by UV-B. Salvador et al., (1999) suggested that the damage of PSII caused by UV-B in the guard cells affected the photophosphorylation, which consequently eliminated the K+ influx and stimulated K+ efflux transport. A second mechanism might be due to a directly UV-B-induced inhibition of the plasmalemma ATPase proton pump. UV-B might also indirectly inhibit the guard cell turgor by modifying the elasticity of the cell walls or the cytoskeleton of guard cells. These effects eliminated the stomata opening, which tended to decrease the stomata conductance.

However, the total aerial biomass yield across clovers was not significantly affected by UV-B (Fig 1), which reflected that photosynthetic system of these clovers might still effectively function. This was supported by the relative chlorophyll content (Table 1), which was not negatively affected by UV-B. These results indicated that these clovers might have adequately photo-protective mechanism, such as enhancing the synthesis of UV-B screening secondary metabolites (Hofmann et al., 2003a). Hofmann et al., (2003a) also reported that photosynthetic pigmentation and photosystem II photochemistry in white clovers were not reduced by UV-B.

Under well-water condition (Fig 1), the total aerial DM of Tienshan and Caucasian clovers did not show significant responses to UV-B, while the total aerial biomass yield of Kupo II was reduced by UV-B. These results indicated that Tienshan and Caucasian clovers were less UV-B sensitive than Kupo II, under well-water conditions.

In addition to UV-B sensitivity, Tienshan and Caucasian clovers also showed drought acclimatization in terms of significantly decreased solute potential by osmotic adjustment (OA), whereas Kupo II clover did not (Fig 4). Osmotic adjustment (OA), which decreases water solute potential by accumulation of compatible solutes in cells, such as proline, can maintain cell turgor under water deficit (Taiz & Zeiger, 2006). This was supported by Hofmann et al., (2003a), who reported the increased proline levels in white clover by drought stress. This acclimatization response indicated that Tienshan and Caucasian clovers might also have higher drought tolerance than Kupo II. This higher drought tolerance in Tienshan clover could also be supported by its higher leaf appearance rate than Kupo II under drought conditions. The synthesis of proline is divided into two pathways: glutamic acid and ornithine pathways, which is mainly catalyzed by P5CS & P5CR, as well as Ornithine Aminotransferase (OAT) respectively (Delauney&Verma,1993).

We may be able to conclude that clovers that have higher drought tolerance are also less UV-B sensitive under well-water conditions. Hofmann et al., (2003b) also suggested that the UV-B tolerance under well-water conditions might be related to other forms of stress, such as drought. Further more, within white clover species, compared with Kupo II, Tienshan clover, which was less UV-B sensitive under well-water condition and higher tolerant to drought, had less productivity in terms of less total aerial biomass yield under control conditions (Fig 1), and had a original habit with multiple forms of stress (see introduction). This relationship was supported by Hofmann et al., (2000), who reported that a higher concentration of flavonols, which functioned as UV-B protective compounds, were found in those white clovers that evolved under multiple forms of stress (Hofmann et al., 2000). Hofmann, et al, (2001, 2003 a, 2003b) also frequently reported similar relationships.

Compared with the well-water treatment, the total aerial biomass yield of Kopu II did not show significant response to UV-B under drought conditions (Fig 1). This

reflected that drought stress reduced UV-B sensitivity in Kupo II clover. Hofmann et al., (2003b) also reported the decreased UV-B sensitivity of white clover with the increase of drought duration. Under UV-B treatment, the concentration of both UV-B absorbing compounds and flavonols, including quercetin and kaempferol, were stimulated by the drought stress (Hofmann et al., 2003a). Elsewhere Grace and Logan (2000, cited in Hofmann et al., 2003b) suggested that the adaptation to other forms of stress contributed to UV-B protection mechanisms, probably via the phenylpropanoid pathway.

In addition to the improvement of UV-B tolerance by drought, UV-B increased water potential by 43% across clovers under drought treatment (Fig 3), and prolonged the time to reach drought (Fig 5), which indicated that UV-B stress also helped to improve the water status during the subsequent drought period. This was supported by Hofmann et al., (2003a), who found that UV-B increased leaf water potential of white clovers by apparent amount under drought conditions. This improvement of drought tolerance by UV-B was attributed to the UV-B-induced changes of leaf morphology and different growth reduction rate among plant organs (Hofmann et al., 2003a; Rozema et al., 1997). The decreased stomata conductance by UV-B led to a reduction of transpiration, which eliminated the water vapour loss from leaves. This was an advantage for the adaptation to the subsequent drought stress. UV-B also led to an increase of root : shoot ratio, which enhanced the water uptake from the soil, and hence improved the water potential in leaves (Hofmann et al., 2001). Further more, UV-B significantly increased leaf damage and leaf senescence across clovers, which reduced leaf area, and consequently decreased the water vapor loss from transpiration before the subsequent drought stress. This could be supported by the increased water potential in Tienshan clover under UV-B treatment with well-water conditions.

Especially, for Caucasian clover, UV-B increased the total aerial DM production under drought conditions. This was partially due to less leaf damage and leaf senescence in Caucasian clover under UV-B treatment. Particularly, this result reflected that UV-B might lead to a higher improvement of drought tolerance in Caucasian clover than in white clover.

In addition, Hofmann et al., (2003a) reported that UV-B increased proline levels, which played a role in decreasing the water solute potential for osmotic adjustment under water-deficit condition, in white clover under well-water treatment. However, in our experiment, UV-B did not significantly decrease the water solute potential under well-water conditions (Figure 3 and 4), which indicated that the pathways of adjusting physiological response would differ between UV-B radiation and water stress. Further more, the synthesis of solute species proline, triggered by the bio-signal of UV-B, would be more sensitive, explaining the mutual enhancement of UV-B and drought tolerance (however, this was considered as the minor mechanism as compared to the discussion below), whereas other compatible solute species involving in osmotic adjustment would be less sensitive to UV-B (UV-B even tended

to eliminate the synthesis of some solute species revealed by the slight increase of water solute potential in Caucasian clover in Figure 3 and by the increased water solute potential in Tianshan clover by 27% (not listed) during well-water conditions). Nevertheless, the significantly increased water solute potential by UV-B radiation during drought conditions, which has been previously explained by the UV-B-induced changes of leaf morphology and different growth reduction rate among plant organs (Hofmann et al., 2003a; Rozema et al., 1997), would be attributed to the UV-B-induced elimination of synthesis of some solute species in cell as well, but this lead to positive effects on DM production, because it is hypothesized that the accumulation of compatible solutes during water stress condition (without UV-B stress) would be usually excessive for maintaining the cell turgor. This hypothesis will be further discussed from the prospective of biochemistry cycling regulated by enzyme in my next article (Liu Huan, 2024).

The main limitation in this experiment might be due to the controlled environment, which isolated the individual stress from the field conditions. For example, controlled environment might lead to disproportionate environment conditions such as high ratios of UV-B to PPF (Hofmann et al., 2003a).

5.Conclusion

In our experiment, the total aerial biomass yield in both white clover and Caucasian clover was significantly decreased by drought. However, Caucasian and Tienshan clover showed higher drought tolerance in terms of osmotic adjustment. Consequently, both Caucasian clover and Tienshan clover had less UV-B sensitivity. Within white clover species, Tienshan clover, which had less UV-B sensitivity and higher tolerance to drought, was less productive and had a original habit with multiple forms of stress. Further more, the combination of drought and UV-B stress helped clovers improve the adaptation to each of them. Via the inter-specific comparison, UV-B might lead to a higher improvement of drought tolerance in Caucasian clover than in white clover. These findings have significantly indicative meanings for the pasture production in NZ, where there is a high level of UV-B radiation.

6.Acknowledge

The data of this article sources from the course of ‘Plant Physiology’ in Lincoln University, 2007, New Zealand.

References

1.Barbour, M., Caradus, J. R., Woodfield, D. R., & Silvester, W. B., (1999). Water stress and water use efficiency of ten white clover cultivars. Grassland Research and Practice Series (6): 159-162. https://doi.org/10.33584/rps.6.1995.3359

2.Black A. D., Moot, D. J., & Lucast, R. J., (2006). Spring and autumn establishment of Caucasian and white clovers with different sowing rates of perennial ryegrass. Grass and Forage Science, 61, 430-441. https://doi.org/10.1111/j.1365-2494.2006.00552.x

3.Delauney.A.J.,Verma,D.P.S., Proline biosynthesis and osmotic regulation in plants[J]. Plant J, 1993, 4(2):215-223. https://doi.org/10.1046/j.1365-313X.1993.04020215.x

4.Hofmann, R.W., Campbell, B. D., Bloor, S. J., Swinny, E. E., Markham, K. R., Ryan, K. G., & Fountain, D. W. (2003). Responses to UV-B radiation in Trifolium repens L.-physiological links to plant productivity and water availability. Plant Cell and Environment (2003) 26, 603-612. https://doi.org/10.1046/j.1365-3040.2003.00996.x

5.Hofmann, R. W., Campbell, B. D., & Fountain, D. W. (2003). Sensitivity of white clover to UV-B radiation depends on water availability, plant productivity and duration of stress. Global Changes Biology (2003) 9, 473-477. https://doi.org/10.1046/j.1365-2486.2003.00578.x

6.Hofmann, R. W., Campbell, B. D., Fountain, D. W., Jordan, B. R., Greer D. H., Hunt,D. Y., & Hunt, C.L., (2001). Multivariate analysis of intraspecific responses to UV-B radiation in white clover (Trifolium repens L.). Plant Cell and Environment (2001) 24, 917-927. https://doi.org/10.1046/j.1365-3040.2001.00749.x

7.Hofmann, R. W., Swinny, E. E., Bloor, S. J., Markham, K. R., Ryan, K. G., Campbell,B. D., Jordan, B. R., & Fountain, D. W. (2000). Responses of nine trifolium repens L. Populations to Ultraviolet-B radiation: Differential flavonol glycoside accumulation and biomass production. Annals of Botany 86: 527-537, 2000. https://doi.org/10.1006/anbo.2000.1216

8.Kopu II White Clover, (2006). Ampac seed company. Retrieved April 11th , 2007. from: http://www.ampacseed.com/kopu2.htm

9.Lindroth, R. L., Hofmann, R.W., Campbell, B. D., McNabb W.C., & Hunt, D. Y., (2000). Population differences in Trifolium repens L. response to ultraviolet-B radiation: foliar chemistry and consequences for two lepidopteran herbivores. Oecologia (2000) 122: 20-28. https://doi.org/10.1007/PL00008831

10.Nogues, S., Allen, D. J., Morison, J. I. L., & Baker, N. R. (1999).Characterization of stomatal closure caused by Ultraviolet-B radiation. Plant Physiology, October 1999, Vol. 121, pp. 489-496. https://doi.org/10.1104/pp.121.2.489

11.Rozema, J., Staaij, J. Van de., Bjorn, L. O., & Caldwell, M. (1997). UV-B as an environmental factor in plant life: stress and regulation. TREE vol. 12, no. 1 January 1997. https://doi.org/10.1016/S0169-5347(96)10062-8

12.Taiz, L., & Zeiger, E., (2006). Plant physiology, 4th ED. Loughborough, UK: Cambridge University Press.

13.Liu Huan (2024). Original Review of Environmental Physiology: Photosynthesis and Systematic Metabolomics. Journal of Biological Sciences (ISSN 2958-4035).2024(07). https://doi.org/10.58473/JBS0024