

## Photosynthetic adaptation of two semi-arid species *Gethyllis* (Kukumakranka) to drought-and-shade stress

C.W. Daniels, W.T. Mabusela, J.L. Marnewick, A.J. Valentine

### Abstract:

*Gethyllis multifolia* and *Gethyllis villosa* are winter-growing, summer-blooming, deciduous and bulbous geophytes that grow naturally in the semi-arid 'Succulent Karoo Biome' of South Africa. *G. multifolia* is threatened in its natural habitat and resides in the 'Vulnerable' category of the 'Red Data List of Southern African Plants'. Previous investigations suggested that *G. multifolia* is more sensitive to drought stress than *G. villosa* and that both species adopted certain morphological changes in their leaves during shade stress. Current models indicate that this biome is being exposed to increasingly drier conditions and shading from encroaching indigenous plant species. In this study, the photosynthetic gas exchange responses of both species to drought and shade stresses were investigated and the 'Vulnerable' conservation status of *G. multifolia*. This investigation found that during drought stress *G. villosa* had a more enhanced photosynthetic performance than *G. multifolia* which appears not to be related to foliar adaptations such as specific leaf mass (SLM), but to the *G. villosa*'s leaves maintaining their stomatal conductance ( $G_s$ ), photosynthetic light compensation (LCP) and photon yields. Furthermore, during shade stress *G. villosa* also had an improved photosynthetic performance by not altering its photosynthetic LCP during reduced light conditions. It can be concluded that *G. multifolia* has a lower capacity than *G. villosa* to adapt its photosynthetic apparatus to changing environments such as increasing drought and shaded conditions. This may be a contributing factor to the threatened conservation status of *G. multifolia*.

### 1. Introduction

The genus *Gethyllis* (family: Amaryllidaceae), indigenous to South Africa, consists of 37 currently accepted species and subspecies (Müller-Doblies, 1986). *Gethyllis* species have medicinal properties (Liltved, 1992; Elgorashi and Van Staden, 2003) and are characterized by four distinct growth phases. The plants that thrive under full sun conditions, are winter-growing, summer-blooming, deciduous and bulbous geophytes (Du Plessis and Delpierre, 1973; Manning et al., 2002). *Gethyllis multifolia* L. Bolus and *Gethyllis villosa* Thunb. grow naturally in the 'Succulent Karoo Biome' of South Africa, which is primarily characterized by low to high winter rainfall and extreme summer aridity. The rainfall varies between 20 and 290 mm per year and during summer the temperatures can be in excess of 40 °C.

*G. multifolia* is threatened in its natural habitat and is listed in the 'Vulnerable' category of the 'Red Data List of Southern African Plants' and 'World Conservation Union List of Plants' (Hilton-Taylor, 1996; IUCN, 1998), while *G. villosa* is not threatened in the same habitats.

In their natural habitat, both these species encounter environmental limitations such as increasing drought stress (Rutherford et al., 1999; Midgeley et al., 2002; Von Maltitz et al., 2006) and light restrictions from shading caused by encroaching indigenous shrubs (Daniels, 2007). It has been observed that both *G. multifolia* and *G. villosa* are limited by drought stress and this phenomenon appears to have a more significant effect on *G. multifolia* (Daniels, 2007). According to preliminary work by Daniels (2007), *G. multifolia* has impaired leaf and flower development during the growth and reproductive phases when exposed to dry conditions. These features are part of a survival strategy during harsh environmental changes (Du Plessis and Duncan, 1989). This concurs with other studies that drought stress increases the rate of pod abortion during the early stages of pod development in soybeans (Liu et al., 2003). The success of plants under stress conditions may be determined by their ability to control carbohydrate utilization for metabolic energy and their ability to allocate enough materials to their reproductive phase (Nielsen et al., 2001). According to Pelleschi et al. (1997) and Kim et al. (2000), drought stress generally decreases the photosynthetic rate and disrupts carbohydrate metabolism in leaves and therefore could increase the rate of reproductive abortion.

In addition to drought stress, *Gethyllis* plants may also encounter light stress in the form of shading from encroaching indigenous shrubs (Daniels, 2007). This encroachment from the invasive shrub, *Galenia africana* is also posing a growing threat in the natural habitat of *G. multifolia*, where many individual plants are found growing in the shade of this 1–1.5 m tall, shrubby species (Daniels, 2007; Klaasen et al., 2009). A previous investigation (Daniels, 2007) revealed that under controlled shade conditions both species produced thinner leaves with no natural spiraling, which is a departure from the natural characteristic of *Gethyllis* species (Esler and Rundel, 1998). The survival and growth of *Gethyllis* species in a changing light environment may be dependent on their shade-tolerance levels, as found for other plants (Daniels et al., 1979; Lorimer, 1983). This concurs with previous work that shade stressed plants can respond to low irradiance via altered leaf morphology for more efficient irradiance capture (Givnish, 1998; Smith and Huston, 1989; Oliver and Larson, 1996) and enhanced photosynthetic investment (Brouwer, 1962; Poorter and Nagel, 2000).

Since both bulbous species occur in a semi-arid area, which is being threatened by progressive aridity due to climate change and increased shading from invasive species, the aim of this work is to therefore investigate the capacity for photosynthetic adaptation of both species to these environmental changes.

## **2. Materials and methods**

### **2.1 Plant materials**

*G. multifolia* and *G. villosa* bulbs were identified by both the curator and resident horticulturist, and compared to living collected samples in the Karoo National Biodiversity

Garden (KNBG) (Worcester, Western Cape, South Africa). The KNBG has a keen interest in the declining numbers of *G. multifolia*, therefore permission was granted to collect samples for the research project from an area where new roads and sewerage lines were planned through the natural habitat of both species. Mature bulbs of both species were collected after their winter growth phase (March to mid-August), from their natural habitat. For conservation purposes and due to the threatened status of *G. multifolia*, the exact location of these species is omitted from this investigation. The bulbs of both species (n = 10 per species per treatment) were potted up in 15 cm nursery pots in sandy, clay soil (pH 4.3–4.4) from the natural habitat. The bulbs were grown under outdoor conditions for 12 months which included one dormant phase (6 months—spring and summer) and one growth phase (6 months—autumn and winter) at the nursery of the Department of Horticultural Sciences, Cape Peninsula University of Technology (CPUT), Cape Town. Table 1 indicates the average rainfall and daily temperatures for the Cape Town area where plants were grown and also indicates the higher rainfall and lower temperatures for the growth phase and lower rainfall and higher temperatures for the dormant phase. Weather data for the Cape Town area (Table 1) was supplied by the South African Weather Bureau (Cape Town WO 0021178A3).

## 2.2. Environmental stresses

Plant samples which represented the control (n = 10 per species) were grown under full sun and irrigated by the ambient rainfall of the Western Cape (Table 1). The mean photosynthetic photon flux density (PPFD) (converted from lux to PPFD) on cloudless days at 12h00 was  $1825 \pm 63 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Temperatures around the plant samples varied from 8 to 24 °C and the relative humidity from 36 to 100%. The PPFD for all treatments was measured with a Toptronic T630 digital light meter (Spraytech, Bellville, Western Cape, South Africa) and the temperatures and relative humidity were measured with a Majortech MT669 digital relative humidity/temperature meter (Spraytech, Bellville, Western Cape, South Africa).

**Table 1**  
The average rainfall (mm) and average daily minimum (min.) and maximum (max.) temperatures (°C) for the Cape Town area (Western Cape, South Africa). Each value was obtained by calculating the mean for two years  $\pm$  SE (n = 2). The data was provided by the South African Weather Bureau and was recorded at the Cape Town weather office (0021178A3).

Month	Mean min. temp. (°C)	Mean max. temp. (°C)	Mean rainfall (mm)
January	17.3 $\pm$ 0.35	27.9 $\pm$ 0.25	0.3 $\pm$ 0.2
February	16.4 $\pm$ 0.15	27.1 $\pm$ 0.65	20.2 $\pm$ 14.2
March	14.2 $\pm$ 0.05	25.9 $\pm$ 0.55	11.7 $\pm$ 8.2
April	12.4 $\pm$ 0.4	23.4 $\pm$ 0.6	47.9 $\pm$ 33.8
May	9.5 $\pm$ 0.2	20.5 $\pm$ 0.6	108.9 $\pm$ 77.0
June	8.1 $\pm$ 0	19.0 $\pm$ 1.1	78.8 $\pm$ 55.6
July	7.9 $\pm$ 0.9	17.3 $\pm$ 0.35	111.5 $\pm$ 78.8
August	8.1 $\pm$ 0.15	17.8 $\pm$ 0.05	78.9 $\pm$ 55.8
September	9.8 $\pm$ 0.55	20.4 $\pm$ 0.55	19.1 $\pm$ 13.5
October	11.7 $\pm$ 0.4	22.9 $\pm$ 0.45	27.9 $\pm$ 19.8
November	13.4 $\pm$ 0.55	23.4 $\pm$ 1.2	39.3 $\pm$ 27.8
December	15.6 $\pm$ 0.15	25.7 $\pm$ 0.65	14.3 $\pm$ 10.1

Plant samples which represented the drought stressed samples (n = 10 per species) were grown under full sunlight and covered with a 6 mm clear glass sheet, placed 300 mm above the plants. The PPFD, temperature and relative humidity environmental conditions were similar to those of the control. The drought stressed plants were

irrigated at a rate of 30% field capacity once a month with de-ionized water (Mortimer et al., 2003).

Plant samples which represented the shade stressed samples (n = 10 per species) were grown under a shade structure covered with 80% neutral black shade cloth (Alnet, Epping, Western Cape, South Africa), which has a neutral effect on light quality (Yates, 1989; Duan et al., 2005).

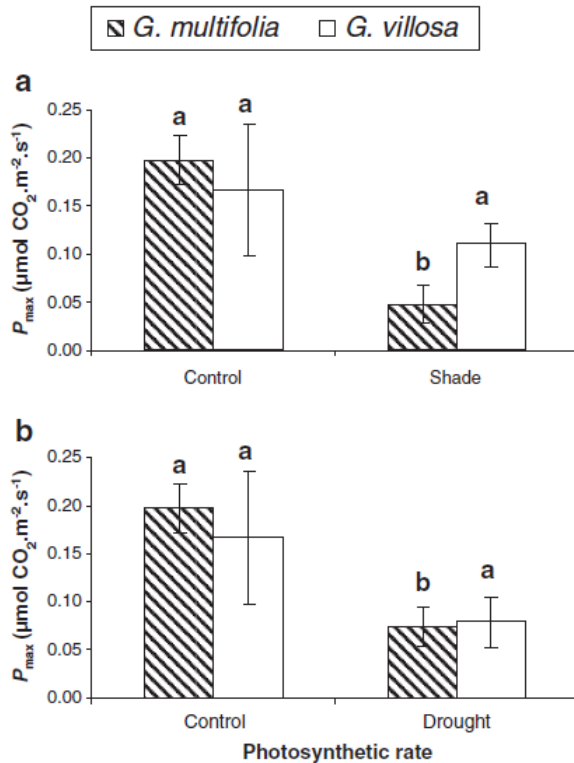


Fig. 1. Leaf photosynthetic rates ( $P_{max}$ ) of *G. multifolia* and *G. villosa* during shade (a) and drought (b) stress. Readings were taken at full leaf emergence during the peak of the growth phase (June). Different letters indicate significant differences between means  $\pm$  SE of treatments ( $P \leq 0.05$ ,  $n = 4$ ), comparisons were done for each species only.

During the experimental period, the mean PPFD on cloudless days at 12h00 was  $365 \pm 26 \mu\text{mol m}^{-2} \text{s}^{-1}$  and was approximately 20% of full sunlight. The temperature around the shade stressed plant samples was  $\sim 1-2^\circ\text{C}$  lower than that of the control, and the relative humidity 2-4% higher than that of the control. The plant samples under shade stress treatment were also irrigated by the ambient rainfall of the Western Cape (Table 1). The readings of all the environmental conditions under all treatments were taken daily at the following time intervals: 09h00, 12h00 and 15h00.

### 2.3. Physiological responses

An infra-red gas analyzer (Licor, Li-6400 Portable photosynthesis system, Lincoln, Nebraska, USA) coupled to a leaf chamber, was used to measure the photosynthetic rates ( $P_{max}$ ), leaf dark respiration rates ( $D_r$ ), stomatal conductance ( $G_s$ ) and transpiration rates ( $E$ ) of the plant samples during the growth phase. The readings were taken on fully expanded leaves at the peak of the growth season during the month of June. *G. villosa* plants have flat leaves ( $\pm 5$  mm in diameter) and a section of one leaf blade per

plant was used for the readings. *G. multifolia* plants consist of thin needle-like leaves ( $\pm 1\text{--}2$  mm in diameter) and 6–8 leaf sections per plant were used for the readings. The infra-red gas analyzer was set to take the net photosynthetic rate readings at the following light photosynthetic photon flux densities (PPFD): 0, 50, 150, 350, 500, 750, 950, 1200 and 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Six readings were taken per PPFD and readings were recorded from four plants per specie per treatment. The corresponding temperature for the photosynthetic rate readings in the leaf chamber was set at 25 °C and the relative humidity 55– 75%. Linear regression analysis was performed on data within the light-limited part of the light response curve to calculate the apparent photon yield. Photosynthetic water-use efficiency (PWUE) was calculated as  $P_{\text{max}}/E$ .

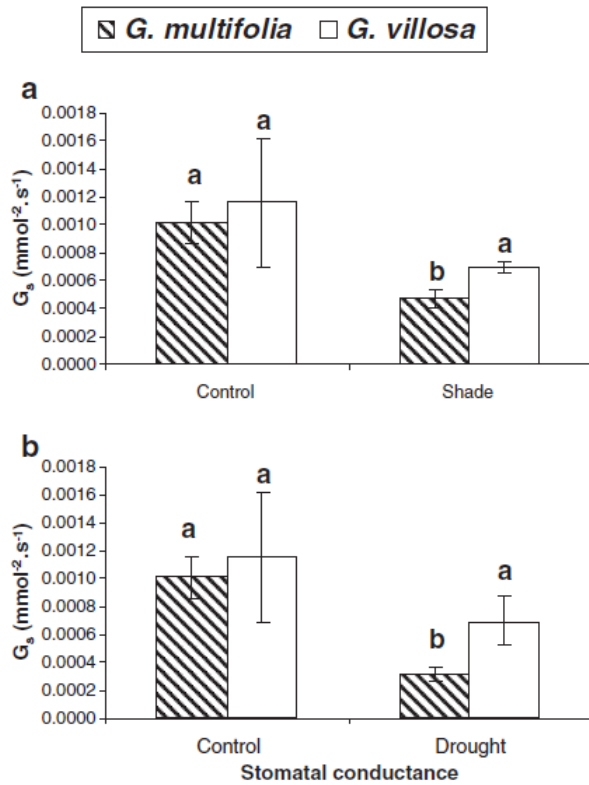


Fig. 2. Stomatal conductance ( $G_s$ ) of *G. multifolia* and *G. villosa* during shade (a) and drought (b) stress. Readings were taken at full leaf emergence during the peak of the growth phase (June). Different letters indicate significant differences between means  $\pm$  SE of treatments ( $P \leq 0.05$ ,  $n = 4$ ), comparisons were done for each species only.

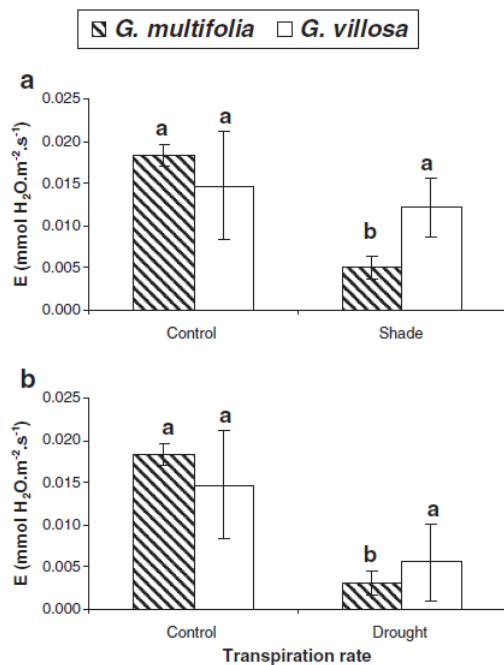


Fig. 3. Transpiration rates (E) of *G. multifolia* and *G. villosa* during shade (a) and drought (b) stress. Readings were taken at full leaf emergence during the peak of the growth phase (June). Different letters indicate significant differences between means  $\pm$  SE of treatments ( $P \leq 0.05$ ,  $n = 4$ ), comparisons were done for each species only.

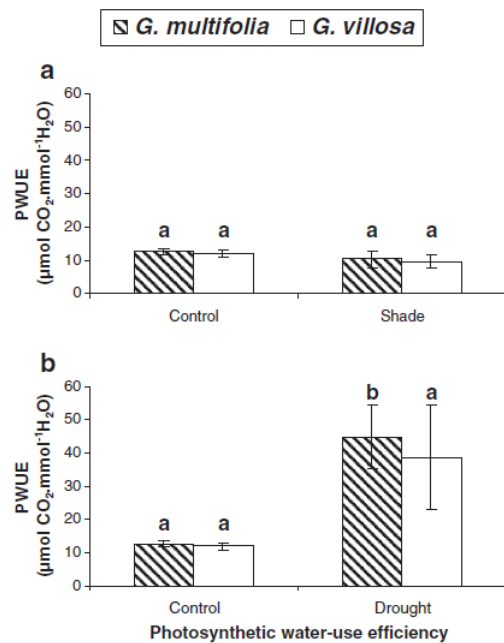


Fig. 4. Water-use efficiency (PWUE) of *G. multifolia* and *G. villosa* during shade (a) and drought (b) stress. Readings were taken at full leaf emergence during the peak of the growth phase (June). Different letters indicate significant differences between means  $\pm$  SE of treatments ( $P \leq 0.05$ ,  $n = 4$ ), comparisons were done for each species only.

## 2.4. Statistical analysis

Significant differences of the means for each species, were separately tested under drought and shade stress. The means were separated using a post hoc Fisher's Protected LSD, multiple comparison test (SuperANOVA, version. 6.11 for Macintosh Abacus Concepts, USA). Different letters indicate significant differences between treatments ( $P \leq 0.05$ ,  $n = 4$ ), and superscript numbers indicate the comparisons for each species only (1 = *G. multifolia*; 2 = *G. villosa*).

### 3. Results

During shade (Fig. 1a) and drought (Fig. 1b) stress, *G. multifolia* had a reduction in its light saturated photosynthetic rates ( $P_{max}$ ), while the  $P_{max}$  for *G. villosa* remained unchanged. These photosynthetic patterns of both species, concur with their respective stomatal conductance ( $G_s$ ) (Fig. 2a, b) and transpiration rates ( $E$ ) (Fig. 3a, b).

In spite of the differences in photosynthetic shade responses in *G. multifolia* and *G. villosa*, the photosynthetic water-use efficiencies (PWUE) remained unchanged in both species during shade stress (Fig. 4a). However, *G. multifolia* had an increase in PWUE under drought stress, while *G. villosa* remained unchanged (Fig. 4b).

The decline in the  $P_{max}$  of *G. multifolia* in response to drought and shade stress, is not related to leaf morphological adaptations such as specific leaf mass (SLM) (Fig. 5a, b), but rather to leaf photochemistry and the associated pigments. In this regard, the *G. multifolia* plants had an increase in the leaf compensation point (LCP) under drought and shade stress, whereas the LCP of *G. villosa* remained unchanged (Fig. 6a, b). Furthermore, the apparent photon yield of *G. multifolia* declined sharply during shade and drought stress, while *G. villosa* remained unaffected (Fig. 7a, b).

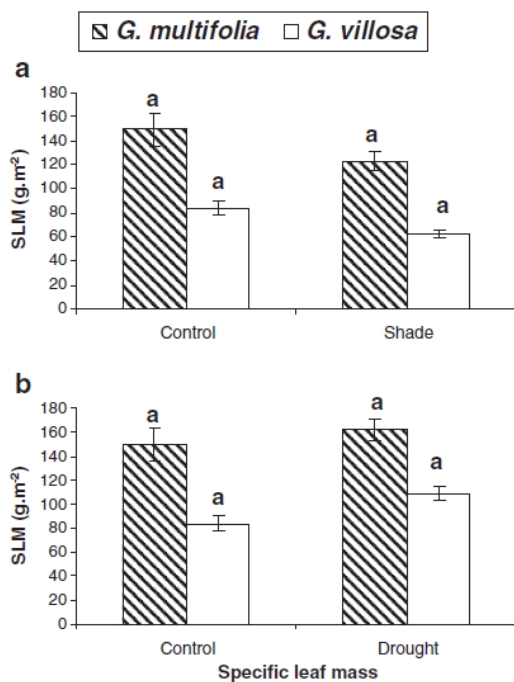


Fig. 5. Specific leaf mass (SLM) of *G. multifolia* and *G. villosa* during shade (a) and drought (b) stress. Readings were taken at full leaf emergence during the peak of the growth phase (June). Different letters indicate significant differences between means  $\pm$  SE of treatments ( $P \leq 0.05$ ,  $n = 4$ ), comparisons were done for each species only.

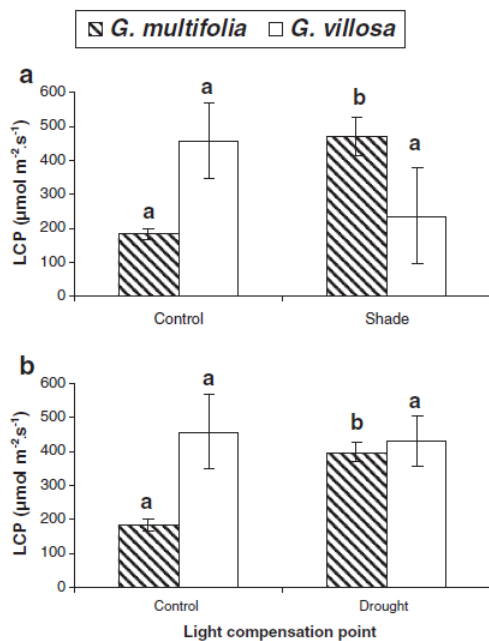


Fig. 6. Light compensation points (LCP) of *G. multifolia* and *G. villosa* during shade (a) and drought (b) stress. Readings were taken at full leaf emergence during the peak of the growth phase (June). Different letters indicate significant differences between means  $\pm$  SE of treatments ( $P \leq 0.05$ ,  $n = 4$ ), comparisons were done for each species only.

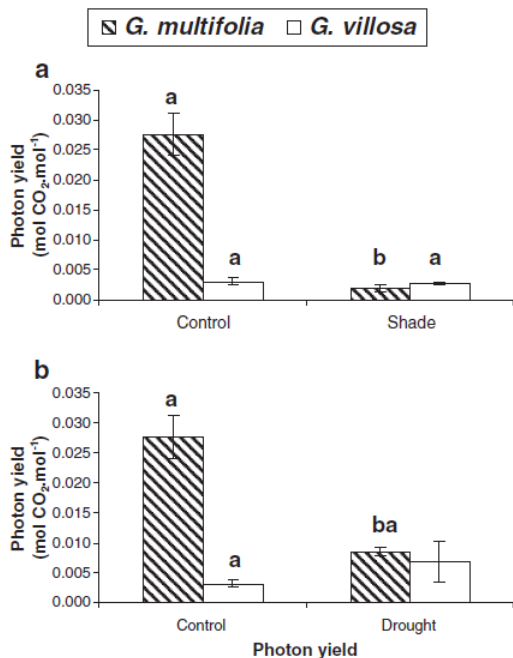


Fig. 7. Leaf photon yield of *G. multifolia* and *G. villosa* during shade (a) and drought (b) stress. Readings were taken at full leaf emergence during the peak of the growth phase (June). Different letters indicate significant differences between means  $\pm$  SE of treatments ( $P \leq 0.05$ ,  $n = 4$ ), comparisons were done for each species only.

These responses were not associated with an alteration in the dark respiratory costs of *G. multifolia* and *G. villosa* leaves (Fig. 8a, b). However, the ratio of photosynthesis to dark respiration indicates that although there was no change in *G. villosa*, that there is a significant decline in *G. multifolia* during shade and drought stress (Fig. 8c, d).

#### 4. Discussion

During drought stress, the ability of leaf photosynthesis to adapt to dry conditions depends on a suite of alterations relating to leaf morphology, stomatal control and



photochemistry. Under drought stress, *G. villosa* had a better photosynthetic performance than *G. multifolia*, which appears not to be related to foliar adaptations such as specific leaf mass (SLM), but to *G. villosa*'s leaves maintaining their stomatal conductance ( $G_s$ ), photosynthetic light compensation (LCP) and photon yields during the dry periods. Stomatal control of photosynthesis is a well-known adaptation in previous work from various ecosystems (Winter and Schramm, 1986; Duan et al., 2005; Valliyodan and Nguyen, 2006; Musila et al., 2009).

In contrast, the inability of *G. multifolia* plants to maintain their photosynthetic performance under drought conditions is underpinned by both stomatal and photochemical factors. In *G. multifolia* plants, the increase in photosynthetic LCP and the decline in apparent photon yield under drought conditions indicate that these leaves are not able to efficiently utilize light energy for photosynthesis. Similar photosynthetic responses were reported for other spring geophytes, *Scilla bifolia* and *Podophyllum peltatum* (Popovic et al., 2006; Constable et al., 2007). Drought-induced responses in plant cells are characterized by a higher net carbon gain during shade.

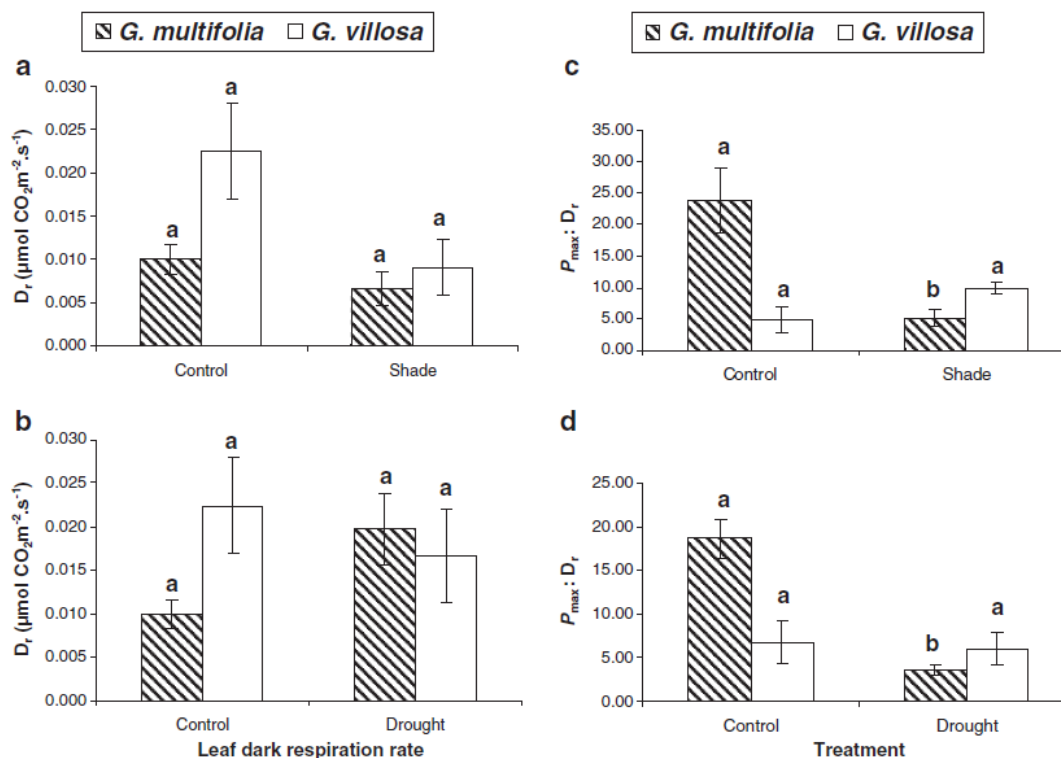


Fig. 8. Leaf dark respiration rates ( $D_r$ ) of *G. multifolia* and *G. villosa* during shade (a) and drought (b) stress and ratio of photosynthesis ( $P_{max}$ ) to dark respiration ( $D_r$ ) under shade (c) and drought (d) stress. Readings were taken at full leaf emergence during the peak of the growth phase (June). Different letters indicate significant differences between means  $\pm$  SE of treatments ( $P \leq 0.05$ ,  $n = 4$ ), comparisons were done for each species only.

These findings indicate that *G. multifolia*'s inability to acclimate to shade is drastically compounded by the lower net gain in carbon during shade. Similarly, in *Tradescantia albiflora*, a reduction in the photosynthetic rate during low light environments, resulted in a lower net carbon gain (Chow et al., 1991).

## 5. Conclusion

These findings indicate that *G. villosa* plants are better able to adapt their  $P_{max}$  to drought and shade conditions, compared to *G. multifolia*. The reduced ability of *G.*

multifolia to adapt to a wider range of environmental extremes such as drought and shade conditions may contribute to its threatened conservation status in this environment. These findings indicate that *G. villosa* plants are better able to adapt their Pmax to drought and shade conditions, compared to *G. multifolia*. The reduced ability of *G. multifolia* to adapt to a wider range of environmental extremes such as drought and shade conditions may contribute to its threatened conservation status in this environment.

### **Acknowledgments**

The authors acknowledge the Cape Peninsula University of Technology (CPUT) and the Department of Horticultural Sciences (CPUT) for financial assistance and use of the nursery and laboratory facilities. Gratitude is expressed to Naomi Daniels for the preparation of the plant samples.

## References

- Brouwer, R., 1962. Distribution of dry matter in the plant. *Netherlands Journal of Agricultural Science* 10, 361–376.
- Chow, W.S., Adamson, H.Y., Anderson, J.M., 1991. Photosynthetic acclimation of *Tradescantia albiflora* to growth irradiance: lack of adjustment of light-harvesting components and its consequences. *Physiologia Plantarum* 81, 175–182.
- Constable, J.V.H., Pepper, B.J., De Nicola, D.M., 2007. Temporal and light-based changes in carbon uptake and storage in the spring ephemeral *Podophyllum peltatum* (Berberidaceae). *Environmental and Experimental Botany* 60, 112–120.
- Daniels, C.W., 2007. A Study of the Propagation and Cultivation of *Gethyllis multifolia* and *G. villosa*. Cape Peninsula University of Technology, Bellville, Cape Town, South Africa 65–71 (MTech dissertation).
- Daniels, T.W., Helms, J.A., Baker, F.S., 1979. *Principles of Silviculture*, second ed. McGraw-Hill, New York 119–121.
- Du Plessis, N., Delpierre, G., 1973. Indigenous flower pride: *Kukumakranka*. *Landbouweekblad*. 37–39 (August).
- Du Plessis, N., Duncan, G., 1989. *Bulbous Plants of Southern Africa*. Tafelberg Publishers, Cape Town, South Africa 104–107.
- Duan, B., Lu, Y., Yin, C., Junntila, O., Li, C., 2005. Physiological responses to drought and Shade in two contrasting *Picea asperata* populations. *Physiologia Plantarum* 124, 476–484.
- Elgorashi, E.E., Van Staden, J., 2003. Pharmacological screening of six Amaryllidaceae species. *Journal of Ethnopharmacology* 90, 27–32.
- Esler, K.J., Rundel, P.W., 1998. Unusual geophytes of the succulent Karoo: how form can relate to function. *Veld & Flora* 84, 6–7.
- Galmés, J., Medrano, H., Flexas, J., 2007. Photosynthetic limitations in response to water stress and recovery in Mediterranean plants with different growth forms. *New Phytologist* 175, 81–93.
- Givnish, T.J., 1998. Adaptation to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiology* 15, 63–92.
- Hilton-Taylor, C., 1996. *Red Data List of Southern African Plants*. National Biodiversity Institute, Cape Town, South Africa 57–58.
- Ierna, A., Mauromicale, G., 2006. Physiological and growth response to moderate water deficit of off-season potatoes in a Mediterranean environment. *Agricultural Water Management* 82, 193–209.
- IUCN, 1998. *Red List of Threatened Plants*. IUCN, World Conservation Union, Cambridge, UK 617–618.
- Kim, J.Y., Mahe', A., Brangeon, J., Prioul, J.L., 2000. A maize vacuolar invertase, IVR2, is induced by water stress. Organ/tissue specificity and diurnal modulation of expression. *Plant Physiology* 124, 71–84.
- Klaasen, J., Knoetze, H., Van Wyk, G., Mali, T., Knowles, C., 2009. Biofuels from indigenous energy crops: a feasibility study. *African Crop Science Conference Proceedings* 9, 735–738.
- Liltved, W.R., 1992. The *Kukumakranka*, past and present. *Veld & Flora* 78, 104–106.
- Liu, F., Andersen, M.N., Jensen, C.R., 2003. Loss of pod set caused by drought stress is associated with water status and ABA content of reproductive structures in soybean. *Functional Plant Biology* 30, 271–280.

- Lorimer, C., 1983. A test of the accuracy of shade-tolerance classification based on physiognomic and reproductive traits. *Canadian Journal of Botany* 61, 1595–1598.
- Manning, J., Goldblatt, P., Snijman, D., 2002. *The Color Encyclopedia of Cape Bulbs*. Timber Press, Cambridge, UK 147–149.
- Midgeley, G.F., Hannah, L., Millar, D., Rutherford, M.C., Powrie, L.W., 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biodiversity* 11, 445–451.
- Mortimer, P., Swart, J.C., Valentine, A.J., Jacobs, G., Cramer, M.D., 2003. Does irrigation influence the growth, yield and water use efficiency of the protea hybrid ‘Sylvia’ (*Protea susannae* X *Protea eximia*)? *South African Journal of Botany* 69, 1–9.
- Müller-Doblies, D., 1986. Enumeration. *Willdenowia* 15, 465–471.
- Musila, C.F., Arnolds, J.L., Van Heerden, P.D.R., Kgope, B.S., 2009. Mechanisms of photosynthetic and growth inhibition of a southern African geophyte *Tritonia crocata* (L.) Ker. Gawl. by an invasive European annual grass *Lolium multiflorum* Lam. *Environmental and Experimental Botany* 66, 38–45.
- Nielsen, K.L., Eshel, A., Lynch, J.P., 2001. The effect of phosphorus availability on the carbon economy of contrasting common bean (*Phaseolus vulgaris* L.) genotypes. *Journal of Experimental Botany* 52, 329–339.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. John Wiley and Sons, New York, USA 137–141.
- Pelleschi, P., Rocher, J.P., Prioul, J.L., 1997. Effect of water restriction on carbohydrate metabolism and photosynthesis in mature maize leaves. *Plant, Cell & Environment* 20, 493–503.
- Poorter, H., Nagel, O.W., 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO<sub>2</sub>, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology* 27, 595–607.
- Popovic, Z., Mijovic, A., Karadzic, B., Mijatovic, M., 2006. Response of growth dynamics of two spring geophytes to light regime in a lime-beech forest. *Journal of Integrative Plant Biology* 48, 527–535.
- Rutherford, M.C., Midgeley, G.F., Bond, W.J., Powrie, L.W., Roberts, R., Allsopp, L., 1999. *Plant Biodiversity: Vulnerability and Adaptation Assessment*. South African Country Study on Climate Change. National Biodiversity Institute, Cape Town, South Africa 34–36.
- Smith, T., Huston, M., 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetatio* 83, 49–69.
- Tabaeizadeh, Z., 1998. Drought-induced responses in plant cells. *International Review of Cytology* 182, 193–247.
- Valliyodan, B., Nguyen, H.T., 2006. Understanding regulatory networks and engineering for enhanced drought tolerance in plants. *Plant Biology* 9, 189–195.
- Von Maltitz, G.P., Scholes, R.J., Erasmus, B., Letsoalo, A., 2006. Adapting conservation strategies to accommodate impacts of climate change in southern Africa. AIACC Working Paper, 35, pp. 2–3.
- Wang, G.G., Bauerle, W.L., Mudder, B.T., 2006. Effects of light acclimation on the photosynthesis, growth, and biomass allocation in American chestnut (*Castanea dentata*) seedlings. *Forest Ecology and Management* 226, 173–180.

- Winter, K., Schramm, M.J., 1986. Analysis of stomatal and nonstomatal components in the environmental control of CO<sub>2</sub> exchange in leaves of *Welwitschia mirabilis*. *Plant Physiology* 82, 173–178.
- Yates, D.J., 1989. Shade factors of a range of shade cloth materials. *Acta Horticulturae* 257, 201–218.