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RESEARCH ARTICLE

# Physiology of African nightshades (*Solanum scabrum* Mill. and *Solanum villosum* Mill.) as Influenced by Soil Water Deficit

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## ABSTRACT

*Limitations in soil water impair physiological processes hence affecting bioproductivity which in turn lowers agricultural production thereby contributing to food insecurity. This research was designed to investigate the effects of soil water deficit on physiology of two African nightshades, (S. scabrum Mill. and S. villosum Mill) which are widely consumed in Kenya due to their high nutritional value. The experiment was conducted at Maseno University, Botanic Garden under glasshouse conditions. The experiment was laid out as a completely randomized design (CRD factorial, consisting of four treatments and three replications. The treatments were: T1-watering daily (control), T2-watering after every three days (the 3rd and 6th day), T3-watering the 9th day and T4-watering the 12th day. Stomatal conductance and leaf temperature were determined by use of a steady-state porometer. Chlorophyll fluorescence was determined by use of a portable fluorescence monitoring system. Soil moisture content was determined gravimetrically. Data collected was analyzed using MSTAT-C statistical computer package. Results showed that the two species of African nightshades were significantly ($p \leq 0.05$) affected by water deficit. Water deficit caused a decrease in stomatal conductance, chlorophyll fluorescence while leaf temperature increased with increasing soil water deficit except during the flowering stage.*

***Key Words:*** *African nightshades, physiology, soil water deficit, Maseno University*

## INTRODUCTION

In Africa, African nightshades *S. scabrum* Mill. and *S. villosum* Mill. are probably the second most important group of indigenous leaf vegetables after Amarathus (Schippers,2002): In some places they even surpass exotic vegetables such as cabbages and kales. In Kenya for instant more than 80% of its landmass is either arid or semi-arid (Luvaha *et al*. 2008), it is characterized by a high population of poor households whose entire livelihood depends on farming as an economic activity, and drought as worsened the poverty status, but Africa nightshades can perform well in areas with limited rainfall Schippers (2002): Therefore there is need of exploiting drought stricken areas by the production of water deficit tolerant African nightshade species. Despite the two species having the potential to alleviate poverty, malnutrition and contribute to food security, there is scarce literature on their physiological response to soil water deficit especially on parameters such as: chlorophyll fluorescence, leaf temperature and gas exchange. According to Colom and Vazzana (2003) water stress causes large reduction in leaf chlorophyll and carotenoid content, which directly affects photosynthesis rates, while Shaw and Laing (1966) observed a decrease in photosynthesis, when water content of the leaves was reduced by 5% to 15% below the maximum leaf saturation and photosynthesis stopped when leaves lost 50% of their maximum water content. The reduction in the soil moisture may lead to lower water content in the leaves, causing guard cells to lose turgor and hence the reduction of stomatal pores. An increase in stomatal resistance may lead to reduced water transport into the leaves, resulting in a decrease in stomatal conductance which in turn decreases transpiration and also limits photosynthesis (Pereira *et al.,* 2000):Mafakheri *et al.* (2010) reported that transpiration and stomatal conductance decreased in chicken pea cultivars exposed to drought stress as one of

the first response of plants to drought is stomatal closure restricting gas exchange between the atmosphere and the inside of the leaf.Environmental stresses that affect PSII efficiency leads to a characteristic decrease in the Fv/Fm ratio (Krause and Weis, 1991; Mamnouie *et al,* 2006): The Fv/Fm ratio is an indicator of plant stress resulting from damage to photosystem II (Demming and Björkman, 1987): Chlorophyll fluorescence is a useful tool for quantification of the effect of abiotic stress on photosynthesis (Krause and Weis 1991: Tezara *et al,* 2005).

Mustafa *et al.* (2011) worked on drip irrigated cotton and observed that water deficit decreased leaf expansion, photosynthesis, rate of leaf production, rate of transpiration, leaf senescence, nutritional quality and total yield in general. Stomatal closure and the resulting $CO_2$ deficit in the chloroplast is the main cause of decreased photosynthesis under water deficit (Flexas and Medrano, 2002), whereas others argue that low ATP content caused by a reduction in ATP synthase is the likely explanation for decreased photosynthesis under water deficit (Lawlor, 2002 and Tang *et al.,* 2002):Studies by Sikuku (2007) on NERICA rice varieties showed no significant effect in maximum photochemical efficiency of water stressed and non water stressed plants while studies conducted by Antelmo *et al.* (2010) observed a decrease in maximum photochemical efficiency in rice varieties. Thobile *et al.* (2010) investigated the response of local wild mustard (*Brassica* species) landraces to water stress and found out significant reductions in their morphology as a result of water stress, yet there is no information on physiological responseof African nightshades to soil water deficit. Muthomi and Musyimi (2009) investigated the growth response of African nightshade (*S. scabrum*) seedlings to water deficit, and observed reductions in growth as a result of water deficit. Efforts to determine differences in chlorophyll fluorescence as a result of water deficit in indigenous vegetables proved to be very limited and this formed the basis for the current research.

## MATERIALS AND METHODS

### 1. SOIL MOISTURE CONTENT

The soil moisture content was determined gravimetrically, whereby samples were scooped from the topsoil, 10 cm from the top using an auger between 10.00a.m and 11.00 a.m. During soil extraction care was taken to minimize root destruction. The scooped samples were immediately placed in polythene tubes (non-perforated) to avoid any moisture loss. The fresh weights ($W_1$) were taken using an electronic weighing balance (Denver instrument, Model XL-31000, Germany): Samples were then dried in an oven for 48 hours at $72^0$C and the dry weight ($W_2$) obtained. The measurements were done at every $13^{th}$ day after initiation of treatments and the average values obtained. The percentage water content (W) was calculated as demonstrated by (Nguyen *et al*., 2013):

$$W = \frac{W1-W2}{W1} \times 100 \quad \text{eqn 1.}$$

Where;

W1 = fresh weight
W2 = dry weight
W = percentage soil moisture content

The determination of field capacity was also done gravimetrically. The upper limit of field capacity was determined by watering soil thoroughly to drainage and then allowed to drain for 24 - 48 hours then soil samples were collected at 10 cm. The scooped samples were immediately placed in polythene tubes (non-perforated) to avoid any moisture loss. The fresh weights ($W_1$) were taken using an electronic weighing balance (Denver instrument, Model XL-31000, Germany): Samples were then dried in an oven for 48 hours at $72^o$C and the dry weight (W1) obtained, and the percentage water content (W) was calculated as shown in equation (1) above. The lower limit for plant water extraction (permanent wilting point) was determined by growing plants to flowering without limiting water intake, after which water intake was limited until permanent wilting was achieved. The percentage water content by

mass was calculated at the permanent wilting point. The levels of moisture deficit imposition for each treatment in terms of percentage were calculated as demonstrated by (Nguyen *et al*., 2013):

$$AWC = FC - WP \quad \text{.....eqn 2.}$$

$$\text{Water deficit} = \frac{FC - T1}{AWC} \times 100 \quad \text{... eqn 3}$$

Where;

AWC = available water content
WP = wilting point
FC = field capacity
T1 = treatments

## 2. LEAF STOMATAL CONDUCTANCE

Leaf stomatal conductance measurements were carried out using a leaf porometer (L1-1600, LICOR, Nebraska, USA): The measurements were conducted between 0900 and 1200 hours on fully sun exposed top leaf from an area of 0.7 $cm^2$. Measurements began from the day treatments were initiated and were done after every 12 days.

## 3. LEAF CHLOROPHYLL FLUORESCENCE AND TEMPERATURE

Chlorophyll fluorescence measurements were carried out using a portable fluorescence monitoring system, (Model FMS 2, Hansatech Instruments, Germany): Measurements began from the day treatments were initiated and were done after every twelve days.Four plants per treatment were sampled and measurements were done on the fourth fully expanded leaf. The leavesused for the measurements were dark adapted for 30 minutes using the dark adaptation clips and then illuminated for 6 seconds with actinic light to induce fluorescence. The initial fluorescence (Fo) and the maximum fluorescence (Fm) was measured and the variable fluorescence (Fv=Fm-Fo) and the Fv/Fo ratio was calculated (Sikuku *et al.,* 2010):

## 4. STATISTICAL ANALYSIS OF DATA

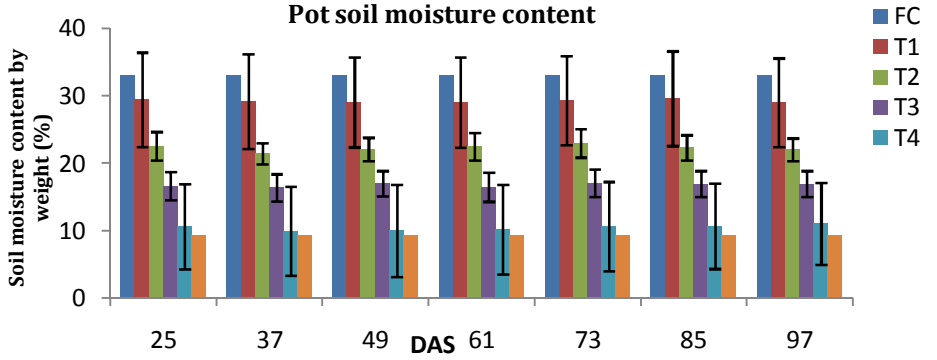
Data collected were subjected to Analysis of variance (ANOVA) using MSTAT-C statistical computer package (Michigan State University, MI): Mean separation was done using the Least Significant Difference (LSD) test at 5% level.

## RESULT

## 1. SOIL MOISTURE CONTENT

There was a significant difference in soil moisture content at($p \leq 0.05$) between all treatments in all days. T1 had the highest moisture content followed by T2, T3 and T4 respectively as shown in Fig 1.

**Fig.1:** The upper limit (FC) and lower limit (WP) levels for soil moisture content and the four treatments (T1, T2, T3 and T4) for *S. villosum* Mill. and *S. scabrum* Mill. grown under different watering regimes. (means of three replicates ± SE): LSD (0.05) T= 0.2506, 0.2282, 0.2326, 0.2889, 0.2125, 0.1419, 0.1931, for DAS 25, 37, 49, 61, 73, 85, and 97 respectively.



## 2. LEAF TEMPERATURE

There was a significant difference in leaf temperature at (p≤0.05) between the two species on days 25 and 37 while there was no observed significant difference at (p≤0.05) on days 49, 61, 73 and 85. All treatments were significant at (p≤0.05) on all days. There was a significant difference at (p≤0.05) between the species and the treatments in all days except on day 25. The highest temperatures were on T4 followed by T3, T2 and T1 respectively as shown in Table 1.

## GAS EXCHANGE PARAMETERS

## 1. STOMATAL CONDUCTANCE

There was no significant difference at (p≤0.05) in stomatal conductance between the two species. There was a significant difference at (p≤0.05) between the treatments in all days except day 25 and day 73. There was no significant difference at (p≤0.05) between the species and the treatments in all days the highest conductance was observed in T1, followed by T2, T3 and T4 respectively as shown in Table 2.

## 2. CHLOROPHYLL FLUORESCENCE

### 2.1. Fv/Fm

There was no significant difference at (p≤0.05) in Fv/Fm between the two species in all days except on 25. There was no significant difference at (p≤0.05) between the treatments in all days except on day 25 and day 61. There was no significant difference at (p≤0.05) between the species and the treatments in all days. The highest Fv/Fm ratio was observed in T1, followed by T2, T3 and T4 respectively in both species as shown in Table 3.

### 2.2. ETR

There was no significant difference (p≤0.05) in ETR between the two species in all days. The treatments were significant (p≤0.05) on days 25 and day 61 only. There was no significant difference at (p≤0.05) between the treatments and the species. There was no clear-cut trend in the ETR between the four treatments in both species. However, higher ETR was observed in the control (T1) on the day 25 followed by T2, T3 and T4 respectively in both species as shown in Table 4.

**Table 1:** The effect of water deficit on leaf temperature of *S. villosum* Mill *(S.v)* and *S.scabrum* Mill. (*S.s*) grown under different watering regimes (T1, T2, T3 and T4): Values represent means of three replicate

| Species | Treatment | Leaf temperature (°C) | | | | | |
|---|---|---|---|---|---|---|---|
| | | Treatments Days After Sowing (DAS) | | | | | |
| | | 25 | 37 | 49 | 61 | 73 | 85 |
| S.s | T1 | 33.2 | 33.87 | 28.67 | 27.47 | 31 | 31.17 |
| | T2 | 35.13 | 31.7 | 28.63 | 27.77 | 31.6 | 32.97 |
| | T3 | 34.63 | 30.53 | 29 | 27.87 | 32.23 | 34.6 |
| | T4 | 34.3 | 29.77 | 29.13 | 28.2 | 32.27 | 34.87 |
| S.v | T1 | 31.63 | 34.17 | 28.63 | 27.27 | 30.47 | 30.63 |
| | T2 | 35.07 | 32.067 | 28.57 | 27.63 | 31.63 | 32.73 |
| | T3 | 34.67 | 30.6 | 29 | 27.83 | 32.07 | 34.33 |
| | T4 | 34.43 | 29.5 | 29.07 | 27.83 | 32.2 | 34.9 |
| **LSD species** | | **0.31** | **0.15** | **0.05** | **0.06** | **0.11** | **0.17** |
| **LSD Treatments** | | **0.44** | **0.21** | **0.08** | **0.08** | **0.16** | **0.24** |

LSD (Least Significance Difference at 5% level of significance), T1-watering daily (control), T2-watering after every three days (the 3rd and 6th day), T3-watering the 9th day and T4-watering the 12th day.

**Table 2:** The effect of water deficit on stomatal conductance of *S. villosum* Mill *(S.v)* and *S.scabrum* Mill. (*S.s*) grown under different watering regimes (T1, T2, T3 and T4): Values represent meansof three replicate

| Species | Treatments | Stomatal conductance (mmol $m^{-2}$ $s^{-2}$) | | | | | |
|---|---|---|---|---|---|---|---|
| | | Days After Sowing (DAS) | | | | | |
| | | 25 | 37 | 49 | 61 | 73 | 85 |
| S.v | T1 | 20.27 | 20.6 | 15.34 | 32.8 | 16.93 | 22.83 |
| | T2 | 15.23 | 14.53 | 13.81 | 20.14 | 16.73 | 15.9 |
| | T3 | 6.47 | 12.23 | 10.59 | 19.03 | 9.13 | 12.47 |
| | T4 | 3.5 | 10.27 | 9.24 | 5.83 | 5.9 | 10.43 |
| S.s | T1 | 17.16 | 13.23 | 18.15 | 22.2 | 24.33 | 17.93 |
| | T2 | 16.8 | 9.71 | 12.1 | 20.63 | 18.7 | 15.33 |
| | T3 | 14.79 | 8.61 | 12.07 | 7.18 | 10.33 | 15.17 |
| | T4 | 14.53 | 7.75 | 11.73 | 4.91 | 8.1 | 8.27 |
| LSD Species | | 3.02 | 1.52 | 1.79 | 3.19 | 3.87 | 2.79 |
| LSD Treatments | | 4.27 | 2.15 | 2.53 | 4.51 | 5.48 | 3.94 |

LSD (Least Significance Difference at 5% level of significance), T1-watering daily (control), T2-watering after every three days (the 3rd and 6th day), T3-watering the 9th day and T4-watering the 12th day.

**Table 3:** The effect of water deficit on Fv/Fm ratio of *S. villosum* Mill *(S.v)* and *S.scabrum* Mill. (*S.s*) grown under different watering regimes(T1, T2, T3 and T4): Values represent means of three replicates

| Species | Treatments | Fv/Fm | | | |
|---|---|---|---|---|---|
| | | Days After Sowing (DAS) | | | |
| | | 25 | 37 | 49 | 61 |
| S.v | T1 | 0.92 | 0.81 | 0.79 | 0.69 |
| | T2 | 0.87 | 0.72 | 0.61 | 0.5 |
| | T3 | 0.76 | 0.63 | 0.53 | 0.5 |
| | T4 | 0.63 | 0.55 | 0.44 | 0.35 |
| S.s | T1 | 0.98 | 0.89 | 0.79 | 0.69 |
| | T2 | 0.87 | 0.79 | 0.67 | 0.52 |
| | T3 | 0.7 | 0.64 | 0.53 | 0.43 |
| | T4 | 0.61 | 0.54 | 0.48 | 0.31 |
| LSD Species | | 0.03 | 0.01 | 0.02 | 0.01 |
| LSD Treatments | | 0.04 | 0.02 | 0.03 | 0.01 |

LSD (Least Significance Difference at 5% level of significance), T1-watering daily (control), T2-watering after every three days (the 3rd and 6th day), T3-watering the 9th day and T4-watering the 12th day.

**Table 4:** The effect of water deficit on ETR of *S. villosum* Mill *(S.v*) and *S.scabrum* Mill. (*S.s*) grown under four watering regimes(T1, T2, T3 and T4): Values represent means of three replicates.

| Species | Treatments | ETR (µmol electrons $m^{-1}$ $s^{-1}$) | | | |
|---|---|---|---|---|---|
| | | Days After Sowing (DAS) | | | |
| | | 24 | 36 | 48 | 60 |
| S.v | T1 | 307.28 | 81.38 | 38.38 | 21.43 |
| | T2 | 163.85 | 66.91 | 31.66 | 21.48 |
| | T3 | 230.02 | 52.58 | 32.79 | 18.78 |
| | T4 | 135.81 | 61.61 | 45.46 | 31.79 |
| S.s | T1 | 275.056 | 64.84 | 39.49 | 21.38 |
| | T2 | 200.33 | 52.51 | 127.03 | 24.87 |
| | T3 | 195.31 | 58.49 | 65.72 | 36.21 |
| | T4 | 210.7 | 75.53 | 50.31 | 18.08 |
| **LSD Species** | | **21.61** | **6.34** | **15.9** | **2.44** |
| **LSD Treatments** | | **30.56** | **8.96** | **22.48** | **3.46** |

LSD (Least Significance Difference at 5% level of significance), T1-watering daily (control), T2-watering after every three days (the 3rd and 6th day), T3-watering the 9th day and T4-watering the 12th day.

## DISCUSSION

### 1. EFFECT OF SOIL MOISTURE CONTENT ON *S. SCABRUM* MILL. AND *S. VILLOSUM* MILL.

Soil water content decreased with decreasing frequency of irrigation. This was in agreement with results of Martim *et al.* (2009), on grapevine and Siddique *et al.* (2000), on wheat plants. According to (Thobile *et al.,* 2010) moisture requirements for plants differ with the species, stage of development and plant age. Decreases in soil moisture may be attributed to surface evaporation, transpiration through the leaves and water absorbed by the roots Luvaha *et al.* (2008): In well watered plants the soil moisture content was more or less similar in both species (Fig. 1), implying that when water is not limiting, the two species have similar rate of water absorption, utilization and water loss.

### 2. EFFECT OF WATER DEFICIT ON LEAF TEMPERATURE AND GAS EXCHANGE PARAMETERS

The significant difference in gas exchange between the two species at the initial stages of growth and the later stages of growth may have been due to less water being acquired for growth and low transpiration rates hence high temperatures. On the other hand during the flowering stage demand for water were high hence high transpiration rates consequently lowering leaf temperature. The highest temperatures were reported in T4 and decreased with a decrease in water deficit. Leaf temperatures increased with increasing water deficit. Generally, well watered plants had low leaf temperatures as compared to stressed plants (Table1).

Stomatal conductance in water stressed plants was generally lower as compared to the well-watered plants (Table 2): A decline in stomatal conductance with increase in water deficit might have helped plants to avoid dessication because severe water deficit could also have increased ABA concentrations that regulate the opening and closing of the stomata. The reduction in stomatal conductance and transpiration in stressed plants might have been due to the reduction in leaf number as observed in T4 that reduced number of stomata, thereby decreasing the rate of water flow into the plant. The reduced stomatal conductance might

have decreased the intercellular $CO_2$ concentration in turn reducing the $CO_2$ assimilation rate (Zhao *et al.,* 2010).

The two species of African nightshades had a reduction in stomatal conductance as a result of increasing water deficit in the leaves. These results are in agreement with those of Upretty and Bhatia (1989), who reported that stomatal conductance in the leaves of mungbean decreased with increase in water deficit. Reduction in stomatal conductance decreases transpiration and limits $CO_2$ assimilation rate (Tezera *et al.,* 2002): The contrary was in sunflower where stomatal closure had a minor effect on photosynthesis because the direct effects on the photosynthetic activity of chloroplast decreased the demand for carbon dioxide and the level of carbon dioxide inside the leaf remained relatively high (Hopkins and Huner, 2004): Nonstomatal limitations such as reduction in photosynthetic pigment concentration and reduction in photosytem II activity may partly account for the decreased rates of photosynthesis (Pierce *et al.,* 2007): According to Cornic and Fresneau (2002), stomatal closing is the main reason reducing photosynthesis rates as a result of water deficit because the maximum value of photosynthesis can be recovered by supplying sufficient amount of $CO_2$ to the leaves. Therefore the causes of low photosynthesis under water deficit depend not only on the stress and plant variety but also on the complex interaction between the age of the plant and the leaves as well as the light intensity (Flexas *et al.,* 2004): Stomatal conductance in T1 and T2 was slightly higher as compared to T3 and T4 might have resulted in increased $CO_2$ diffusion into the leaves to attain higher photosynthetic rates which favoured higher biomass in T1 and T2 (Siddique *et al.,* 2000).

## 3. EFFECT OF WATER DEFICIT ON CHLOROPHYLL FLUORESCENCE

The patterns of changes in fluorescence parameters observed in this study are consistence with those reported under water deficit conditions in barley (Mamnouie *et al.,* 2006) and Bambara groundnuts (Vurayai *et al.,* 2011): Estimates of ETR describe the ability of photosytems to use incident light thereby giving an indication of the overall photosynthetic capacity of the plant (Uku and Bjork, 2005), while the flow of electrons through photosystem II is indicative under many conditions of the overall rate of photosynthesis (Pereira *et al.,* 2004; Flexas *et al.,* 2004): Although there was no significant difference in ETR between the two species *S. villosum* had a higher ETR rates with increase in water deficit (Table 3), implying that it was more tolerant to water deficit since low ETR under water deficit suggests low tolerance to water deficit (Santos *et al.,* 2009): In severe water deficit Fv/Fm ratio decreased indicating a reduction in efficiency of PSII centers, or possibly due their damage, because according to Zanella *et al*. (2004) low Fv/Fm ratio is the main consequence of photoinhibitory damage and may be attributed to the down regulation of photosystem II activity and impairment of photochemical activity. Water deficit reduces photosynthesis directly hence dehydrated protoplasm has a lowered photosynthetic capacity (Vurayai *et al*., 2011): The decrease in Fv/Fm indicates, to some extent, the occurrence of photoinhibition which may be due to photoinactivation of PSII centers (Bjorkman and Powles, 1984): The constant Fv/Fm values for *S. villosum* in DAS 61 for T1 and T2 is an indication that there is no loss in the yield of PSII photochemistry and confirmed the resistance of the photosynthetic machinery to water deficit stress, as earlier reported by Chaves *et al.* (2002) and Cornic and Fresneau, (2002), while high Fv/Fm values in T1 for the two species in all days, may have resulted in an increase in dry matter production.The standard Fv/Fm ratio is 0.83 but typically ranges from 0.75 to 0.85 for normal healthy plants (Demming and Björkman, 1987): In the present study, Fv/Fm ratio of the two species ranged from 0.980 to 0.787 for T1 in DAS 25, 37 and 49, these values were slightly high possibly due to higher temperatures that increased enzymatic activity (Viera and Necchi, 2006): Similar results were obtained in beans as indicated by Miyashita *et al.* (2005) and in NERICA rice varieties as reported by Sikuku *et al.* (2012): While the decrease in electron transport along with photosystem II may also be due to the inhibition of energy transfer from carotenoids to chlorophyll or according to (Sikuku *et al.,* 2012) in rice among the NERICA varieties. The higher ETR (Table 4) in well-watered plants observed in this study agree with those of Maricle *et al.* (2007): ETR

describes the ability of photosystems to use incident light thereby giving an indication of the overall photosynthetic capacity of the plants which is exhibited by the flow of electrons through PSII under many conditions of the overall rate of photosynthesis.

## CONCLUSIONS

Stomatal conductance was higher in well-watered plants compared to water stressed plants. Generally, leaf temperature increased with increase in soil water deficit. Water deficit caused a general reduction in Fv/Fm ratio, and thismay be attributed to down regulation of photosystem II activity and photoinhibition due to photoinactivation of PSII centers, possibly due to the resistance of the photosynthetic machinery to water deficit stress.The results indicate that T1-watering daily (control), T2-watering after every three days (the 3rd and 6th day), and T3-watering the 9th day gave the best physiological responses plant species under study and *S.scabrum* Mill. (*S.s*) performed better than *S. villosum* Mill *(S.v*) under soil water deficit conditions.

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