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Effect of increased temperature and drought associated to climate change on productivity of nodulated alfalfa

I. Aranjuelo, J.J. Irigoyen and M. Sánchez-Díaz
Departamento de Fisiología Vegetal, Facultades de Ciencias y Farmacia, Universidad de Navarra, Irunlarrea s/n, 31008 Pamplona, Spain, e-mail: jirigo@unav.es

SUMMARY – Alfalfa productivity is frequently limited by environmental factors such as temperature and water availability. The aim of our study was to investigate the effect of a 3ºC increase in air temperature (28ºC vs. 25ºC) and low water availability upon dry matter production in nodulated alfalfa. Two month-old plants inoculated with *Rhizobium meliloti* were grown in growth chambers at 25ºC well (W25) or partially irrigated (30% lower volumetric soil water content) (D25) and at 28ºC well (W28) or partially irrigated (30% lower volumetric soil water content) (D28). Both groups of droughted plants (D25 and D28) suffered the same degree of water stress in soil and leaf tissues. Drought and elevated temperature reduced the plant dry matter (DM) production and leaf area, especially when they were applied simultaneously. Lower leaf area and net photosynthetic rates induced by elevated temperatures explained the reduction in DM production at leaf level. Most of the photosynthetic limitations were due to lower Rubisco activity. Also, lower nodule mass and activity reduced the nitrogen available to the plants subjected to elevated temperature. Results are discussed in connection to the effect of a potential temperature increase associated to elevated CO_2 in atmosphere.

Key words: Alfalfa, drought, productivity, temperature.

RESUME – *"Effet de l'augmentation de la température et la sécheresse associées au changement climatique sur la productivité de la luzerne nodulée". La production de luzerne peut être limitée par des facteurs environnementaux, tels que la sécheresse et les températures élevées. L'objectif de notre étude est l'évaluation des effets de la sécheresse et des températures élevées sur la production des plantes de luzerne en symbioses avec* Rhizobium meliloti. *Des plantes ont poussé pendant deux mois dans des chambres de croissance à 25ºC, avec une irrigation complète (W25) ou partielle (de 30% de moins de teneur volumétrique d'eau dans le sol) (D25), et à 28ºC, avec une irrigation complète (W28) ou partielle (de 30% de moins de teneur volumétrique d'eau dans le sol) (D28). Les plantes de luzerne étudiées sont dépendantes de la fixation biologique de l'azote. Les plantes des deux traitements de sécheresse (D25 et D28) ont été soumises au même niveau de stress dans le sol et dans les tissus. L'augmentation de la température n'a pas eu d'effet sur la teneur hydrique des plantes. Concrètement, l'augmentation de la température a réduit la production de matière sèche (DM) et la superficie foliaire, spécialement chez les plantes partiellement irriguées (D28). La réduction de la photosynthèse et de la superficie foliaire sont deux effets qui pourraient expliquer la réduction de la production de DM. Au niveau de la photosynthèse, c'est surtout l'activité de Rubisco qui se voit sensiblement affectée par l'augmentation de la température (W28 et D28). La teneur totale en azote des plantes se voit significativement affectée par l'augmentation de la température, et spécialement chez les plantes soumises en même temps à la sécheresse (D28). Les raisons de cette réduction d'azote dans les plantes sont : une diminution de la quantité de masse nodulaire (effet de la sécheresse) et/ou la réduction de l'activité nodulaire (effet de la température). Nous concluons donc que l'augmentation de la température (de 25ºC à 28ºC) et la sécheresse ont affecté l'activité foliaire et nodulaire des plantes de luzerne, limitant ainsi la réponse positive à l'augmentation de CO_2 atmosphérique.*

Mots-clès : *Luzerne, production, sécheresse, température élevée.*

Introduction

It is expected that plant photosynthesis and growth may be stimulated by the increase in atmospheric CO_2 concentration. However plant response to elevated CO_2 may be limited by endogenous (plant species, development stage, source demand, etc.) and exogenous factors (water and mineral supply, temperature, etc.). In the Mediterranean area, low water availability and elevated temperature are common situations which affect plant performance. In previous studies, we have demonstrated that nodulated alfalfa plants are very responsive to elevated CO_2, growth being significantly stimulated. This effect on growth is observed in both well and partially watered plants (De Luis *et al.*, 1999). However, when air temperature was increased 3ºC (25ºC to 28ºC) the growth improvement induced by CO_2 was reduced significantly, especially under low water availability conditions (De Luis, 2000).

The main goal of our study was to investigate the effect of increased temperature and drought on leaf and nodule activities and their implications for nodulated alfalfa plant production.

Materials and methods

Alfalfa plants (*Medicago sativa* L. cv. Aragón) inoculated with *Rhizobium meliloti* strain 102F78 were grown in 2 l pots (ten per pot) filled with wet perlite, in a greenhouse at 25/15ºC (day/night) and 14 h photoperiod during one month. Pots were irrigated alternatively with nitrogen free nutrient solution (Evans N-free) and distilled water. When plants were thirty days old, they were randomly distributed among four treatments: (i) W25, fully irrigated, grown at 25ºC and 45% RH (1.74 kPa VPD); (ii) D25, partially irrigated, grown at 25ºC and 45% RH (1.74 kPa VPD); (iii) W28, fully irrigated, grown at 28ºC and 54% RH (1.74 kPa VPD); and (iv) D28, partially irrigated, grown at 28ºC and 54% RH (1,74 kPa VPD). Plants were grown for another month under growth chamber conditions (PGV-36 Conviron, Canada) in their respective temperature and RH, 14 h photoperiod, 600 µmol/m^2/s and ambient CO_2 concentration (around 350 ppm). Partially irrigated plants (D25 and D28) were fed with a portion of the amount applied to fully irrigated treatments (W25 and W28) in order to reach a volumetric soil water content ( ) 30% lower (around 0.35 m^3/m^3) than that of the fully irrigated ones (around 0.47 m^3/m^3). At the end of the experiment, the following parameters were measured: leaf and soil (5 cm depth) temperatures, dry matter (DM), total leaf area, leaf and soil water status by measuring relative water content (RWC) and volumetric soil water content ( ), net photosynthesis (NP), dark adapted leaf chlorophyll fluorescence (Fm/Fv), total leaf soluble proteins (TSP), Rubisco activity, plant total nitrogen content and nodule specific activity (NSA).

Results and discussion

As expected leaf and soil temperatures (5 cm depth) were around 3ºC higher in the high temperature treatments (Table 1) and no effect of the water regimen was observed.

Table 1. Leaf (adaxial) and soil (5 cm depth) temperature (ºC) of 60 days old nodulated alfalfa subjected to 25 or 28ºC and irrigated (W) or droughted (D). Values are the mean ± SE (n = 8). Means followed by the same letter are not significantly different (P > 0.05)

	Treatments			
	W25	D25	W28	D28
Leaf	28.2 ± 0.3 a	27.5 ± 0.3 a	31.2 ± 0.3 b	31.3 ± 0.2 b
Soil	25.5 ± 0.7 a	26.8 ± 0.5 a	28.5 ± 0.7 a	28.5 ± 0.3 b

The soil volumetric water content ( ) of droughted plants (D25 and D28) were 30% lower than the values measured in well watered treatments (W25 and W28) (Table 2). As differences were not observed in the values between D25 and D28 we can deduce that both groups of plants were subjected to the same soil water stress. Leaf relative water content (RWC) was also significantly lower in droughted treatments (D25 and D28).

Table 2. Effect of elevated temperature and drought on leaf relative water content (RWC, %) and volumetric soil water content (m^3/m^3). Otherwise as for Table 1

	Treatments			
	W25	D25	W28	D28
RWC	87 ± 2 a	76 ± 3 b	85 ± 1 a	76 ± 2 b
	0.48 ± 0.01 a	0.34 ± 0.01 b	0.47 ± 0.01 a	0.31 ± 0.01 b

Dry matter (DM) and total leaf area per plant (Table 3) were negatively affected by 3ºC increase in air temperature, and drought (D28). The DM and leaf area measured in D28 plants were 77% and 70% respectively lower than those observed in W25.

Table 3. Effect of elevated temperature and drought on plant total dry matter (DM, g/plant) and leaf area (cm^2/plant). Otherwise as for Table 1

	Treatments			
	W25	D25	W28	D28
DM	2.2 ± 0.2 a	1.3 ± 0.1 b	1.28 ± 0.2 b	0.5 ± 0.0 c
Area	91 ± 10 a	44 ± 19 bc	66 ± 10 ab	27 ± 3c

The DM reduction in W28 and D28 plants can be explained on the basis of lower net photosynthetic rates (NP) (Table 4) and leaf area (Table 3). In our study, low NP appears associated with a significant reduction in extractable Rubisco activity (Table 4). As the total leaf soluble proteins were not affected (Table 4), the reduction in Rubisco activity could be related to an inactivation of the enzyme rather than to a low amount of Rubisco protein. Dark adapted leaf chlorophyll fluorescence parameter (Fv/Fm) discarded at least photosystem II malfunction (Table 4).

Table 4. Effects of elevated temperature and drought on net photosynthesis (NP, µmol of $CO_2/m^2/s$), optimal quantum yield of photosystem II (Fv/Fm), total leaf soluble proteins (TSP, mg/g DM) and Rubisco activity (µmol/g DM/min). Otherwise as for Table 1

	Treatments			
	W25	D25	W28	D28
NP	13 ± 1 a	14 ± 1 a	8 ± 1 b	10 ± 2 b
Fm/Fv	0.81 ± 0.01 a	0.80 ± 0.01 a	0.79 ± 0.00 a	0.78 ± 0.01 c
TSP	78 ± 1 a	66 ± 1 a	70 ± 4 a	68 ± 4 a
Rubisco	20 ± 1 a	19 ± 1 a	11 ± 0 b	12 ± 0 b

The total N of plants was also negatively affected by temperature and drought (Table 5). Especially in D28 plants (25% of the W25 plants). The lower amount of fixed N was due to: reduction in nodule mass and lower nodule activity. The same conclusion was obtained when the nodule specific activity was analysed (Table 5).

Table 5. Total nitrogen content (mg N/plant), nodule dry matter per plant (mg nodule DM/plant), and nodule specific activity (NSA; mg N/mg nodule DM). Otherwise as for Table 1

	Treatments			
	W25	D25	W28	D28
Total N	64 ± 7 a	38 ± 4 b	43 ± 5 b	16 ± 2 c
Nodule DM	39 ± 5 a	23 ± 3 a	43 ± 5 a	16 ± 2 c
NSA	1.6 ± 0.2 a	1.7 ± 0.3 a	1.0 ± 0.2 b	1.0 ± 0.2 b

Conclusions

According to the results, we can conclude that the DM production of the nodulated alfalfa plants is limited under drought and elevated temperature conditions, but especially when both stresses are applied

simultaneously. Leaf photosynthesis and nodule nitrogen fixation were adversely affected. Thus the response of the nodulated alfalfa to elevated atmospheric CO_2 concentration may be strongly limited under these conditions.

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