

HELIOtropISM AND WATER AVAILABILITY EFFECTS ON FLOWERING DYNAMICS AND SEED PRODUCTION IN *Macroptilium lathyroides*¹

ARMANDO MARTINS DOS SANTOS², LUIS MAURO GONÇALVES ROSA³, LUCIA BRANDÃO FRANKE⁴, CARLOS NABINGER⁵

ABSTRACT - The experiment was carried out in pots in a glasshouse, with one plant per pot and nine repetitions per treatment. The treatments consisted of free or restricted leaves, submitted to 90-100% or 60-70% soil field capacity (FC). Only independent effects of water availability or leaf movement were observed on yield components. Plants under well-watered conditions and with freely orienting leaves were taller, and had a larger number of ramifications. The greater development favored the setting of a higher number of inflorescences per plant in these treatments. This behavior resulted in a high number of flowers, green and mature legumes per plant, thus resulting in high seed production which was the most evident response to water availability. Although individual seed weight was higher in the water stress treatment, total seed production was higher for well-watered plants, with no statistically significant effect of leaf movements.

Index terms: water stress, leaf movements, phasey bean, flowers production.

EFEITO DO HELIOtROPISMO E DA DISPONIBILIDADE HÍDRICA NA DINÂMICA DE FLORESCIMENTO E PRODUÇÃO DE SEMENTES DE *Macroptilium lathyroides*¹

RESUMO - O experimento foi conduzido em casa de vegetação, em vasos, com uma planta por vaso e nove repetições por tratamento. Os tratamentos constituíram: plantas com folhas livremente orientadas ou restritas, submetidas às condições hídricas de 90-100% e 60-70% da capacidade de campo. Foram observados efeitos independentes da disponibilidade hídrica e da movimentação foliar para os componentes do rendimento de sementes ao longo do período experimental. Plantas submetidas a alta disponibilidade hídrica e com folhas livremente orientadas apresentaram maior número de ramificações por planta. Este melhor desenvolvimento favoreceu a emissão de maior número de inflorescências por planta, proporcionando maior número de flores, legumes verdes e legumes maduros por planta que, por sua vez, gerou maior produção diária de sementes. Esta resposta foi evidenciada ao se avaliar o efeito da disponibilidade hídrica. Apesar da massa individual da semente ter apresentado valores superiores para o tratamento com restrição hídrica, a produção total de sementes foi superior no tratamento com alta disponibilidade hídrica, não se observando efeito significativo para a movimentação foliar.

Termos para indexação: estresse hídrico, movimentos foliares, feijão-dos-arrozais, produção de flores.

INTRODUCTION

Almost all of the physiological processes of plants are directly or indirectly affected by the water supply (Fisher and Turner, 1978). Water is also one of the main ecological

factors dictating the patterns of the local vegetation, through the relationship precipitation/transpiration. Water's ecological importance comes from its physiological importance, and this is a result of the functions carried out in the plant (Kramer and Boyer, 1995). The reduction of the plant water content is

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² MSc., Estudante de Doutorado em Ciências Animais, UFRGS; amando_martins@uol.com.br;

³ PhD., Professor Adjunto, Departamento de Plantas Forrageiras e

Agrometeorologia, Faculdade de Agronomia, UFRGS; lmrosa@ufrgs.br;

⁴ Dra., Professor Adjunto, Departamento de Plantas Forrageiras e Agrometeorologia, Faculdade de Agronomia, UFRGS; lbfranke@ufrgs.br;

⁵ Dr., Professor Adjunto, Departamento de Plantas Forrageiras e Agrometeorologia, Faculdade de Agronomia, UFRGS; nabinger@ufrgs.br.

followed by turgor loss and wilting, stopping cellular elongation, closing stomata, reducing photosynthesis, and interfering in various basal metabolic processes (Angelocci, 2002). These effects may affect plant productivity and, especially, seed production, therefore reducing the ability of a species to disseminate (Chiarello and Gulmon, 1991). In this relationship between vegetative and reproductive development, it is known that the latter is more sensitive to water stress than the first. This sensitivity comes from the fragility of the reproductive development (Bazzaz and Ackerly, 1992).

Like many other species on the legume family, *M. lathyroides* presents turgor mediated leaf movements in response to the sun's direct rays (heliotropism). Considered an adaptive response mechanism to environmental stress (Forseth, 1990), heliotropism involves rapid and reversible leaf movements in response to the intensity and direction of the sunlight. Heliotropic movements were divided by Darwin (1881) into two distinct classes, diaheliotropism, movements in which the leaf lamina are perpendicular to the light beam, and paraheliotropism where leaf lamina are parallel to the direct beam.

Similar to *Phaseolus vulgaris* (Fu and Ehleringer, 1989), *Strophostyles helvola* (Prichard and Forseth, 1988) and *Glycine max* (Rosa and Forseth, 1995), diurnal patterns of leaf movements *M. lathyroides* represent a mixture between dia and paraheliotropism. In the early morning hours, the illuminated leaves orient towards the sun (diaheliotropism), while at midday, sunlit leaves avoid direct sunlight (paraheliotropism) through steep inclination angles. Finally, by late afternoon sunlit leaves again face towards the sun.

The primary role of these leaf movements is to regulate the amount of solar radiation incident on a leaf, maximizing it in diaheliotropic leaves and minimizing it for paraheliotropic leaves (Ehleringer and Forseth, 1980; Forseth, 1990; Koller and Cohen, 1990). On clear days paraheliotropism can reduce total radiant energy on the leaf blade by 20-30% (Forseth and Ehleringer, 1980). Therefore, these leaf movements have an influence on leaf energy balance, leaf temperature, transpirational water loss, carbon gain through photosynthesis, water use efficiency (WUE), photoinhibition, and the return in carbon of the nitrogen invested in photosynthesis (Koller et al., 1985; Ludlow and Bjorkman, 1987; Fu and Ehleringer, 1989 and 1991; Berg and Heuchelin, 1990; Forseth, 1990; Bielenberg et al., 2003). The regulation of all these factors may give these plants an advantage in growth and seed production when compared to plants with stationary leaves.

The objective of this study was to verify the effects of water availability and heliotropism on flowering dynamics and seed production of *Macropitilium lathyroides*.

MATERIAL AND METHODS

Seeds of *M. lathyroides*, harvested in a previous experiment, were scarified and inoculated with a *Rhizobium* strain specific for this species, sown on germination flats on December 12, 2002, and kept in a greenhouse at the UFRGS School of Agronomy (Porto Alegre, Brazil, 30°05'S, 51°39'W), from December 2002 through April 2003. After germination, seedlings with an approximate size of 80mm were transferred to 10kg pots (3 seedlings per pot, later reduced to only one per pot), filled with soil, classified as a red dystrophic argisole, collected from the first 200mm of depth (arable layer) at the Agronomica Experimental Station (EEA/UFRGS). Prior to potting, the soil was air dried and sieved. Soil humidity was estimated from the difference between the weight of air dried soil and after 72 hours of oven drying at 102°C. All the pots were watered to soil field capacity before initiating the treatments. The relationship between soil volumetric humidity and matric potential (Figure 1) was plotted from data obtained at the same site (Cunha, 1991)

Plants were either watered to 100% soil field capacity (A) or 60% field capacity (S) by weighing the pots daily and adding water as needed to keep the experimental proportions. The water stress treatment was initiated only after the complete expansion of the third trifoliate leaf. Leaf orientation treatments consisted of plants with leaves allowed to move freely (L) or leaves held horizontally (H), by painting the pulvinus, organ responsible for the leaf movements, with a water soluble, non allergenic ink. Painting the pulvinus did not completely restrict leaf movement, especially at times of high air temperature.

All plants received 100mL of a one mmolar urea solution as a starter N to reduce problems of differential bacterial activity at the early stages of growth. Weed control in the pots was conducted manually.

Monitoring of flowering dynamics and of the components of seed production was initiated at the time of the opening of the first flower on the first inflorescence. Counts of number of branches, number of inflorescences, number of flowers, number of mature and immature legumes, number of seeds, were performed on a per plant basis every 2 days for a period of 58 days for all treatments. Number of flowers per

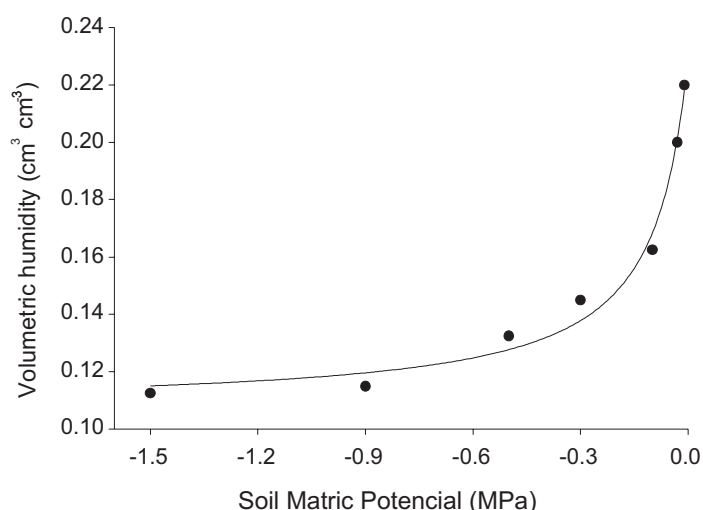


FIGURE 1. Variation in the volumetric humidity of a red dystrophic argisil soil, in the first 200mm of depth as a function of soil matric potential. Data adapted from Cunha 1991 at the Agronomical Experimental Station (EEA/UFRGS).

inflorescence, number of seeds per legume, mean seed weight, rate of seed production, total seed production, and mean number of days to the beginning of flowering were also recorded for each treatment.

Statistical analysis was performed as a completely randomized design, considering each pot as a replicate. Number of branches, mean number of days for the beginning of flowering, and total seed production were tested by ANOVA (SAS Institute, 2001) and mean comparison performed by a Tukey *post hoc* test ($\alpha = 0.05$). For all other variables a repeated measures ANOVA (SAS Institute, 2001) was used. A regression analysis was performed following the repeated measures for all statistically significant main effects and/or interactions.

RESULTS AND DISCUSSION

The favourable environmental conditions in the greenhouse (air temperature higher than 30°C), the low competition for light (one plant per pot), the lack of herbivory or harvest resulted in a vigorous development of the plants, especially in those under well-watered conditions. Because of this luxurious growth, which made evaluation difficult due to the height and degree of intertwining of the plants, the experiment had to be stopped at 58 days after the beginning of flowering.

Heliotropism ($p = 0.3327$), water availability ($p = 0.6062$) or their interaction ($p = 0.7452$) did not significantly influence the average period of flower initiation, not even these factors

interaction. Plants with freely orienting leaves under 100% and 60% of field capacity (FC) presented an average flowering initiation on the 63rd and 66th day after the sowing (DAS), respectively, while plants with restricted leaves had started flowering on the 64th DAS at 60% FC and on the 68th DAS at 100% FC. These responses can be attributed to the short length of the treatment period until the beginning of flowering, as the stress treatments were implemented only on the 35th DAS and the first experimental plant flowered on the 60th DAS. Klafke et al. (2003) working on the effects of leaf orientation on *M. lathyroides* flowering found that plants with freely moving leaves started to flower earlier (an average of 10 days) than plants with restricted leaves ($p = 0.0001$).

M. lathyroides is a photoperiodically neutral species that depends on the accumulation of thermal units to the flower (Skerman et al., 1988; Ledezma, 2000; Ferreira, 2002), therefore it is suggested that the combination of the diaheliotropic and paraheliotropic movements during the day, in the treatment with freely moving leaves, could have facilitated the accumulation of thermal units, compared to the treatments with restricted leaves, stimulating the phenological events, which are necessary to flower initiation.

The average number of branches on the 58th day after the beginning of the flowering (DAF) showed significant effects of the interaction between water availability and leaf orientation ($p = 0.0445$). Plants with heliotropic leaves developed a higher number of branches under well water conditions, while the water availability did not influence the number of branches in plants with restricted leaves (Table 1). At the same level of water availability, the heliotropic and restricted plants did not present statistically significant differences, although the absolute value of the number of branches in the 100% FC treatment was higher than in the 60% FC for both leaf orientation treatments. This response indicated that plants with heliotropic leaves, under a low water

TABLE 1. Average number of branches of *M. lathyroides* at the 58th day after flowering, cultivated in pots, in a greenhouse and submitted to two water (100 and 60% field capacity) and two leaf orientation treatments (leaves freely orienting and restricted leaves). Porto Alegre, RS – 2003.

	100% FC	60% FC
Heliotropic leaves	4.11 ± 1.28Aa	1.77 ± 1.28Ab
Horizontally restricted leaves	3.33 ± 1.28Ab	2.77 ± 1.28Ab

Means followed by the same capital letter are not significantly different in the columns, means followed by lower case letters are not significantly different on the same line as compared by a Tukey multiple mean comparison test ($\alpha = 0.05$)

availability, may minimize the interception of the direct solar radiation (paraheliotropism), therefore, reducing the amount of photo assimilates available above ground, especially in the branches.

According to Carambula (1981), the components of seed yield are determined from the beginning of the vegetative development until the end of the reproductive development. During the vegetative development, environmental and management conditions resulted in changes in the number of branches, which was responsible for the first seed production component, the number of inflorescence per area and/or per plant. The analysis of variance of the number of inflorescences per plant (NI/P) showed a significant effect ($p = 0.0151$) for the interaction heliotropism x water availability x days after the flowering (DAF). NI/P increased linearly from the beginning of flowering until the 58th DAF (Figure 2), showing on this date an average number of inflorescences per plant of 23.0 in the treatment with freely oriented leaves, under 100% FC (AL), 18.4 in the treatment with restricted leaves, under 100% FC (AH), 9.6 in plants with freely orienting leaves, under 60% FC (SL) and 8.9 in the treatment with restricted leaves, under 60% FC (SH). Baseggio (1997) found that the NI/m² for *Desmodium incanum* increased linearly, reaching a maximum point at 2172 degrees day, from which the emission rate of new inflorescences decreased, gradually reducing the NI/m² until it reached zero at 3933 degrees centigrade day. *Macroptilium lathyroides* presents a long flowering period (about 6 months in the south of Brazil), therefore its NI/P behaviour could be the same as for *D. incanum*. However, the evaluations were performed over a short period (2 months), which may be located in the linear phase of NI/m² of *D. incanum*.

Comparing the treatments with the same degree of leaf orientation (AL x SL and AH x SH), it is observed that the reduction in soil humidity from 100% to 60% FC reduced flowering 58.43% and 52.0% in plants with free and restricted leaves, respectively. According to Bazzaz and Ackerly (1992), moderate water restriction at the beginning of the reproductive period favours flowering in plants of indeterminate growth, because it inhibits growth on the apical meristem and favours the allocation of resources to the development of the reproductive apparatus. However, more severe water stress, as is the case of this experiment, inhibits both the vegetative growth and the reproductive development (Chiarello and Gulmon, 1992).

The effects of heliotropism on NI/P can be observed by comparing the treatments with the same water availability

(AL x AH and SL x SH). Under a low water condition, the difference in the NI/P on the 58th DAF, among plants with free and restricted leaves, was very small. In the high water treatment plants with free leaves showed an average of 5.0 inflorescences more than plants with restricted leaves. This response indicated that water was the main controller of inflorescence emission, and that heliotropism was a complementary factor under high water conditions.

The number of flowers per plant (NF/P) was affected by either water availability or heliotropism x DAF ($p < 0.0001$, $p = 0.0093$, respectively). There were two peaks of flower production in both water treatments (Figure 3). This behaviour was related to the type of flowering shown by *M. lathyroides* which, despite being indeterminate in the plant was determinate on the stem. Initially, the main stem produces inflorescences, which will flower, reaching a point of maxima, represented by the first production peak (Figure 3A). The exhaustion of the main stem resources due to pod and grain filling and relocation to branches caused a reduction in NF/P up to the 24th DAF. On this date, the flower emission restarted on the primary and/or secondary stems, reaching a 2nd peak of flower production on the 36th and 50th days, for plants under 60% and 100% of FC, respectively.

Among all the factors that may affect flower formation, water availability has a distinctive role. This, associated to a

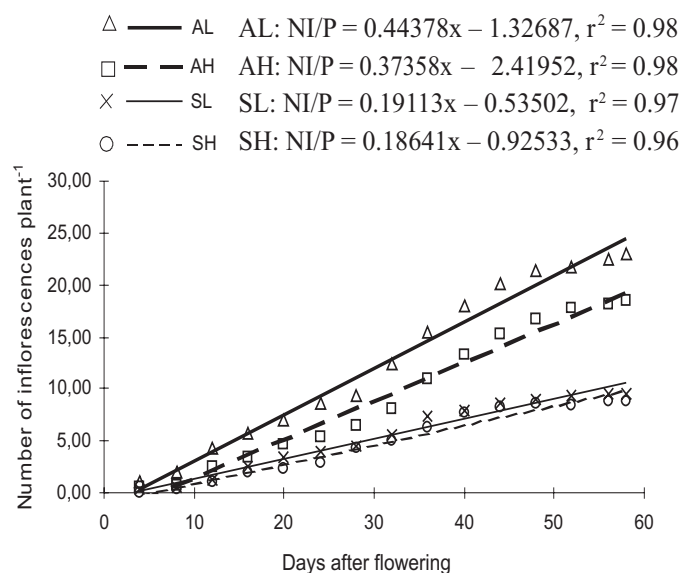


FIGURE 2. Evolution of the total number of inflorescences per plant of *M. lathyroides* as a function of days after flowering. Plants were cultivated in a greenhouse and submitted to two water (100% (A) and 60% (S) FC) and two leaf orientation treatments (freely orienting, L, and horizontally restricted, H). Porto Alegre, RS – 2003.

2A	100 % FC: NF/P = $-0.0002x^4 + 0.0197x^3 - 0.7292x^2 + 10.551x - 12.106$	$r^2=0.8929$
	60 % FC: NF/P = $4E-06x^5 - 0.0005x^4 + 0.0298x^3 - 0.735x^2 + 8.5168x - 23.196$	$r^2=0.8378$
2B	Heliotropic leaves NF/P = $-5E-07x^6 + 9E-05x^5 - 0.0071x^4 + 0.2651x^3 - 4.9745x^2 + 42.94x - 94.589$	$r^2=0.8270$
	Restricted leaves NF/P = $-9E-05x^4 + 0.0102x^3 - 0.3676x^2 + 5.8839x - 14.524$	$r^2=0.9560$
2C	100% FC: NLV/P = $-0.0002x^4 + 0.0268x^3 - 0.9275x^2 + 13.408x - 41.334$,	$r^2=0.9436$
	60% FC: NTGL/P = $-8E-05x^4 + 0.0073x^3 - 0.2009x^2 + 2.9393x - 9.137$,	$r^2=0.9383$
2D	Heliotropic leaves: NLV/P = $-0.0002x^4 + 0.0225x^3 - 0.7687x^2 + 10.962x - 32.086$,	$r^2=0.9314$
	Restricted leaves: NLV/P = $-0.0001x^4 + 0.0131x^3 - 0.4034x^2 + 5.8007x - 19.399$,	$r^2=0.9578$
2E	100% FC: NLM/P = $0.0006x^3 - 0.0544x^2 + 1.7553x - 13.336$,	$r^2=0.9427$
	60% FC: NLM/P = $3E-06x^5 - 0.0005x^4 + 0.0374x^3 - 1.2361x^2 + 19.342x - 112.44$,	$r^2=0.9362$
2F	Heliotropic leaves: NLM/P = $-4E-05x^4 + 0.0066x^3 - 0.3488x^2 + 7.605x - 53.328$,	$r^2=0.9417$
	Restricted leaves: NLM/P = $2E-05x^4 - 0.0021x^3 + 0.0882x^2 - 1.3085x + 6.7328$,	$r^2=0.9104$

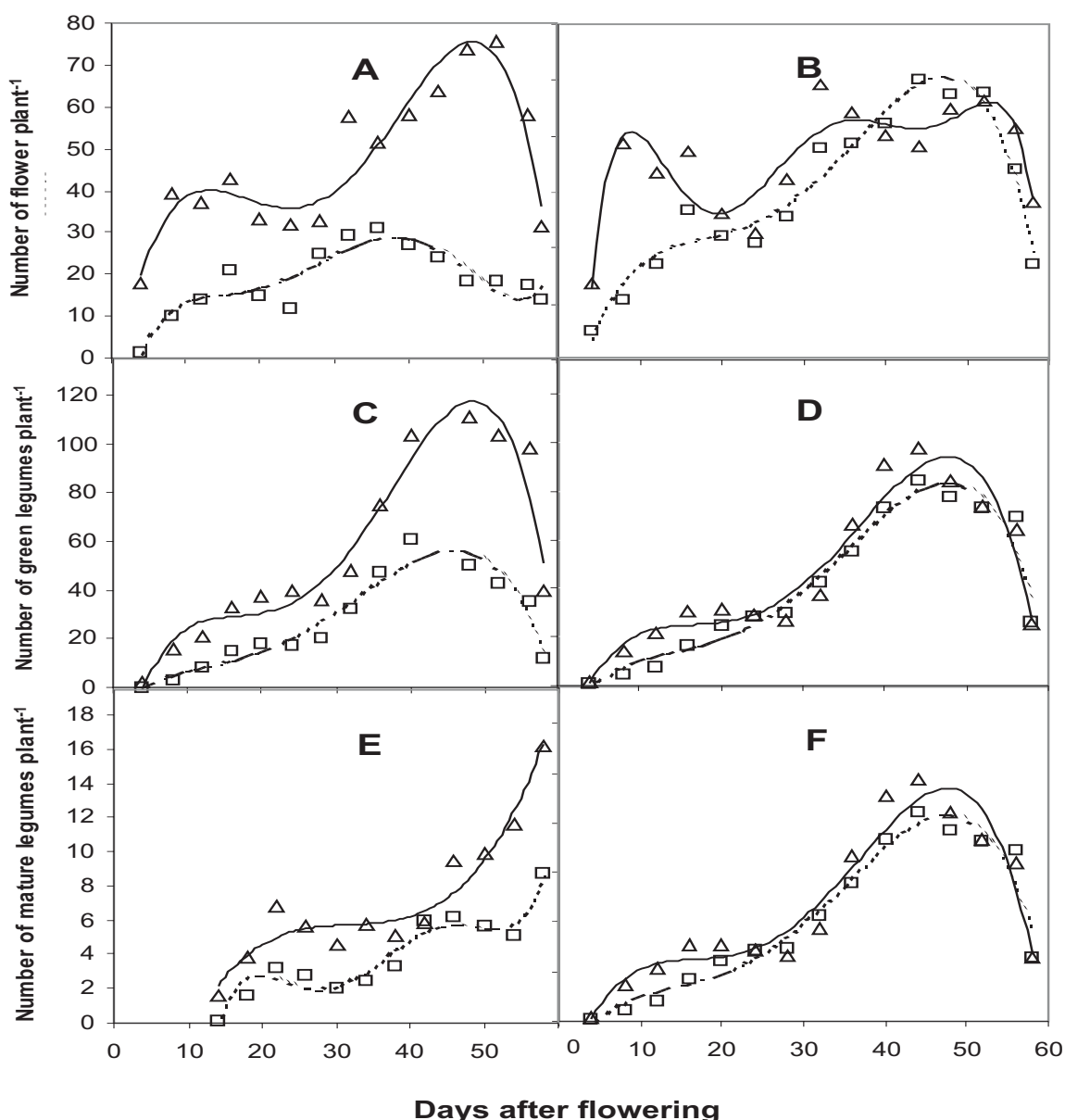


FIGURE 3. Flowering Dynamics of *M. lathyroides* as a function of days after flowering in response to water availability (A, C, E) and leaf orientation (B, D, F). Open triangles, plants under 100% field capacity over all leaf orientation treatments (A, C, E) and for heliotropic leaves over all water availability treatments (B, D, F). Open squares plants under 60% field capacity over all leaf orientation treatments (A, C, E) and for restricted leaves over all water availability treatments (B, D, F). Porto Alegre - RS, 2003.

higher number in the 100% FC treatments resulted in higher flower production throughout the experiment.

Leaf orientation showed a similar effect on NF/P as the water treatment (Figure 3B). Three peaks of flower production were observed in plants with heliotropic and restricted leaves, but no evident reduction between flower production peaks was observed. As the NI/P was very similar in both treatments, this difference may be mainly attributed to the higher number of flowers per inflorescence (NF/I) in plants with freely oriented leaves (Figure 4).

The number of green legumes per plant (NLV/P) was also affected by the interaction of water availability x DAF (Figure 3C) and by the interaction of heliotropism x DAF (Figure 3D).

The number of ripe legumes per plant (NLM/P) also presented independent effects in the interactions water availability x DAF and heliotropism x DAF (Figure 3E). The responses in both treatments (leaf orientation and water availability) were similar, showing an increase in the initial NLM/P, followed by a stable period, and finally a new increase until the end of the evaluations.

M.lathyroides is a plant with indeterminate growth habits, and has a long flowering period (about six months), and the evaluations performed in this study lasted only 58 days. This is probably the reason why the NLM/P showed an increase until the last evaluated date, according to the flowering dynamic observed for the flowers and green legumes.

No interaction of the effects of heliotropism, water and

DAF could be detected on the average number of seeds per legume. Values of S/L in this experiment varied between 16.5 and 20.5, in agreement with the results of Skerman et al. (1988) who reported an average number of 20 seeds per legume for this species.

The number of seeds per plant (NS/P, Figure 4) showed significant effects of water availability ($p=0.0092$), and leaf orientation ($p=0.0007$) over time. Plants under 100% FC showed the highest NS/P (Figure 4A). The same overall behaviour was observed for those plants where the leaves were allowed to move freely, although they produced a smaller number of seeds per plant (Figure 4B). Sixty percent FC resulted in low seed production, but it still showed the two peak behaviours seen in the 100% FC. On the other hand, plants with restricted leaves showed a different NS/P pattern over time. There was a constant increase in NS/P, coming to a saturation type of response at 50 to 60 DAF. As the number of seeds per legume (S/L) did not change in either treatment, the response of NS/P may be attributed to the number of mature legumes per plant (NLM/P).

Daily seed production per plant (PDS/P) during the flowering period is shown in Figure 5. Two production peaks may be observed in the AL and AH treatments, the first on the 18th and 20th DAF and the second on the 55th DAF for AL. The second peak of AH was not observed because the experiment was stopped before the plants could reach it. In the SH treatment, two seeds production peaks (PS) were observed on the 20th and 42nd DAF, and also the beginning of a third

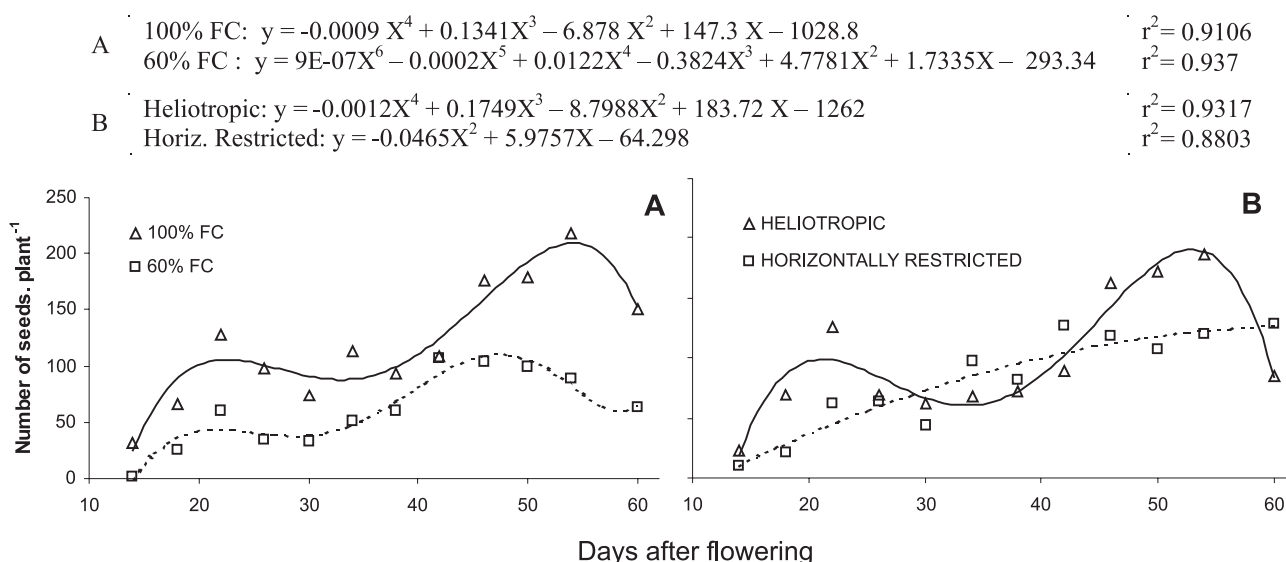


FIGURE 4. Evolution of the number of seeds per plant of greenhouse grown *M. lathyroides* as a function of days after flowering under two water availability treatments (100% and 60% field capacity, A) and two leaf orientation treatments (freely moving or horizontally restricted, B). Porto Alegre - RS, 2003.

$$\text{AL TPS/P} = -1\text{E-}05x^4 + 0.0022x^3 - 0.1161x + 2.5098x - 16.719, r^2 = 0.607$$

$$\text{SH TPS/P} = 1\text{E-}07x^5 - 0.0002x^4 + 0.0141x^3 - 0.4727x^2 + 7.5205x - 44.39, r^2 = 0.6119$$

$$\text{SL TPS/P} = 9\text{E-}07x^5 - 0.0002x^4 + 0.016x^3 - 0.4373x^2 + 7.137x - 42.708, r^2 = 0.8382$$

$$\text{AHTPS/P} = 6\text{E-}07x^5 - 0.0001x^4 + 0.008x^3 - 0.2706x^2 + 4.3154x - 23.921, r^2 = 0.8529$$

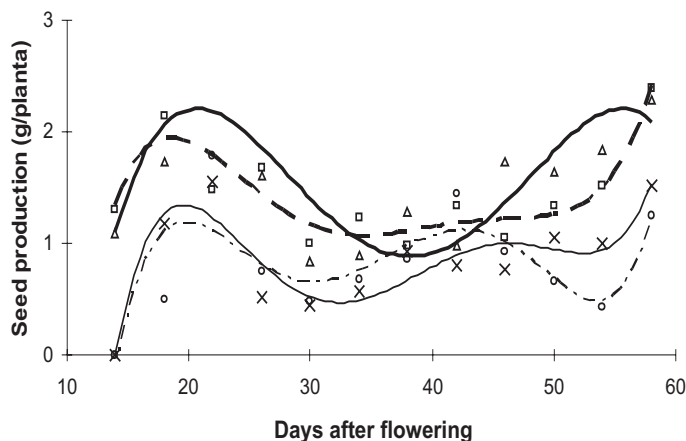


FIGURE 5. Evolution of the daily seed production per plant (PDS/P) in greenhouse grown *M. lathyroides* as a function of days after flowering under two levels of water availability (100%, A, and 60%, S, FC), and two leaf orientation treatments (freely orienting leaves, L, and horizontally restricted, H). Porto Alegre, RS – 2003.

one. The SL treatment showed the same trend as SH, with a first peak of PS on the 20th day, another on the 45th, and the beginning of a third one at around 58 days.

The cyclic behaviour observed in all treatments can be justified by the indeterminate growth habit of the species. The *M. lathyroides* inflorescences emitted flowers staggeringly during the evaluated flowering period.

The seed production (PS/P) was obtained through the sum of PDS/P throughout the flowering period. Water availability had the only significant effect observed on this variable ($p=0.0008$), no significant effect was observed for heliotropism ($p=0.2135$) or the interaction water availability x heliotropism (0.5513).

Plants under 60% of the field capacity (FC) presented an average reduction of 44% in the total seed production, regardless of leaf orientation. This treatment showed an average of 6.8g seeds per plant throughout the experimental period, while the 100% FC treatment showed an average of 12.1g seeds per plant. This difference may be attributed to some of the seed yield components, because the PS/P is a function of the S/L, PIS, and NLM/P, and this last component depends on the NI/P and NF/I. Although the PIS was superior in plants under 60% FC, and the S/L did not show any difference between the treatments, NLM/P showed much higher values

on plants under 100% FC.

Plants with restricted leaves showed a reduction of about 20% in PS when compared to the heliotropic leaves (average of 10.35g in heliotropic leaves and 8.53g in restricted leaves), although this difference was not significantly different ($p=0.2135$). The partial movement of the leaves with painted pulvinus (especially the ones at the top of the canopy) on very hot days may have influenced this response. Therefore, the differences in NF/P, NLV/P and NLM/P between plants with freely oriented and restricted leaves may have been reduced because of the reduced heliotropism presented by the painted pulvini leaves.

CONCLUSIONS

Under favourable water availability, heliotropism induced an increase in yield components. This response was due to the higher vegetative/reproductive development of the plants. However, under low water availability, leaf orientation had no effect on the yield components.

Total seed production per plant was influenced only by the degree of soil moisture.

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