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Growth of the crabgrass species *Digitaria ciliaris* and *Digitaria nuda*

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GROWTH OF THE CRABGRASS SPECIES *Digitaria ciliaris* and *Digitaria nuda*¹

*Crescimento das Espécies de Capim-Colchão *Digitaria ciliaris* e *Digitaria nuda**

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ABSTRACT - The aim of this research paper was to compare the growth of *D. ciliaris* and *D. nuda* crabgrass species under non-competitive conditions. To this end, two experiments were conducted, one from March - July 2010 and the other from February - June 2011. The experimental design of both trials was completely randomized making a factorial (2 seasons x 2 species crabgrass x 12 evaluation periods) with four replications. Assessments began at 15 days after sowing (DAS), and repeated weekly until 92 DAS. The variables evaluated were total dry matter (roots+leaves+stems), leaf area, leaf number and tiller. The results were submitted to analysis of variance and the absolute growth rate, relative growth rate and leaf area ratio were calculated using the means, which were adjusted regression models. The crabgrass species were significantly different in leaf area, leaf number, tiller number and dry matter per plant. *D. ciliaris* for all variables was statistically higher than *D. nuda*. Regarding the speed at which the growth of the species occurred, the absolute growth rate and relative growth rate of *D. ciliaris* was also greater than *D. nuda*. In addition, *D. ciliaris* also had a lower leaf area ratio indicating greater efficiency in converting light energy into carbohydrates. It can be concluded that *D. ciliaris* has a higher growth rate in conditions where there is no limitation of nutrients and water availability in relation to *D. nuda*, mainly due to *D. ciliaris* have greater leaf area, number of leaves and dry matter accumulation per plant.

Keywords: growth curve, competitive ability and weed biology.

RESUMO - O objetivo da presente pesquisa foi comparar o crescimento das espécies de capim-colchão *D. ciliaris* e *D. nuda*, em condições não-competitivas. Para isso, foram conduzidos dois experimentos, um de março a julho de 2010 e outro de fevereiro a junho de 2011. O delineamento experimental de ambos os ensaios foi inteiramente casualizado, perfazendo um esquema fatorial (2 épocas x 2 espécies de capim colchão x 12 períodos de avaliação), com quatro repetições. As avaliações iniciaram-se aos 15 dias após a semeadura (DAS), e repetidas semanalmente até os 92 DAS. As variáveis avaliadas foram massa seca total (raízes+folhas+colmos), área foliar, número de folhas e de perfilho. Os resultados foram submetidos a análise de variância e com as médias foram calculadas a taxa de crescimento absoluto, taxa de crescimento relativo e a razão de área foliar, as quais foram ajustadas a modelos de regressão. As espécies de capim-colchão diferiram entre si quanto a área foliar, número de folhas, número de perfilho e matéria seca por planta. *D. ciliaris* para todas as variáveis obteve média estatisticamente superior em relação a *D. nuda*. Em relação à velocidade com que o crescimento das espécies ocorreu, a taxa de crescimento absoluto e relativo de *D. ciliaris* também foi superior a *D. nuda*. Além disso, *D. ciliaris* também teve menor razão de área foliar indicando maior eficiência na conversão de energia luminosa em carboidratos. Pode-se concluir que *D. ciliaris* apresentar maior crescimento, em condições onde não há limitações de nutrientes e disponibilidade hídrica, em relação a *D. nuda* principalmente por apresentar maior área foliar, número de folhas e acúmulo de matéria seca por planta.

Palavras-chave: curva de crescimento, habilidade competitiva e biologia de plantas daninhas.

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INTRODUCTION

Among known weeds, there are some species of crabgrass that stand out as important in Brazilian agriculture such as *Digitaria ciliaris*, *D. nuda*, *D. bicornis*, and *D. horizontalis*. They are plants belonging to the botanical family Poaceae (Gramineae), subfamily of Panicoideae, the Paniceae tribe, with fairly wide distribution in Brazil, present in the Northeast, Midwest, Southeast and South (Canto-Dorow, 2001; Dias et al., 2007). These species of crabgrass are highly aggressive and reported as being a problem in 60 countries, infesting more than 30 economically important crops. In Brazil, they constitute serious problems in many annual crops and semi-annual crops such as sugarcane. They are particularly skilled in the process of competition, causing damage to crops and nurseries. They also have advantages over crops under dry conditions, in addition to having allelopathic effects on several crops (Kissmann & Groth, 1997).

However, in the Brazilian southeastern sugarcane fields, a change has been observed in the population dynamics of *Digitaria* species occurrence, popularly known as the “*Digitaria* species complex.” Among the observed proportions in the complex *D. nuda* has dominated communities in which it was previously considered rare (Dias et al., 2007). One reason for this change in the dynamics of the *Digitaria* species is the continuous application, for several years, of herbicides inhibiting photosystem II (PSII) and/or herbicides of the imidazolinone chemical group (inhibitors of acetolactate synthase (ALS). To these herbicides, *D. nuda* presents a lower differential susceptibility than other species of *Digitaria*, thus justifying the increased frequency of this species in the *Digitaria* complex of sugarcane fields (Dias et al., 2005).

In studies conducted by Dias et al., (2003) *D. nuda* showed greater tolerance in relation to *D. ciliaris*, but the mechanism of tolerance is not yet fully understood. It was observed that the differential foliar absorption and translocation of herbicides by *Digitaria* plant are not related to the mechanisms tolerance. The differential susceptibility, presented by

the crabgrass species, has undermined the effectiveness of some commercial products used in chemical control in the sugarcane crop (Dias et al., 2007).

In addition to the selection pressure that herbicides have on the population dynamics of weed species, it is also important to consider the ecological adaptability of the species present in the plant complex. Knowledge of ecological adaptability may partly explain the reasons for the predominance of one species over another in the weed community, especially when these species are of the same genus. Ecological adaptability is usually defined as reproductive success or the proportion of genes that an individual plant leaves in the gene pool of the population (Christoffoleti, et al., 1994). The two fundamental components of ecological adaptation are survival and reproduction (Silvertown, 1987).

Herbicides impose a great selection pressure, which can lead to changes in the weed community. Thus, in quite restrictive environments such as those subject to herbicides, the adaptation of a species into this new environment can often be accompanied by the development of negative pleiotropic genes affecting the fitness to the original environment. This phenomenon is called the cost of adaptation (Purrington, 2000; Vila-Aiub et al., 2009). There may be differences in the pattern of growth and development of resistant and tolerant plants in relation to susceptible plants in conditions where there is no picker herbicide effect, causing the susceptible individuals have greater competitive ability and high frequency in environments with low selection pressure (Baucom & Mauricio, 2004). Implementing the integrated management of weeds effectively is fundamental to understanding the biology of the weed species present in the area (Ravindra et al., 2008). Thus, integrated management of the *Digitaria* species complex is necessary in order to expand the knowledge of the biology of the genus *Digitaria* species, tolerant and susceptible to herbicides.

In general, if a plant has greater competitive ability in relation to other plants, these basically have fast leaf expansion, rapid initial growth and a long development cycle to ensure advantage in the use of environmental

resources (Balbinot Jr et al., 2003). Therefore, if a plant is tolerant and/or resistant, the fitness cost can be detected by comparing its growth and development to that of susceptible plants. A widely used and easy way to infer the contribution of different physiological processes for plant growth is with growth analysis (Benincasa, 2003; Carvalho et al., 2008), making available the knowledge of the kinetics of plant biomass production, distribution and efficiency, along with the plant ontogeny. The objective of this study was to compare the growth between crabgrass species, related to the hypothesis that the larger development of *D. ciliaris* inhibits the occurrence of *D. nuda* where herbicide factors are not present.

MATERIAL AND METHODS

The study was carried out in a greenhouse (without environmental control) over two seasons: from March-July 2010 and February-June 2011. The experimental design used in each experiment (season) was completely randomized in factorial arrangement with four replications. The factors were two crabgrass species (*Digitaria ciliaris* and *Digitaria nuda*) and 12 evaluation periods: 15, 22, 29, 36, 43, 50, 57, 64, 71, 78, 85 and 92 days after sowing (DAS) in each period. The experimental units were pots with 1.1 L capacity, filled with soil fertilized with doses proportional to the application of 500 kg ha⁻¹ of the commercial formula 10-10-10 (NPK), and irrigated daily through an automatic irrigation system to eliminate potential water deficiency. The pots were maintained free of infestations of other weed species manually. The physico-chemical properties of soil used in both experiments are available in Table 1. The diaspores of both species were collected from commercial areas of sugarcane crops in Sao Paulo state, Brazil. After collection, they were taxonomically identified according to the analytical identification key proposed by Canto-Dorow (2001) and packed in paper bags (and kept) in a dry place at room temperature until the onset of labor. The diaspores of each of the two grass species were sown in pots separately in quantities necessary for the emergence of five seedlings. When they were in the developmental stage of two true leaves,

thinning was carried out in order to leave only one plant per pot.

In each evaluation, the plants were sampled by the destructive method and washed in running water to remove the remaining substrate from the roots. The leaves were spent on a leaf area meter LICOR LI-3100(LI-COR, inc., Lincoln, Nebraska, USA) model. Then the leaves were placed in paper bags and other parts of the plant were separated into stems and roots for the drying of the material in an oven at 70 °C for 72 hours. Moreover, the number of green leaves and number of tillers produced by species of crabgrass throughout the experimental period were counted.

The data of total dry matter (leaves+stems+ roots), leaf area, number of green leaves and tiller number were subjected to analysis of variance. The data were submitted to the Tukey test (p<0,05) to verify differences between species in each evaluation. The absolute growth rate (g day⁻¹), which provides an estimate of the average speed of plant growth throughout the development cycle, and the relative growth rate (g g⁻¹ day⁻¹) which expresses the growth in grams dry matter per unit of material present in an observation period, were calculated with the averages of these variables (Benincasa, 2003; Carvalho et al., 2008). The leaf area ratio (LAR) (cm² g⁻¹), which is the amount of leaf area needed to produce one gram of dry matter (Benincasa, 2003; Silva et al., 2005), was also calculated. All variables were subjected to nonlinear regression in order to model the growth of the species.

Table 1 - Physicochemical analysis of the soil used in the experiments (March-June 2010 and February-May 2011) growth and development of *D. ciliaris* and *D. nuda*

Texture (%) ^{1/2}			pH	O.M.	P	V
Sand	Silt	Clay	(CaCl ₂)	(g dm ⁻³)	(mg dm ⁻³)	(%)
77	3	20	4.4	48	4	48
Exchangeable cations (mmol _c dm ⁻³)						
K ⁺	Ca ²⁺	Mg ²⁺	SB	H+Al	CEC	
0,1	15	9	24.1	26	50.1	

^{1/2} Medium textured sandy. SB – sum of bases; CEC – cation exchange capacity; V – base saturation; O.M. – organic matter.



The total dry mass, number of tillers, the relative growth rate and leaf area ratio were adjusted to the nonlinear regression model of the logistic type, adapted from Streibig (1988):

$$y = \frac{a}{1 + \left(\frac{x}{b}\right)^c}$$

where y is the response variable of interest, x the number of accrued days and a , b , and c are estimated parameters of equation (a is the amplitude between the peak and minimum of the variable; b is the number of days needed for the occurrence of 50% of the variable response and c is the slope of the curve around b) (Carvalho et al., 2008).

Leaf area, leaf number and the absolute growth rate were adjusted to the nonlinear regression of the log-normal type, with three parameters (adapted from Limpert et al., 2001; Ferreira Junior, 2010):

$$y = a \exp \left[-0,5 \left(\frac{\ln(x/b)}{c} \right)^2 \right]$$

where y is the response variable of interest, x the number of accrued days and a , b , and c are estimated parameters of equation (a is the amplitude; b is the value of x in which y is the maximum and c indicates the degree of decay of the variable y).

RESULTS AND DISCUSSION

Significant differences were found among the days after sowing for all variables (Table 2). This fact was expected given that the growth of a plant over time is directly related, by means of size variation, to some resulting aspect of photosynthesis liquid (Benicassa, 2003). Significant differences between the seasons of the study, for all variables, were also found (Table 2). This indicates that the species suffered influences of the environment in which they were studied, mainly because there was no environmental control of the greenhouse where the studies were conducted.

Even with the environmental changes, the species differed in all variables (Table 2). It was found that *D. ciliaris* obtained more leaf area, leaf number, number of tillers and dry matter in relation to *D. nuda*. For a greater understanding of the behavior of the species, an unfolding of the interaction of the species with days after sowing along with the nonlinear equations that model the growth, were presented. The behavior of the species is better understood when one observes the species unfolding with days after sowing. This is represented by the nonlinear characteristics of the growth variables of the species (Figures 1-7). The parameters of the models used to describe the behavior of the dry matter, leaf area, leaf number, tiller number, absolute growth rate, relative growth rate and leaf area ratio during the development cycle of the crabgrass species are shown in Table 3. They indicate that the equations used have good

Table 2 - Average of variables of the two study seasons of growth of two crabgrass species, with the results of analysis of variance

Specie	Leaf area	N° of leaves	N° tiller	Dry matter
<i>D. ciliaris</i>	131.287A	31.489A	13.057A	5.823A
<i>D. nuda</i>	86.693B	28.176B	11.142B	2.415B
F DAS ^{1/}	241.571**	105.698**	75.823**	294.708**
F sp. ^{2/}	291.095**	15.257**	22.062**	994.574**
F season	1050.83**	417.286**	348.305**	1639.263**
F DAS x sp. ^{2/}	29.893**	13.736**	5.959**	45.480**
F DAS x season	123.002**	55.156**	33.171**	211.119**
F sp. x season	12.257**	0.266	16.225**	193.423**
F sp. x season x DAS	14.985**	5.947**	6.382**	41.074**
CV(%)	15.91	18.86	22.35	17.40

^{1/} DAS = days after sowing; ^{2/} sp. = specie; ** significant (p<0,01); * significant (p<0,05).

Table 3 - Model parameters and determination coefficient obtained for the modeling of the variables of growth and development of two crabgrass species

Variable	Specie	Parameters			R ²	F
		a	b	c		
Leaf area ^{2/} (cm ²)	<i>D. ciliaris</i>	239.258**	52.616**	0.329**	0.867	33.667
	<i>D. nuda</i>	146.502**	55.887**	0.348**	0.791	19.950
N° Leaves ^{2/} (per plant)	<i>D. ciliaris</i>	49.812**	55.953**	0.369**	0.855	30.559
	<i>D. nuda</i>	41.296**	66.205**	0.431**	0.817	23.269
N° tiller ^{1/} (per plant)	<i>D. ciliaris</i>	18.685**	37.275**	-4.303*	0.817	23.329
	<i>D. nuda</i>	15.098**	38.152**	-5.664*	0.815	23.081
Dry matter ^{1/} (g per plant)	<i>D. ciliaris</i>	12.580**	57.347**	-4.240**	0.953	103.012
	<i>D. nuda</i>	5.243**	57.704**	-4.606	0.689	12.117
Abs.Growth rate ^{2/} (g day ⁻¹)	<i>D. ciliaris</i>	0.397**	71.066**	0.527**	0.591	6.049
	<i>D. nuda</i>	0.599**	73.698*	0.145	0.909	41.031
Rel.Growth rate ^{1/} (g g ⁻¹ day ⁻¹)	<i>D. ciliaris</i>	0.685**	35.357*	15.894	0.946	71.114
	<i>D. nuda</i>	0.545**	37.459**	7.787*	0.938	46.133
Leaf area ratio ^{1/} (cm ² g ⁻¹)	<i>D. ciliaris</i>	2376.417	7.313	2.075*	0.995	1036.719
	<i>D. nuda</i>	312.856**	35.188**	3.373*	0.967	162.874

^{1/} Model: $y = a/(1+(x/b)^c)$; ^{2/} $y = a \exp(-0,5(\ln(x/b)/c)^2)$; ** significant ($p < 0,01$); * significant ($p < 0,05$).

application for biological interpretation of the growth of *D. ciliaris* and *D. nuda*, evidenced by the high coefficient of determination of the curves.

The leaf area of crabgrass plants varied over the experimental evaluation cycle (Figure 1). In the beginning of the cycle, 15 and 22 DAS, the species did not differ. But from 29 DAS *D. ciliaris* showed a leaf area per plant quantitatively greater than *D. nuda* for most of the cycle. Finally, the two species reduced the leaf area at the end of the cycle due to the senescence of the plants, which were not statistically different from each other at this point in the cycle. In addition, the first had reached its maximum growth at 52 DAS while *D. nuda* peaked at 55 DAS (parameter *b* in Table 3). Similarly to what happened in leaf area, leaf number of the species did not differ at 15 and 22 DAS (Figure 2). After this, *D. ciliaris* had a greater number of leaves compared to *D. nuda* most of the cycle. In addition *D. ciliaris* reached the maximum number of leaves at 55 DAS, while *D. nuda* reached this parameter to 66 DAS (parameter *b* in Table 3). This indicates that *D. ciliaris* has a tendency to complete its growing season earlier than *D. nuda* (Figure 2).

As the leaf area is responsible for the interception of photosynthetically active radiation and subsequent conversion of light energy into biomass, this is a variable that greatly influences plant growth (Lisazo et al., 2003). Thus, the behavior exhibited by *D. ciliaris* makes this species have greater potential for biomass production in relation to *D. nuda*. In addition, *D. ciliaris* completes the cycle more quickly, because the leaf development stage involves the issuing of new leaves, leaf expansion and senescence newly issued from old leaves (Pourreza et al., 2009). This is evidenced by the fact that *D. ciliaris* obtains a maximum leaf area and number of leaves above the *D. nuda*. Another fact that has to be noted is that in some cases the leaf area may influence interspecific competitive ability because of the potential biomass production.

In studies with cultivars of wheat (*Triticum aestivum*) in an attempt to select some morphological characteristics to increase the competitive ability against *Avena fatua*, the authors concluded that the plant cultivars that had the largest number of productive tillers per plant, height, leaf area and fast growth rate in height are those with strong



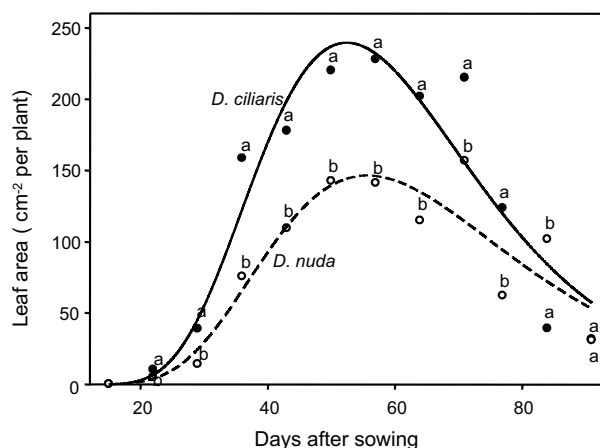


Figure 1 - Leaf area of crabgrass plants as a function of days after sowing of the species *D. ciliaris* and *D. nuda*. The values † represent the average of two periods evaluated. Different letters indicate significant differences between crabgrass species within the same day after sowing. ($p < 0.05$, Tukey's test).

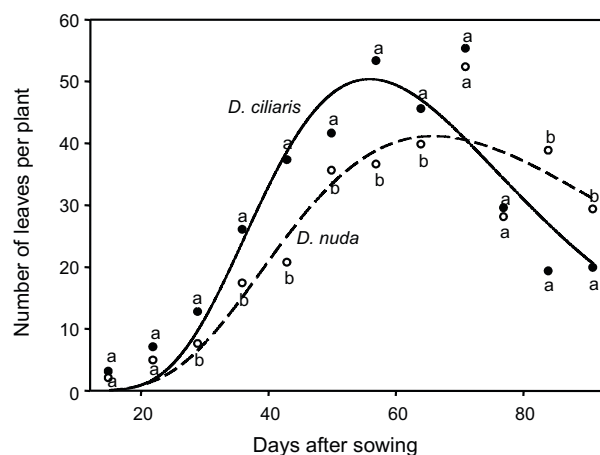


Figure 2 - Number of leaves of crabgrass plants as a function of days after sowing of the species *D. ciliaris* and *D. nuda*. The values † represent the average of two periods evaluated. Different letters indicate significant differences between crabgrass species within the same day after sowing. ($p < 0.05$, Tukey's test).

competitive ability (Bogale et al., 2011). Carvalho et al. (2008) observed differences in the number of leaves and leaf area of weed species belonging to the same genus, which evaluated the growth and development of species of the genus *Amaranthus*. *A. viridis* which showed greater leaf area during the initial phase of the vegetative cycle had the greater ecological adaptability in relation to

others. In addition to these factors, other factors must be taken into consideration, such as allelopathy and plant plasticity in the environment, in the ecological adaptations of the species (Zuo et al., 2008).

The number of tillers of crabgrass species varied over the experimental evaluation cycle. The species differed at 43, 57 and 92 DAS, where *D. ciliaris* had a greater number of tillers (Figure 3). *D. ciliaris* needed 37 DAS to issue 50% of the maximum tiller while *D. nuda* spent 38 DAS to reach this parameter (parameter *b* in Table 3). The specie with the highest leaf area and leaf number also obtained more tillers per plant. Therefore *D. ciliaris*, due to its greater ability to capture light energy, was able to generate more tillers per plant and consequently higher biomass in relation to *D. nuda*.

As did the leaf area, the dry matter of crabgrass plants varied during the cycle of the species studied (Figure 4). Plants with higher leaf area, number of leaves and tillers during the experimental period (*D. ciliaris*) produced higher amounts of dry matter compared to plants with lower variables (*D. nuda*). However, the species reached only 50% of its maximum dry matter at 57 and 58 DAS, respectively (parameter *b* in Table 3). The dry matter accumulation during the course of a species' cycle is closely related to its ability to compete with other plants. It directly reflects resource capture ability. This fact was observed by Gaudet & Keddy (1988) when they tested the competitive abilities of 44 herbaceous plant species in experiments with pots and found that biomass was a good predictor of competitiveness. It explained 63% of the variation in competitive ability. Lopez-Ovejero et al. (2007), through studies of plant populations of *D. ciliaris*, resistant (R) and susceptible (S) to ACCase inhibitor herbicides found that the R and S biotypes show no difference in dry matter accumulation in non-competitive conditions. Therefore these biotypes are competitive equivalents, and the R biotype showed no fitness cost for the development of resistance. But in some cases, the R and S biotypes may differ in dry matter of plants and fitness cost, as in the case of *Amaranthus powellii*, which is resistant to ALS herbicides (Tardif et al., 2006). Thus, the

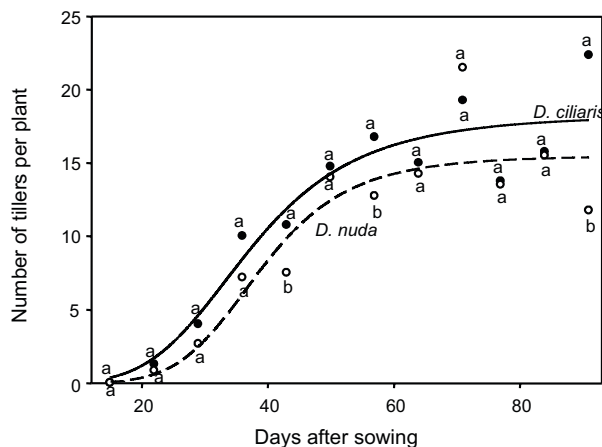


Figure 3 - Number of tillers of crabgrass plants as a function of days after sowing of the species *D. ciliaris* and *D. nuda*. The values † represent the average of two periods evaluated. Different letters indicate significant differences between crabgrass species within the same day after sowing. ($p < 0.05$, Tukey's test).

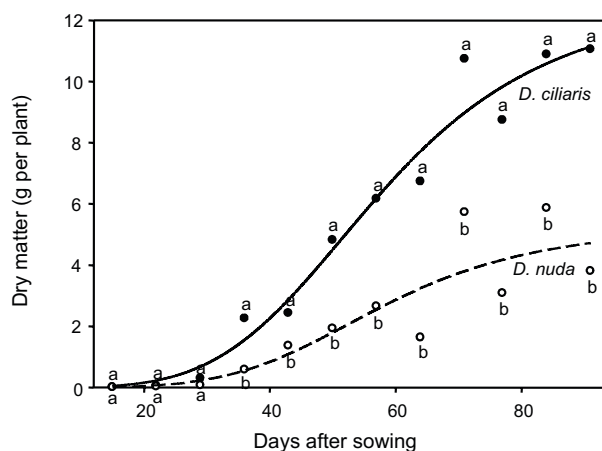


Figure 4 - Dry matter of crabgrass plants as a function of days after sowing of the species *D. ciliaris* and *D. nuda*. The values † represent the average of two periods evaluated. Different letters indicate significant differences between crabgrass species within the same day after sowing. ($p < 0.05$, Tukey's test).

species of crabgrass have distinct competitive ability and a possible fitness cost for the tolerance shown by *D. nuda*, which accumulated less dry matter.

The absolute growth rate of the species of crabgrass increased slowly at the beginning of the experimental period (Figure 5). The rate remained higher during growth of *D. ciliaris*

in relation to *D. nuda*. Thus, the model employed by *D. ciliaris* reached an absolute maximum growth rate at 71 DAS, while *D. nuda* reached this parameter at 73 DAS (parameter b in Table 2). This fact contributed to the greater accumulation of dry matter per plant for *D. ciliaris* in relation to *D. nuda*. Another factor that contributed to *D. ciliaris* having greater plant dry matter was that it had a higher relative growth rate than *D. nuda* in the initial phase of the cycle (Figure 6). The growth rate has been a key feature used to describe plants with different ecological strategies. Plants with high relative growth rate in the early stages of the cycle of growth,

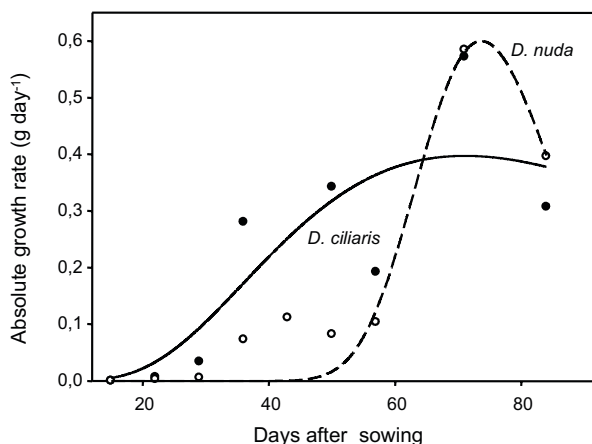


Figure 5 - Absolute growth rate of crabgrass plants as a function of days after sowing of the species *D. ciliaris* and *D. nuda*. The values † represent the average of two periods evaluated.

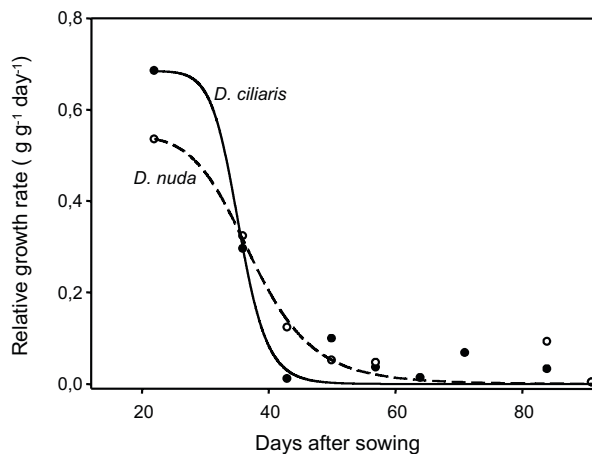


Figure 6 - Relative growth rate of crabgrass plants as a function of days after sowing of the species *D. ciliaris* and *D. nuda*. The values † represent the average of two periods evaluated.



aimed at rapid acquisition of nutrients in environments without limitations is a feature associated with annual grasses in general (James et al., 2011).

Finally, the leaf area ratio also proved to be different between crabgrass species (Figure 7). The species with the highest leaf area and dry matter accumulation was the one with the lowest LAR during most part of the cycle. Thus, there is evidence of greater efficiency in converting solar energy into carbohydrates by *D. ciliaris*. The lower efficiency in the production of dry matter of *D. nuda* may be associated with reduced photosynthetic potential, as in cases where exists resistance to triazines, where resistant biotypes, because of this low potential, exhibit reduced growth rate, low competitive ability for resources and poor sexual reproduction, depending on the environmental conditions to which the plants are subject (Arntz et al., 2000).

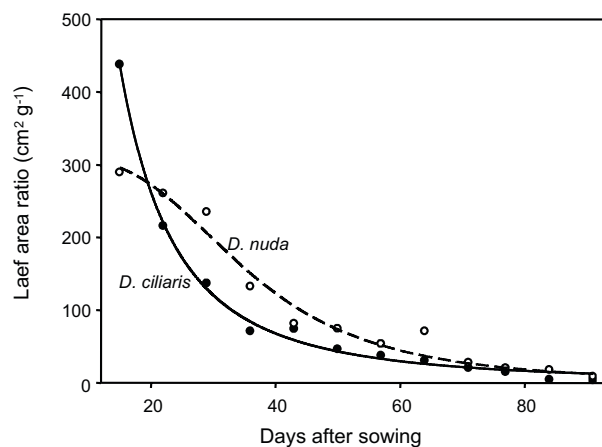


Figure 7 - Relative growth rate of crabgrass plants as a function of days after sowing of the species *D. ciliaris* and *D. nuda*. The values † represent the average of two periods evaluated.

With these results, further studies are suggested for a better understanding of the fitness costs presented by *D. nuda*. In addition to vegetative growth, there may be other costs such as those relating to the process of seed production, a fact already observed in relation to the tolerance of glyphosate presented by *Ipomoea purpurea* (Baucom & Mauricio, 2004). It is also suggested the discovery of a molecular

and biochemical basis of tolerance by *D. nuda*, in order to advance the knowledge of fitness costs related to this species (Vila-Aiub et al., 2009). It can be concluded that *D. ciliaris* has a higher growth under conditions where there are no limitations of nutrients and water availability in relation to *D. nuda*, mainly due to its greater leaf area, number of leaves and dry matter accumulation.

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