



Interaction between increased CO₂ and temperature enhance plant growth but do not affect millet grain production

Gabriela Viana de Oliveira Lima¹, Yumi Oki¹, Leandra Bordignon², Wallison Kenedy Siqueira¹, Marcel Giovanni Costa França³, Daniela Boaneres³, Augusto César Franco⁴ and Geraldo Wilson Fernandes^{1*} 

¹Departamento de Genética, Ecologia e Evolução, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos, 6627, Cx. Postal 486, 31270-901, Belo Horizonte, Minas Gerais, Brazil. ²Centro Multidisciplinar, Universidade Federal do Acre, Cruzeiro do Sul, Acre, Brazil.

³Departamento de Botânica, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil. ⁴Departamento de Botânica, Universidade de Brasília, Brasília, Distrito Federal, Brazil. *Author for correspondence. E-mail: gw.fernandes@gmail.com

ABSTRACT. The intergovernmental panel on climate change predicts a progressive increase in atmospheric CO₂ concentration and temperature; however, their effects on cereals have been shown for a limited number of species. This study evaluates the effects of increased CO₂ concentration and temperature separately and combined on millet growth and grain production in open-top chambers where the microclimate was adjusted to the following conditions: ambient CO₂ and temperature; CO₂ enriched (~ 800 ppm) and ambient temperature; ambient CO₂ and higher temperature (+3°C); and CO₂-enriched and higher temperature. For each treatment, two chambers were used, each containing 15 7 L pots. Each pot received five seeds at the beginning of the experiment and thinning to one plant per pot at 15 days after sowing. Ten plants were harvested from each chamber 65 days after sowing and the plant height, the number of leaves and the longest root length as well as shoot and root biomass were measured. The remaining plants were harvested 130 days after sowing to evaluate grain production. The results indicate that high CO₂ levels did not affect plant growth and biomass. On the other hand, plants subjected to high temperature grew 7% taller than those grown under ambient temperature. Contrastingly, plants submitted to both elevated CO₂ and temperature were 19% taller and had 22% more shoot biomass than plants under ambient CO₂ and temperature. However, grain production did not change in any of the environmental conditions. We provide evidence that millets are tolerant of the predicted climate changes and that grain production potential may not be affected.

Keywords: climate change; C₄ plants; grain production; adaptive responses.

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Introduction

Carbon dioxide (CO₂) concentration in the atmosphere has increased since the industrial revolution. In the mid-eighteenth century, it was 280 ppm (Intergovernmental Panel on Climate Change [IPCC], 2013), increasing to 403 ppm in 2016 (World Meteorological Organization [WMO], 2017), and the forecast is between 700 and 1010 ppm by 2100 (IPCC, 2013). The predicted high level of CO₂ may lead to a substantial temperature increase of up to 4.8°C by the end of this century (Sage & Kubien, 2007; IPCC, 2013). Several studies have shown that plants will respond directly to the increase in atmospheric CO₂ and temperature (Friend, 2010; Martinez, Oliveira, Mello, & Alzate-Marin, 2015). The CO₂ is assimilated in photosynthesis and its concentration increase in the atmosphere may influence carbon uptake and assimilation rate and therefore plant growth (Shine, Fuglestedt, Hailemariam, & Stuber, 2005; Leakey, 2009; Gray & Brady, 2016).

Temperature also has an important role in plant physiology due to the close relationship with transpiration, respiration and photorespiration (Sage & Kubien, 2007). However, above the optimum temperature range, metabolic activity may become unfeasible, leading to losses in plant growth, reproduction and survival (Streck, 2005; Gray & Brady, 2016). The effect of CO₂ and temperature may vary according to the plant photosynthetic mechanism of CO₂ fixation (Liang, Xia, Liu, & Wan, 2013; Martinez et al., 2015). Generally, in the absence of limitations by nutrients or water, plants with C₃ metabolism increase biomass accumulation in response to a rise in CO₂ concentration (Liang et al., 2013; Bishop, Betzelberger, Long, & Ainsworth, 2014; Gray & Brady, 2016). In contrast, an atmospheric CO₂ concentration increase is expected to have little or no direct effect on RuBisCO activity in C₄ plants and consequently in the CO₂ assimilation of

these species (Leakey, 2009). Because C_4 plants can concentrate CO_2 in RuBisCO active sites, they are also less bound to suffer carbon losses from photorespiration (Sage & Kubien, 2003; Martinez et al., 2015). In fact, they reach maximum rates of CO_2 assimilation in higher temperatures (> 25 to $30^\circ C$), when compared to C_3 plants (below $20^\circ C$; Ehleringer, Cerling, & Helliker 1997; Sage & Kubien, 2003).

Despite the atmospheric CO_2 increase being associated with temperature increase (IPCC, 2014), most of the studies have considered such factors separately (Sá, Negreiros, Fernandes, Dias, & Franco, 2014; Gray & Brady, 2016). In truth, they affect plants jointly (IPCC, 2014). In C_3 plants under CO_2 addition and temperature increase, there is a growth reduction if compared to those only exposed to high CO_2 concentrations (Gray & Brady, 2016). For C_4 plants, the responses to such conditions are still varied and indefinite (Leakey et al., 2006). Some studies reported increases in shoot and root biomass production, while others did not (Vu, Allen Jr., & Gesch, 2006; Ruiz-Vera, Siebers, Drag, Ort, & Bernacchi, 2015; Bordignon, Faria, França, & Fernandes, 2019).

Pearl Millet (*Pennisetum glaucum* [L.] R. Br.) (Poaceae) is an annual warm climate plant from Africa (Bezançon et al., 2009), and together with corn, sorghum and sugarcane, it is among the most cultivated C_4 plants worldwide in tropical regions (Leakey, 2009; Yadav & Rai, 2013). Millet in Brazil is processed almost exclusively for animal food (Pereira Filho et al., 2003). Furthermore, millet is an interesting species to be used as crop cover in tropical areas, particularly in the Cerrado (Brazilian Savannah) (Rosolem, Calonego, & Foloni, 2005). However, considering all the challenges imposed by climate change on biomass, it is essential to understand the effects it may have on millet and how it may influence the application of this planting practice. After all, one of the determinants for the success of no-till systems in tropical regions is the amount of straw accumulated on the soil surface (Rosolem et al., 2005). Therefore, this study aimed at testing the following hypotheses about the effects of CO_2 and temperature increase on millet: i) high CO_2 concentration under ambient temperature will not affect growth and grain production, irrespective of the CO_2 level; ii) warmer temperatures will have a positive effect on growth and grain production; and iii) the positive effect of warmer temperatures on growth and grain production will be more evident on plants subjected to higher CO_2 concentration.

Material and methods

Plant material and experimental design

Pennisetum glaucum seeds from cultivar 'BRS 1501' supplied by Embrapa Milho e Sorgo were used for this experiment. They were cultivated in open-top chambers (OTC) in a greenhouse at the Federal University of Minas Gerais, Belo Horizonte, state of Minas Gerais, Brazil. The chambers had aluminium structures covered by PVC plastic according to Aidar et al. (2002), modified by the inclusion of electrical resistances to increase the temperature inside the chambers, and internal volume of 1.53 m^3 .

To simulate the conditions foreseen by IPCC for 2100 (IPCC, 2013; 2014) the chambers were calibrated and monitored by sensors to keep the following treatments: Control (Ctrl, ambient CO_2 and temperature); +T (ambient CO_2 and increased air temperature at $3^\circ C$ above ambient); +C (high CO_2 at ~ 800 ppm and ambient temperature); and +C+T (high CO_2 and temperature). Eight open-top chambers were used, two for each tested treatment. The CO_2 sources were from pressurised cylinders containing 99.8% CO_2 , 58.3 KgF cm^{-2} . The atmospheric CO_2 concentration in the chambers was constantly monitored through an auto CO_2 meter SBA-4 OEM® (PP Systems). The air moisture content inside the chambers was not controlled.

The experiment was conducted under a natural photoperiod. Measurements of CO_2 , temperature and air relative humidity were stored every 15 min in a computer through a Remote Integrated Control System application (RICS 3.7, Evco), which also regulated temperature and CO_2 concentration in the heated and high CO_2 chambers, to keep experimental conditions stabilised relative to the non-heated, ambient CO_2 chambers. All chambers contained temperature sensors that performed comparisons every 15 min between those exposed to ambient air temperature and those exposed to $+3^\circ C$ and automatically activated the resistance, elevating temperature by $\sim 3^\circ C$ in the high temperature simulating chambers. Temperature averages ($^\circ C$) during the experiment were higher in the +C+T treatment, followed by the +T treatment, the +C treatment, and the Ctrl (Figure 1A). Average relative humidity (%) was lower in the +C+T treatment, followed by the +T treatment, the +C treatment, and the Ctrl (Figure 1B).

The averages of CO_2 concentration (ppm), temperature ($^\circ C$), and relative humidity (%) in the treatments were for (1) the Ctrl 407.0 ppm of CO_2 , $22.95^\circ C$ and 60.1% of relative humidity (RH); (2) +C+T: 771.5 ppm, $25.95^\circ C$ and 49.65% of RH; (3) +C: 783.0 ppm, $24.0^\circ C$ and 59.1% RH; and (4) +T: 386.5 ppm, $26.65^\circ C$ and 54.7% of RH.

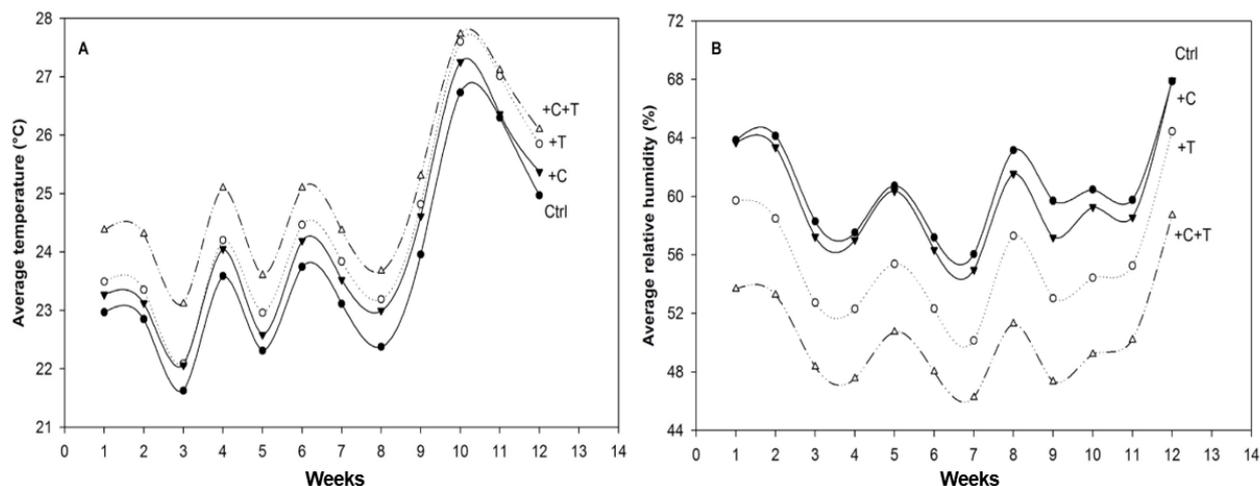


Figure 1. Average air temperature (°C) and relative humidity (%) in open-top chambers exposed to the following environmental conditions: (1) Ctrl (ambient CO₂ and temperature); (2) +T (ambient CO₂ and elevated air temperature at 3°C above ambient); (3) +C (high CO₂ ~ 800 ppm and ambient temperature) and (4) +C+T (high CO₂ and temperature).

PVC pots of 32.5 cm height and 7 L volume filled with Terral® commercial sterilised substrate were used. For each treatment, 30 pots (15 per chamber, a total of 120 pots) were numbered, identified, and in each, five seeds were planted. The pots were placed in the open-top chambers and irrigated daily with 300 mL of distilled water (Sá et al., 2014) and 50 mL full-strength Hoagland nutrient solution (Hoagland & Arnon, 1950) every three days. Fifteen days after planting, thinning was performed and only one plant remained in each pot. To avoid possible environmental differences among chambers, pots were exchanged weekly among chambers of the same treatment.

Plant growth measurements

Plant height and number of leaves were measured weekly from 22 to 63 days after planting. To determine the plants' relative growth rate (RGR) in the interval between 22 and 63 days after planting, the following expression was used, according to McGraw and Garbutt (1990): $RGR = (\ln B_2 - \ln B_1) / (t_2 - t_1)$, where: ln, natural logarithm; B, average total height; t, time. After the panicle development phase (65 days of growth), 20 plants of each treatment were randomly selected and removed from the pots and separated into roots, stems, leaves, and panicles. Roots were washed in running water using a sieve and the length of the longest root (cm) was measured using a measuring tape.

After millet maturation, about 130 days of growth, we verified the same number of panicles per plant for each treatment (average \pm standard error): Ctrl = 3.8 ± 0.57 ; +C = 3.6 ± 0.4 ; +T = 3.8 ± 0.3 ; +C+T = 3.7 ± 0.37). We collected the main panicle from 40 plants (10 plants for each treatment) to evaluate the total grain production of the main panicle per plant. Panicles were weighed on an analytical scale (0.0001 g). Subsequently, grains were removed from panicles, placed in a forced-air oven at 60°C and weighed after reaching constant mass (Vu & Allen Jr., 2009). Afterward, we calculated the total grain mass in the main panicle.

Data analysis

The analyses were performed in R software (R Core Team, 2018). Generalised linear models (GLM) were built with adequate distribution error and corrections of distribution performed whenever necessary (Crawley, 2013). The test of each GLM was done through an analysis of variance (Crawley, 2013) and the results with $p < 0.05$ were considered statistically significant.

To investigate the effect of CO₂ increase, the factors high CO₂ (+C) and combined high CO₂ and temperature (+C+T) were grouped into the category '+C ambient' and compared to the category 'C ambient', compounded of the high temperature (+T) and control (Ctrl) factors. Likewise, to investigate the effect of temperature increase, the factors high temperature (+T) and combined high CO₂ and temperature (+C+T) were grouped into the category '+T ambient' and compared to the category 'T ambient', the compound of the high CO₂ (+C) and control (Ctrl) factors. Thus, the explicative variable was composed of treatments +C ambient vs C ambient, +T ambient vs T ambient and +C+T ambient vs Ctrl. Relative growth rate, plant height, number of leaves, longest root length, shoot biomass, mass and number of grains in the main panicle were used as variable responses.

Results and discussion

Millet grown under increased CO₂ concentration had similar relative growth rates, cumulative numbers of leaves formed, numbers of grains produced, grain mass in the main panicle, and total biomass per plant compared to those exposed to ambient CO₂ ($p > 0.05$, Table 1). These results corroborate our first hypothesis that plant growth and grain production in millets are not expected to change under CO₂ enrichment in OTC chambers. Likely, the millet under the increased atmospheric CO₂ was not enough to further increase RuBisCO activity already operating at its maximum rate of catalysis (Edwards & Walker, 1983; Barnaby & Ziska, 2012).

Contrastingly, millets subjected to elevated temperature had an increase in height (6.75% higher, $p = 0.0007$, Table 1, Figure 2A), length of the longest root (5.82% higher, $p = 0.0042$, Table 1, Figure 2B), shoot biomass (8.90% higher, $p < 0.001$, Table 1, Figure 2C), and root biomass (5.82% higher, $p = 0.0008$, Table 1, Figure 2D). However, the elevated temperature did not statistically affect grain production ($p = 0.6096$) and grain mass in the main panicle ($p = 0.6858$, Table 1). These responses under elevated temperature partially corroborate our assumption that millet grown in warmer temperatures presents higher growth and grain production. In general, extremely high temperatures during the reproductive stage affect grain and/or fruit formation (Hatfield et al., 2011). However, the expected temperature rise for the next century from global warming could not affect grain production, although it could favour millet growth. Yet, this scenario of temperature increase has already been observed during El Niño events and intensified by climate changes (IPCC, 2013). It is known that C₄ plants may have a greater capacity for photosynthetic acclimation to high temperature (Yamori, Hikosaka, & Way, 2014), which can result in a modest increase in photosynthetic rate and plant biomass (Dwyer, Ghannoum, Nicotra, & von Caemmerer, 2007).

Table 1. Results of the statistical models (GLM) according to each response variable: 1. CO₂ concentration; 2. Temperature; 3. CO₂ and temperature interaction. The set of statistical models are separated by lines according to the response variable. Values of $p < 0.05$ are in bold.

Response variable	Error distribution	Explicative variable	Df	Deviance	Resid. df	Resid. dev	F	p
Relative growth rate	Gaussian	CO ₂	1	1.4e ⁻⁰⁶	78	0.0021	0.053	0.8179
		Temperature	1	9.6e ⁻⁰⁶	78	0.0021	0.343	0.5594
		CO ₂ and temperature	1	9.3e ⁻⁰⁶	38	0.0013	0.263	0.6110
Plant height	Gaussian	CO ₂	1	1531.2	78	41116	2.904	0.0922
		Temperature	1	5790.2	78	36857	12.25	0.0007
		CO ₂ and temperature	1	6638.4	38	16168	15.60	0.0003
Longest root length	Gaussian	CO ₂	1	9.0245	75	2627	0.257	0.6132
		Temperature	1	273.94	75	2362.1	8.697	0.0042
		CO ₂ and temperature	1	180.6	37	1168.3	5.719	0.0219
Leaf production	Quasipoisson	CO ₂	1	0.03415	78	18.74	0.143	0.7064
		Temperature	1	0.74392	78	18.031	3.240	0.0757
		CO ₂ and temperature	1	0.53232	38	9.9193	2.076	0.1578
Shoot biomass	Gaussian	CO ₂	1	3.1265	74	713.32	0.324	0.5707
		Temperature	1	170.04	74	546.4	23.02	8.0e-06
		CO ₂ and temperature	1	110.2	37	241.11	16.91	0.0002
Root biomass	Gaussian	CO ₂	1	0.1175	78	49.528	0.185	0.6683
		Temperature	1	4.2349	78	45.411	7.274	0.0085
		CO ₂ and temperature	1	1.4708	38	17.93	3.117	0.0855
Grain production in the main panicle	Negative binomial	CO ₂	1	59.607	38	10726	0.242	0.6255
		Temperature	1	66.315	38	10719	0.265	0.6096
		CO ₂ and temperature	1	0.0812	18	6534.1	0.000	0.9870
Grain mass in the main panicle	Gaussian	CO ₂	1	6.3873	38	579.11	0.419	0.5213
		Temperature	1	2.3812	38	583.11	0.1552	0.6958
		CO ₂ and temperature	1	0.4843	18	407.38	0.0214	0.8853

Millets simultaneously subjected to elevated CO₂ and warmer temperatures grew 18.9% more ($p = 0.0003$, Table 1, Figure 2E), had a 9.4% increase in the length of the longest root ($p = 0.0219$, Table 1, Figure 2F), and 22.02% in shoot biomass. However, grain production and grain mass of the main panicle under increased CO₂ and temperature did not vary relative to plants under ambient CO₂. Considering the scenario predicted for climate changes in terms of CO₂ and temperature increases, this millet cultivar would not be affected. Plant growth rate and development are dependent on the optimal average temperatures for each species (Hatfield et al., 2011). However, for most plant species, as the atmospheric temperature rises beyond the ideal, the losses in crop yields accelerate instead of falling at a rate proportional to the temperature increment (Hatfield

& Prueger, 2015). Maximum growth and yields for corn, soy and cotton are reached with temperatures between 29 and 32°C but decrease dramatically with any increase beyond this temperature interval (Schlenker & Roberts, 2009). It is feasible to consider that temperature increases from 23 to 26-27°C would expose millets to a temperature close to the optimum range for CO₂ assimilation. According to Streck (2005), the two most important metabolic functions in determining the extent of plant growth are CO₂ assimilation and water use efficiency, as indicated for C₄ grasses also grown in OTC chambers (Faria, Marabesi, Gaspar, & França, 2018), the same conditions in which millet was grown.

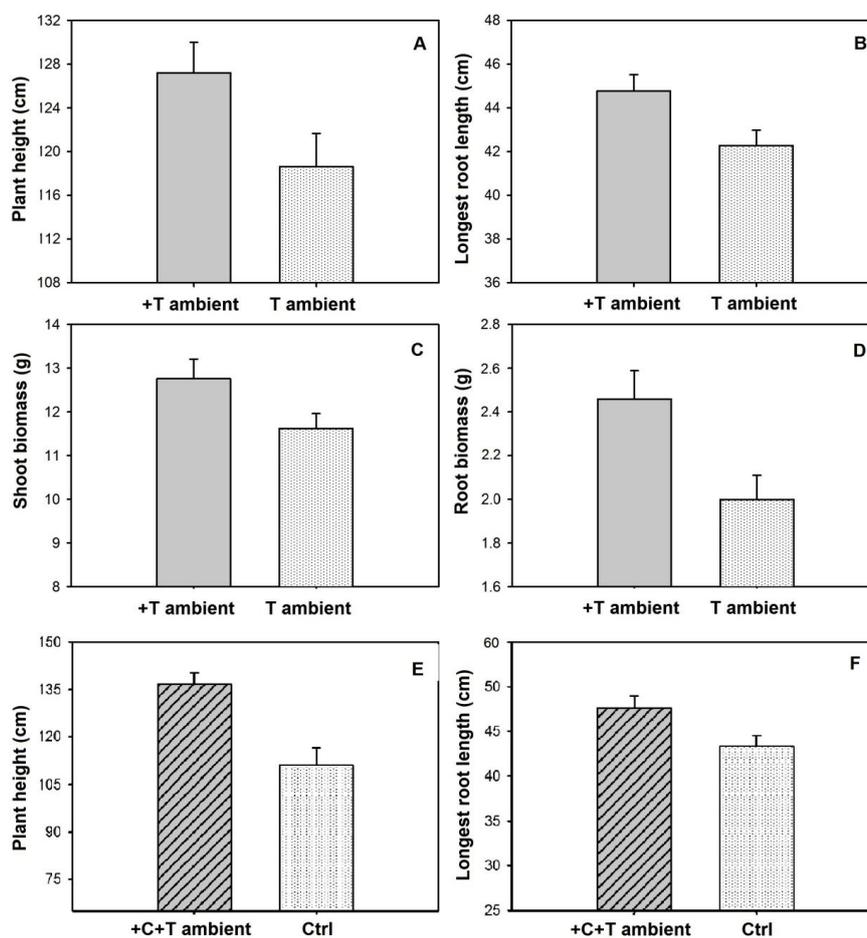


Figure 2. Comparison of growth parameters of millet in open-top chambers. 1. Average (\pm standard error) of height (cm); (A) length of the longest root (cm); (B) shoot biomass (g); (C) and root biomass (g); (D) subjected to elevated temperature (+T ambient, 3°C above ambient temperature) and ambient temperature (T ambient). 2. Average (\pm standard error) of height (cm); (E) and length of the longest root (cm); (F) of millet under both elevated CO₂ and temperature (+C+T ambient) and ambient CO₂ and temperature (Ctrl).

The more significant growth in shoot height and biomass in millets could be an advantage for this cultivar since it is mainly used as forage for feeding cattle and other animals and as silage (Pereira Filho et al., 2003). Indeed, keeping the millet straw on the soil surface provides a considerable reserve of nutrients that can easily become available for the next harvest (Gassen & Gassen, 1996). The longest root length was also higher under these changed environmental conditions. Moreover, the high lignin content of straws could allow an increase in carboxylic and humic acids, making the soil less susceptible to compaction and erosion, improving the structure and stabilisation of soil aggregates (Lanzanova et al., 2007). These changes also promote greater efficiency and a sustainable no-tillage system needed in the face of climate change scenarios (Lanzanova et al., 2007).

Several studies suggest a drop in grain production for plants growing under elevated CO₂ concentration and temperature (Streck, 2005; Ruiz-Vera et al., 2015). However, unlike *Zea mays* (Ruiz-Vera et al., 2015), the grain production of millet was not affected negatively by the treatments. The temperature increase may affect the reproductive development of plants anticipating reproductive events or causing damages by heat in reproductive structures (Gray & Brady, 2016). The lack of negative effects in grain production is likely related to the 'BRS 1501' millet cultivar used in this study, which is considered good for grain production and as a cover crop (Pereira Filho et al., 2003; Rosolem et al., 2005).

Conclusion

We provide evidence that the increased CO₂ concentration or temperature or both conditions predicted by IPCC could positively affect biomass accumulation of *Pennisetum glaucum* without affecting grain production. This increased biomass production represents a greater amount of straw that can assist in covering the soil and recycling nutrients or as forage for animals. This species can, therefore, be resistant to climate change and can be an alternative crop for coverage of soil and as a cover crop in a new environmental scenario.

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