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ALLOCATION OF DRY MATTER AND CARBON IN *Pinus taeda* L. SEEDLINGS SUBJECTED TO THIGMOMORPHOGENESIS

PARTIÇÃO DA MATÉRIA SECA E DE CARBONO EM MUDAS DE *Pinus taeda* L. SUBMETIDAS À TIGMOMORFOGÊNESE

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ABSTRACT

The present study aimed at quantifying the effects of thigmomorphogenesis induced by stem bending in the hardening phase of seedlings of *Pinus taeda* L. on the partitioning of dry matter and carbon. Seedlings of *Pinus taeda* 22 cm high grown in tubes were subjected to five intensities of stem bendings (0, 5, 10, 20 and 40 bendings) performed daily using a mechanical device, for 60 days. Subsequently we quantified the leaf area and the increments in height and diameter. Afterwards, it was determined the increments in dry weight of roots and shoots, which were subdivided into five components: taproot, lateral roots, needles, bark and wood. Along with the resulting dry matter, we determined the carbon concentration and content. The experiment followed a completely randomized design with four replications. The obtained data were subjected to regression analysis at 5% error probability. The thigmomorphogenesis induced by stem bendings resulted in a reduced height growth, leaf area and shoot dry weight, but with up to 20 stem bendings increased the growth rate in diameter and the root dry weight. The changes in primary and secondary growth was a result of the redistribution of carbon and dry matter content in the stem and root system, especially in lateral roots through of reduced leaf area, in terms of area and dry matter. The results suggest that on mechanically disturbed seedlings increase in leaf area ceases to be the preferred sink of carbon, predominating the growth of stem and root.
Keywords: hardening; stem bendings; mechanical disturbances.

RESUMO

O presente trabalho objetivou quantificar os efeitos da tigmomorfogênese induzida por flexões caulinares na fase de rustificação de mudas de *Pinus taeda* L. sobre a partição da matéria seca e de carbono. Mudas de *Pinus taeda* com 22 cm de altura, produzidas em tubetes, foram submetidas a cinco intensidades de flexões caulinares (0, 5, 10, 20 e 40 flexões) realizadas diariamente, com o auxílio de um aparato mecânico, por 60 dias. Ao final, quantificou-se a área foliar e os incrementos na altura e no diâmetro do coleto. Posteriormente, determinaram-se os incrementos na massa de matéria seca de raízes e da parte aérea foram subdivididas em cinco componentes: raiz pivotante, raízes laterais, acículas, casca e lenho. Na matéria seca resultante, foi determinado o teor e conteúdo de carbono. O experimento seguiu o delineamento inteiramente ao acaso com quatro repetições. Os resultados foram submetidos à análise de regressão a 5% de probabilidade de

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erro. A tigmomorfogênese induzida por flexões caulinares resultou na redução do crescimento em altura, área foliar e matéria seca da parte aérea, mas, com até 20 flexões caulinares, promoveu o aumento da taxa de crescimento em diâmetro e matéria seca do sistema radicular. A alteração no crescimento primário e secundário foi resultante da redistribuição de carbono e do conteúdo de matéria seca no caule e no sistema radicular, principalmente em raízes laterais, através de redução de área foliar. Os resultados sugerem que em mudas perturbadas mecanicamente o aumento em área foliar deixa de ser o dreno preferencial de carbono, predominando o crescimento de caule e sistema radicular.
Palavras-chave: rustificação; flexão caulinar; distúrbios mecânicos.

INTRODUCTION

Carbon is the most abundant element in the plant biomass. It is estimated that 45-55% of the biomass is structural carbon or is present in organic compounds. The carbon content depends on the type of organ, plant age and rainfall season (TEDESCO et al., 1995; LACOINTE, 2000). Around 80% of the carbon assimilated by photosynthesis is translocated from the leaves to meet the metabolism of non-photosynthetic cells to maintain growth respiration and other physiological processes (FERNANDES; SOUZA, 2013).

The exposal of terrestrial plants to external mechanical forces results in avoidance, as well as tolerance strategies that may benefit the plant through reducing the risk of mechanical failure, therefore increasing the probability of survival. Biomass and carbon allocation in seedlings of terrestrial woody species are altered by environment stimuli (MALAVASI; MALAVASI, 2001; VILLAR-SALVADOR et al., 2004; COUTAND et al., 2008). Natural disturbances such as wind, hail, soil conditions, gravity, slope, friction, weight load either by overlapping branches or by neighbor plants and accumulation of rainwater affect growth and development as well as limit seedling survival under field conditions (LI; GONG, 2011).

Measurements of changes in carbon uptake and allocation among plant components (i.e. leaves, stem, and roots) because of mechanical disturbances (MD) allows understanding plant growth plasticity. Determination of the effects of MD enlightens morphological changes that promote seedling hardiness in the nursery, enabling survival and fast development after planting. MD can be applied in many ways (GARTNER, 1994) one of which is brushing plant shoots (LATIMER, 1990; WANG et al., 2009).

Studies of allocation of plant biomass and carbon subjected to MD reported a lower biomass accumulation in shoots at the expense of root growth. Reported results showed a lower productivity of plants through reduction of leaf area (WANG et al., 2010; MOREL et al., 2012).

Plant recognition of MD results in a series of physiological changes that culminate in reducing primary growth and increasing secondary growth (TELEWSKI; PRUYN, 1998; COUTAND et al., 2010). Growth response to mechanical stimuli was named thigmomorphogenesis by Jaffe (1973). Among the various physiological effects on growth such as changing wood mechanical properties (CORDERO, 1999; LITTLE; EKLUND, 1999) and stimulation of lignin biosynthesis (ALVAREZ-CLARE; KITAJIMA, 2007; RAMOS et al., 2012), thigmomorphogenesis alters biomass partitioning and carbon allocation resulting in increased number of roots and larger dry root biomass (TAMASI et al., 2005; REUBENS et al., 2009).

Furthermore, CO_2 uptake and its conversion to organic molecules by leaves is directed to areas of growth such as division of xylem cells, formation of a secondary cell wall and extension of the root system (JAEGHER et al., 1985; PRUYN et al., 2000; KERN et al., 2005; COUTAND et al., 2008; MOURA et al., 2010). However, carbon allocation may be reversible, usually linked to seedling acclimation to field conditions (LACOINTE, 2000; MARTIN et al., 2010).

The effects of MD upon carbon dynamics in plants is still not fully elucidated and little evidenced in *Pinus taeda* L. Therefore, knowledge of changes in the carbon uptake and partitioning between plant main components (leaves, stem, and roots) in terms of dry biomass resulting from MD would allow better understanding of growth plasticity.

Determination of the intensity of stimuli through studies of growth in response to MD evidences morphological changes in seedling components that promote greater hardiness in the nursery, enabling acclimation to environmental conditions prevailing at planting. The effects of applying a variable number of stem bending were studied on young *Ulmus americana* L. by Telewski and Pruyn (1998) and *Prunus avium*

L. by Coutand et al. (2008) as well as on seedlings of *Maytenus ilicifolia* (Schrad.) Planch by Volkweis et al. (2014), and *Cordia trichotoma* (Vell.) Arrab. ex Steud by Cadorin et al. (2015).

Conifers represents a large economic potential for the Brazilian southern states, given that 84.7% of the total area is planted with *Pinus* species (1,562,782 ha) with 40% at the state of Paraná (approximately 658,707 ha). Therefore, pine seedling production is important to supply corporative demand for production of cellulose, saw timber and energy (ASSOCIAÇÃO BRASILEIRA DE PRODUTORES DE FLORESTAS PLANTADAS, 2013).

In this context, this study aimed to quantify the effects of thigmomorphogenesis induced by stem bending on the partitioning of dry biomass and carbon in seedlings of *Pinus taeda* L. during the nursery hardening phase.

MATERIAL AND METHOD

Seedlings of *Pinus taeda* L. (RNC 04705) were produced by seeds in a nursery located in Cascavel, Paraná state. Sowing was performed in January 2011, using 90 cm^3 plugs filled with commercial substrate (Mecplant®) placed in flat plastic trays with capacity for 192 plugs. Fertilization consisted of 200 g of controlled-release fertilizer (8 month Osmocote® Plus) of the formulation N_2-P_2O_5-K_2O (15-9-12) in 25 kg of substrate. During this phase no environment monitoring was done.

Seedling production lasted for 8 months in which they remained in the greenhouse for the first four months and exposed to full sun for the four remaining months when tray capacity was reduced to 96 plugs. Seedlings were watered daily close to the saturation capacity.

When seedlings were (mean ± standard deviation) 21.4 ± 1.8 cm high and 3.85 ± 0.38 mm in stem diameter they were transported to facilities located in Marechal Cândido Rondon, Paraná, where treatments were applied for 60 days. The average temperature during that period was 24.43 °C and relative humidity was 62.33%.

The experiment was conducted as a completely randomized design. Treatments consisted of five intensities (0, 5, 10, 20 and 40 bendings) of stem bending performed daily. All seedlings were mechanically bent by a mechanical device developed by Volkweis et al. (2014), comprising a polyvinyl chloride (PVC) pipe bar, 25 mm in diameter filled with cement, horizontally disposed and attached to a metal frame with rollers, which allowed the displacement of the bar on the bench.

The seedlings were bent vertically no more than 45° by passing the bar over the upper third of the seedling, striking the stem at 5.0 cm from the apical bud, in forward/backward direction. Each movement was counted as one bending. The movements were conducted at a speed of 0.10 m s^{-1} once daily in the morning always at 09:00 (local time). Stem bending lasted from September to November 2011, totaling sixty days after which seedlings were outplanted.

Seedling increment in height, stem diameter, and dry biomass of roots (taproot, lateral roots) and shoots (needles, bark and stele) were measured after treatment in four replicates of five seedlings each. We separated lateral roots from taproot with a pruning scissors.

Dry biomass determination used samples in Kraft paper bags kept in air circulation oven at 60 °C for 72 h until constant weight. Dry biomass values of seedling components before treatments were 0.173 ± 0.084 g, 0.502 ± 0.128 g, 0.562 ± 0.174 g, 0.189 ± 0.061 g and 0.207 ± 0.058 for taproot, lateral roots, needles, bark and stele, respectively. The percentage contribution of each seedling component was calculated based on the total dry biomass accumulation.

Plant dry biomass was ground in Wiley mill, passed through a 40 mesh sieve and analyzed for organic carbon according to Tedesco et al. (1995) with results expressed in g kg^{-1}. Accumulation of organic carbon resulted from multiplying dry biomass by its carbon content.

Additionally, seedling leaf area was determined by digital images using the QUANT 1.0 software (VALE et al., 2001). The number of leaf samples to estimate leaf area per seedling was determined by the method of simple random sampling, based on the mean variance of 20 needles per treatment from different crown positions in the seedling. It was admitted the error limit of 15% with 95% probability by Student's t-test for a population that tends to infinity, as suggested by Pellico Netto and Brena (1997). Mean leaf area was multiplied by the number of needles to obtain seedling leaf area.

Data were subjected to Lilliefors test for normal distribution of residuals and Cochran and Bartlett test for homogeneity of variance, followed by analysis of variance. Whenever significant by F-test, the data was broken down by polynomial regression at 5% error probability with software SigmaPlot version 12.0 (SIGMAPLOT, 2011).

RESULTS AND DISCUSSION

Stem bendings of *Pinus taeda* seedlings during 60 days altered plant growth (Figure 1). Seedlings subjected to 40 bendings showed reduced leaf area (Figure 1C) and increased shoot dry biomass (Figure 1D) by 41% and 21%, respectively compared to control seedlings.

Stem diameter (Figure 1B) increased with up to 20 bendings resulting in a growth rate of 34% higher than that of control seedlings. Together with the above mentioned bending intensity, seedlings of *Pinus taeda* showed a 27% reduction in height (Figure 2A) and a 74% increase in root dry biomass (Figure 1E).

The results for the increments in height and in stem diameter are similar to reports with various plant species subjected to thigmomorphogenesis (JAEGHER et al., 1985; LUNDQVIST; VALINGER, 1996; TELEWSKI; PRUYN, 1998; KERN et al., 2005; COUTAND et al., 2010; WANG et al., 2010; MOREL et al., 2012). The reduction in height growth rate with the increase in bending frequency can be explained by the reduction of leaf area, which triggered redistribution of assimilated carbon to support growth in diameter and of roots (WANG et al., 2010; MOREL et al., 2012).

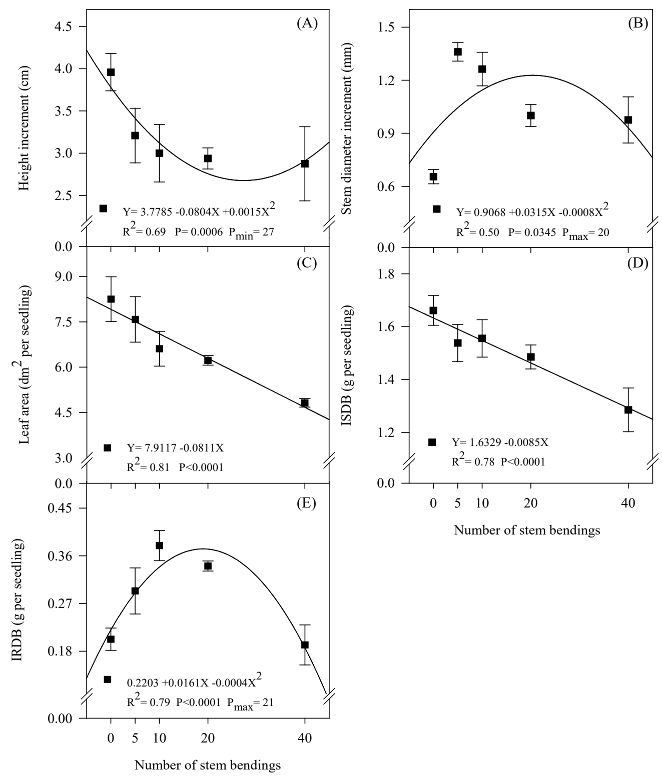

FIGURE 1: Morphological attributes of 10-month old *Pinus taeda* seedlings subjected to mechanical bendings. (A) height increment; (B) stem diameter increment; (C) Leaf area; (D) Increase in shoot dry biomass (ISDB); (E) Increase in root dry biomass (IRDB). Bars represent standard deviation. n=4. P_{max} or P_{min}: maximum or minimum inflection point.

FIGURA 1: Atributos morfológicos em mudas de *Pinus taeda* com 10 meses submetidas a perturbações mecânicas. (A) incremento na altura. (B) incremento no diâmetro do coleto. (C) área foliar. (D) incremento na massa seca da parte aérea. (E) incremento na massa seca de raízes. As barras representam desvio padrão. n=4. P_{max} ou P_{min}: Ponto de máxima ou mínima inflexão.

The rate of needle dry biomass accumulation decreased linearly with increasing frequency of stem bending (Figure 2A) resulting in a reduction of 33% with 40 bending compared to the control. For the other seedling components, the mean values were fitted to a quadratic polynomial model which resulted in increased rate of dry biomass accumulation of 42%, 21%, 128% and 35% for stem (Figure 2B), bark (Figure 2C), lateral roots (Figure 2D) and taproot (Figure 2E) respectively for seedlings subjected to 20 bending compared to undisturbed seedlings.

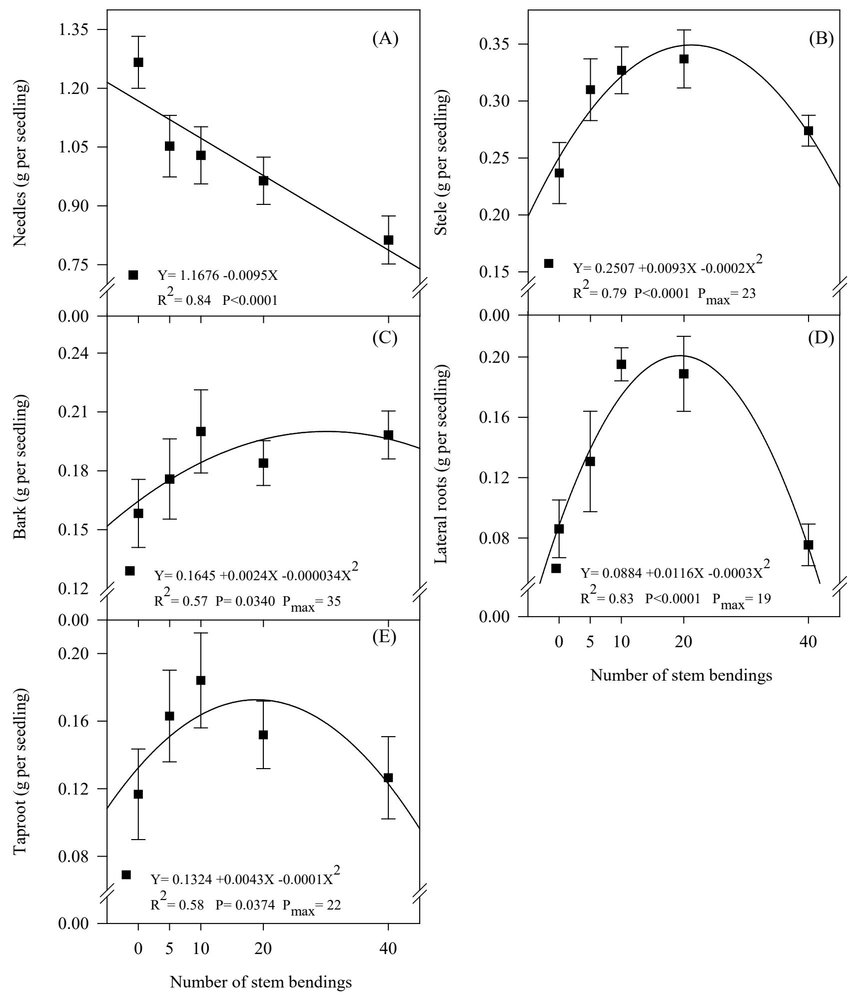

FIGURE 2: Increments in dry matter in different parts of seedlings of *Pinus taeda* subjected to stem bendings in the hardening phase. (A) needles; (B) stele; (C) bark; (D) lateral roots; (E) taproot. Bars represent standard deviation. P_{max}: maximum inflection point.

FIGURA 2: Incrementos na matéria seca nos diferentes componentes de mudas de *Pinus taeda* submetidas a flexões caulinares na fase de rustificação. (A) acículas. (B) cerne. (C) casca. (D) raízes laterais. (E) raiz pivotante. As barras representam desvio padrão. P_{max}: Ponto de máxima inflexão.

For stem components (i.e. stele and bark), thigmomorphogenesis stimulates xylogenesis in woody species (BIRO; JAFFE, 1984; LITTLE; EKLUND, 1999) and changes the orientation, from transverse to longitudinal, of cellulose microtubules and microfibrils of the primary cell wall and cytoplasm. Consequently, turgor pressure occurs in the longitudinal direction, resulting in radial growth and the stem becomes more cylindrical (BJÖRKLUND, 2007). Therefore, the increase in rate of dry matter accumulation in the stele and in the bark would cause increase in diameter and therefore in the volume of the stem.

Dry biomass allocation to lateral roots due to the increasing frequency of MD is prioritized at the expense of taproot growth, because the increase in lateral roots was 128% greater than the control while taproot increment and was 35%. Mechanical perturbation induces division of pericycle resulting in increased dry matter and number of roots in seedlings of *Robinia pseudoacacia* L. (REUBENS et al., 2009), and in seedlings of *Prunus avium* L. cv Monteil (COUTAND et al., 2008). Additionally, root growth in the branching zone promotes stability and anchoring of seedling to the soil, indicating a strategy of induced tolerance to forces naturally generated by wind or by slope, as observed by Tamasi et al. (2005) in *Quercus rubur* L. seedlings and Sun et al. (2008) in *Pinus yunnanensis* Franch.

Because of the larger leaf area and dry biomass, the increment of leaf dry biomass from control seedlings corresponded to an increase of 24% compared to seedlings subjected to MD (Figure 3). Seedlings of *Pinus taeda* mechanically stimulated invested in allocation of dry biomass in other components such as stem and root system, rather than the formation of new needles. This fact is strongly supported when compared to the allocation rate in stele dry biomass (43%) and lateral roots (128%) at the calculated maximum response in contrast to the control treatment (i.e. no stem bending).

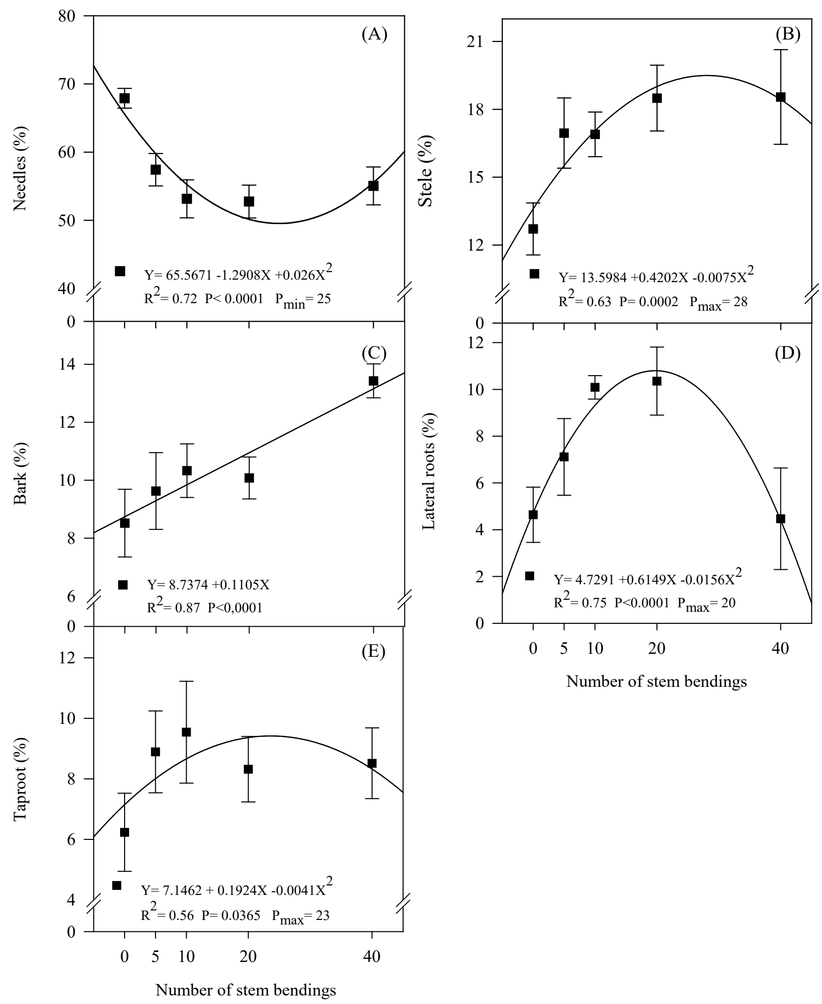

FIGURE 3: Contribution of seedling components to dry biomass increments in seedlings of *Pinus taeda* subjected to stem bendings. (A) Needles; (B) Stele; (C) Bark; (D) Lateral roots; (E) Taproot. Bars represent standard deviation. P_{max} or P_{min}: maximum or minimum inflection point.

FIGURA 3: Contribuição dos componentes nos incrementos na matéria seca de mudas de *Pinus taeda* submetidas a flexões caulinares. (A) acículas. (B) caule. (C) casca. (D) raízes laterais. (E) raiz pivotante. As barras representam desvio padrão. P_{max} ou P_{min}: Ponto de máxima ou mínima inflexão.

The measured value of stem dry biomass supports the hypothesis of reduction in cell elongation, because of reduced height increment (Figure 1A) and the increase in dry biomass with the number of stem bendings applied. The increase of stem dry biomass may be associated with increased lignin content. Lignin is a polymer of high molecular weight and its biosynthesis is stimulated by mechanical disturbances

(COLEMAN et al., 2008; MOURA et al., 2010; RAMOS et al., 2012). The increase in lignin content of cell walls, especially in the xylem cells, confers higher rigidity to the stem and fluidity to the water transport between the soil - plant - atmosphere continuum, resulting in increased resistance to embolism (KITIN et al., 2010; VOELKER et al., 2011).

In the root system (Figure 3D and 3E), the biomass increment of lateral roots and taproot followed similar behavior to that verified in Figure 2D and 2E, indicating that growth of lateral roots has a high requirement of carbohydrates synthesized in the needles. This requirement is a response to mechanical disturbances, because taproot growth was approximately 32% higher in seedlings subjected to MD while for lateral roots it was 128%.

The results indicated significant changes in carbon concentration because of the increase in the frequency of seedling stem bendings (P <0.05). All components fitted a quadratic polynomial model (Figure 4). Points of maximum inflection occurred in the 20-30 stem bendings interval with the exception of needle carbon concentration.

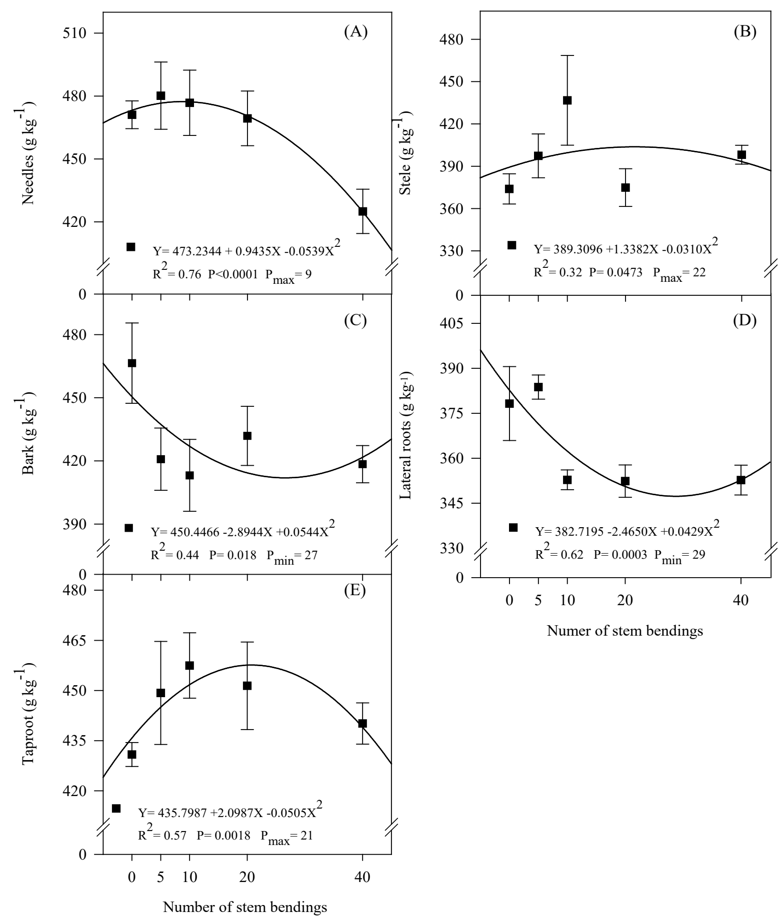

FIGURE 4: Carbon concentration in the different components of seedlings of *Pinus taeda* subjected to stem bendings in the hardening phase. (A) Needles; (B) Stele; (C) Bark; (D) Lateral roots; (E) Taproot. Bars represent standard deviation. P_{max} or P_{min}: maximum or minimum inflection point.

FIGURA 4: Teor de carbono nos diferentes componentes de mudas de *Pinus taeda* submetidas a flexões caulinares na fase de rustificação. (A) acículas. (B) cerne. (C) casca. (D) raízes laterais. (E) raiz pivotante. As barras representam desvio padrão. P_{max} ou P_{min}: Ponto de máxima ou mínima inflexão.

The application of 40 bendings reduced carbon concentration of needles by 10% compared to the other treatments (Figure 4A). This reduction in carbon concentration resulted from the increase in demand for organic compounds by other growing organs, which have become larger than the capacity of uptake by needles.

MD increased carbon by 4% in the stele compared to the control (Figure 4B). The low increment rate in carbon of this seedling component in relation to the other components may be associated with the advancement of vascular differentiation, regarding the deposition of secondary cell wall constituents (BIRO; JAFFE, 1984; FUKUDA, 1996).

The increase in frequency of stem bendings reduced carbon concentration of bark and lateral roots (Figures 4C and 4D). The maximum reduction was observed with 27 and 29 bendings, calculated from the adjusted equations respectively, resulting in reductions of 9.0% and 10.0% compared with control seedlings. Those results suggest that the increase in growth rate of those components resulted in a reduction of carbon necessary to support growth, as might be compared with the results in Figures 2C and 2D.

The increase in carbon concentration up to 5% with the application of 21 bendings (Figure 4E) in dry biomass may be indicative of lignin accumulation in taproots, thus enhancing its tolerance to the pendulum movement of shoots. The thigmomorphogenesis induced by mechanical bending resulted in increased lignin content in the taproot of seedlings of *Populus nigra* (L.) especially in the area of root branching and the first-order lateral roots responsible for promoting stability of shoots (TRUPIANO et al., 2012).

Carbon content in the components of seedlings of *Pinus taeda* (Figure 5) shows that applying up to 20 MD changes carbon allocation. In seedlings mechanically disturbed, carbon ceased to be directed to growth of new needles to sustain growth of the stele and root system, considering the linear reduction of the content in needles and the increased content in the stem and root system (taproot + lateral roots).

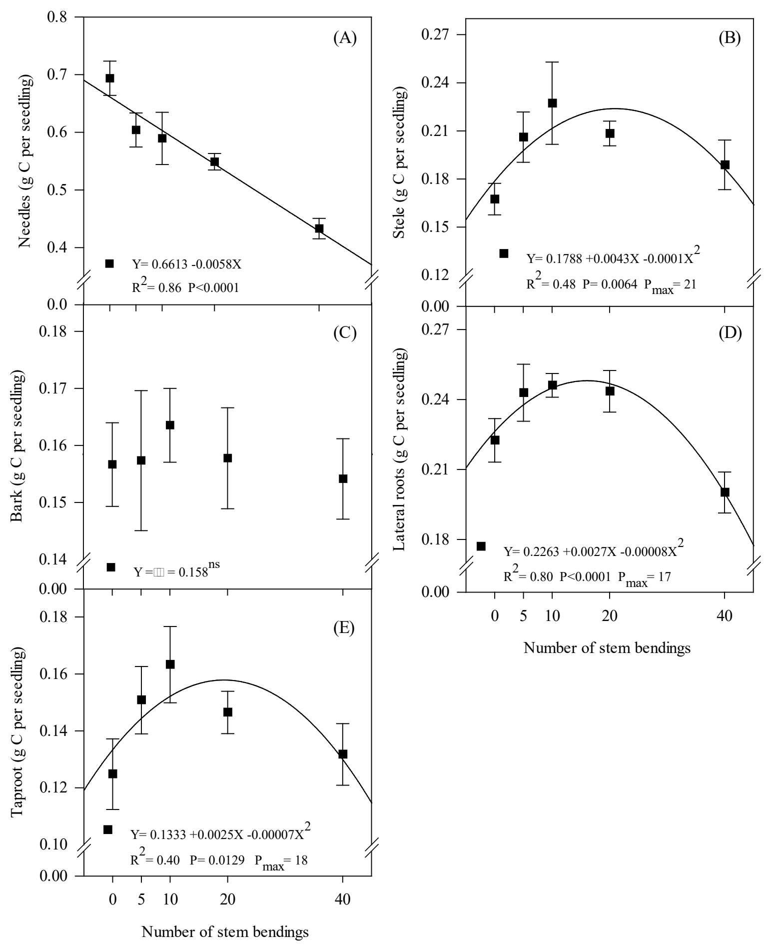

FIGURE 5: Carbon content in different components of seedlings of *Pinus taeda* subjected to stem bendings in the hardening phase. (A) Needles; (B) Stele; (C) Bark; (D) Lateral roots; (E) Taproot. Bars represent standard deviation. P_{max}: maximum inflection point.

FIGURA 5: Conteúdo de carbono nos diferentes componentes de mudas de *Pinus taeda* submetidas a flexões caulinares na fase de rustificação. (A) acículas. (B) cerne. (C) casca. (D) raízes laterais. (E) raiz pivotante. As barras representam desvio padrão. P_{max}: Ponto de máxima inflexão.

Carbon re-allocation is commonly observed in seedlings subjected to different forms of mechanical disturbances as reported by Coutand et al. (2008) for seedlings of *Prunus avium* ('Monteil') and by Awad et al. (2012) for seedlings of *Populus canescens* (Aiton.)Sm. The lack of statistical significance (P> 0.05) in bark carbon content reflects the effect of increased radial growth of the stem, expressing the dilution effect on this carbon component.

CONCLUSIONS

The results of this essay suggested that mechanical stimulus by stem bendings changes allocation of biomass and carbon in seedlings of *Pinus taeda* because leaf area is no longer the preferred carbon sink, resulting in increased growth of stem diameter and roots in treated seedlings.

The results from the application of 20 stem bendings does not represent the threshold for increase in dry biomass and carbon of seedling components in spite of the fact that the average difference between the maximum or minimum inflection points from the fitted models and those resulting from 20 bendings is only 1%.

Thigmomorphogenesis induced by stem bending with frequency of 20 bendings applied in the hardening phase of *Pinus taeda* seedlings promoted an increase in the rate of dry biomass accumulation of stem and root system and altered carbon allocation to sustain secondary stem and root growth.

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