INFLUENCE OF SHADING ON THE GROWTH OF TROPICAL TREE SPECIES SEEDLINGS AND ITS ECOLOGICAL AND SILVICULTURAL IMPLICATIONS

VERA LEX ENGEL
UNESP/Depto. de Ciências Florestais
Caixa Postal 237
18603-970 – Botucatu, SP

FÁBIO POGGIANI
ESALQ/USP – Depto. de Ciências Florestais
Caixa Postal 9
13400-970 – Piracicaba – SP

ABSTRACT - The present work studied the most adequate light intensity for the growth of four native tree species which occur in the State of São Paulo, with the objective of determining its shade tolerance rank at the juvenile phase. The species studied were: (1) Amburana cearensis (Fr. Ali.) A.C.Sm., "cerejeira", family Fabaceae; (2) Zeyhera tuberculosa (Vell) Bur., "ipê-felpudo", family Bignoniaceae; (3) Tabebuia avellanedae Lorentz ex Grisbach, "ipê-roxo" family Bignoniaceae and (4) Erythrina speciosa Andr., "suinã" family Fabaceae, whose seedlings were grown under the shade levels of 0, 41, 68 and 82% in relation to the full daylight. Height and diameter growth rates in relation to the shade level, as well as the variation of final height and diameter, shoot dry weight and leaf area as a function of relative light intensity were analyzed. It's stressed the adaptive importance of the results, as well as its silvicultural implications. It was possible to establish an increasing order of shade tolerance as follows: E. speciosa < Z. tuberculosa < T. avellanedae < A. cearensis.

RESUMO - O presente trabalho estudou as intensidades de luz mais adequadas ao crescimento de quatro essências florestais que ocorrem no Estado de São Paulo, com o objetivo de determinar seu grau de tolerância à sombra na fase de mudas. Foram estudadas mudas de (1) Amburana cearensis (Fr. Ali.) A.C.Sm., "cerejeira", família Fabaceae; (2) Zeyhera tuberculosa (Vell) Bur., "ipê-felpudo", família Bignoniaceae; (3) Tabebuia avellanedae Lorentz ex Grisbach, "ipê-roxo" família Bignoniaceae, e (4) Erythrina speciosa Andr., "suinã", família Fabaceae, crescendo sob níveis de sombreamento de 0, 41, 68 e 82% em relação à luz plena do dia. Avaliaram-se taxas de crescimento em altura e diâmetro do colo em função do sombreamento, bem como a variação da altura e diâmetro finais, matéria seca da parte aérea e área foliar em função da intensidade relativa de luz. Discutiu-se a importância adaptativa dos resultados e suas implicações silviculturais. Pode ser estabelecida uma ordem crescente de tolerância à sombra na seguinte sequência: E. speciosa < Z. tuberculosa < T. avellanedae < A. cearensis.

INTRODUCTION

In spite of the fact that individual environmental factors do not act isolatedly upon the plants, the factor light is fundamental as na essential and direct source of energy to the development of all green plants. The local distribution of one species inside a forest
community is hardly affected by the difference in light availability, which limits direct or indirectly most of the growth processes in plants.

The light, mainly concerning its intensity, has been recognized as the most important factor for the processes of regeneration and growth of forests (Lugo, 1970; Walter, 1971; Bazzaz, 1979; Nygren & Kelloaki, 1983/1984; Amo, 1985; Koike et alii, 1986). The species adaptation to the environmental luminosity is important primarily at the juvenile phase, by conditioning morphogenetical and physiological changes in their structure and function (Whatley & Whatley, 1982), and then determining the success or not of the regeneration.

The importance of this factor has led several authors to classify the forest species in distinct ecological groups according to its capability of adapting themselves to the light environmental conditions, whose knowledge is a key to understand the forest dynamics and its management (Amo, 1985).

Several parameters have been used to establish the bases of plant adaptability to different shade levels conditions, such as physiological (Bohning & Burnside, 1956; Bjorkman & Holmgren, 1963; Inoue, 1977; Bazzaz 1979; Koike et alii, 1986), morphological (Blackman & Wilson, 1951; Boardman, 1977) and ecological (Grime, 1977, 1982; Amo & Gomez-Pompa, 1979; Martinez-Ramos, 1985).

The present study has the objective of studying the shade adaptability of 4 forest tree species that occur naturally in the State of São Paulo, by the analysis of some growth aspects, as a basis for the understanding of their ecological role in the dynamics of forests regeneration and for the establishment of some silvicultural guidances to those species.

**MATERIAL AND METHODS**

The following species were studied: (1) *Amburana cearensis* (Fr. All.) A.C. Sm.: “cerejeira”, finally Fabaceae; (2) *Zeyheria tuberculosa* (Vell) Bur., “ipê-felpudo”, family Bignoniaceae; (3) *Tabebuia avellanedae* Lorentz ex Grisebach, “ipê-roxo”, family Bignoniaceae and (4) *Erythrina speciosa* Andr., “suinã”, family Fabaceae. The species choice was based on their ecological and silvicultural importance, as well as on the hypothesis that they would present contrasting characteristics in their degree of shade tolerance.

Four shade levels were tested: 0% (full daylight), 41%, 68% and 82% of shade in relation to full daylight, according to measurements made with a luximeter. The shade covers were roof-shaped, made with wood frame covered with polyethylene black screen, measuring 12.25m² of area and 1.50 m of height in its central part.

The seedling s were produced by direct sowing in polyethylene bags with about 1600cm³ of volume, using a mix of clay subsoil, sandy soil and organic compound at the proportion of 4:1:1. The conditions of germination of seedling establishment were the same for all species, at full daylight.

The statistica design was the randomized blocks, each shade level being an individual essay with 4 treatments (species) and 3 repetitions, which later were analysed together. The experimental sample plots had 9 plants each.

The total height and diameter were measured periodically up to 425 days after germination for *A. cearensis*, 355 days for *Z. tuberculosa*, 339 days for *T. avellanedae* and 220 days for *E. speciosa*, which depended on the growth rate of each species. After the
latest measurement, 4 plants by plot were sampled for the shoot dry weight and leaf area analysis.

The growth data were studied by regression analysis in function of the age for each specie in each shade level, using the models of equation (1) and eq. (2) as following, respectively for height and diameter.

\[
\ln (y) = a + b(x) \quad (1)
\]

\[
\ln (y) = a + b \ln (x) \quad (2)
\]

After the parameters estimate, it was possible to establish growth curves by species and shade level. These curves were compared two by two in relation to the parameters a and b of the regression, by means of Test “t” for 2 samples means with different number of observations and unequal variances, according to STEEL & TORRIE (1960). This analysis permitted to verify if the curves for different shade levels and the same species differed from each other primarily in relation to the parameter b, indicating the influence of shade on the growth rates.

The data of final height and diameter, as well as shoot dry weight and leaf area were studied by simple regression analysis as a function of relative light intensity (1 – shade level %/100), as in the model:

\[
Y = a + bx + cx^2 \quad (3)
\]

The mortality by species in each shade level was also analysed through the percentage of plants alive at the end of the nursery period.

RESULTS AND DISCUSSION

SURVIVAL

The seedlings of *T. avellanedae* and *E. speciosa* presented an excellent survival in all shade levels. *Z. tuberculosa* showed 100% of survival on 41% of shade, and 96.3% on the others. This was not considered to correlate with its shade tolerance.

On the hand, the seedlings of *A. cearensis* showed a low survival at full daylight—only 29.3%, which sensibly increased at the other levels: 85.2, 96.3%, respectively for 41.68 and 82% of shade.
TABLE 1. Simple regression analysis for height growth (cm) of seedlings at the different shade levels as function of age (days). Model: In (y) = a + b (x). Species: (1) A. cearensis; (2) Z. tuberculosa; (3) T. avellaneade; (4) E. speciosa.

<table>
<thead>
<tr>
<th>Species</th>
<th>Shade Level (%)</th>
<th>N²</th>
<th>Parameter¹ a</th>
<th>Parameter¹ b</th>
<th>r²</th>
<th>F³</th>
</tr>
</thead>
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<td>0.0011 a</td>
<td>03938</td>
<td>129.939**</td>
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<tr>
<td>1</td>
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<td></td>
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<td>T. avellaneade</td>
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<td>659.222**</td>
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</table>

(1) Parameters of the same species followed by the same letters are not statistically different at 5% level of probability
(2) Number of observations
(3) Values of F of regression analysis of variance significant at 1% probability

This result may denote the intolerance of the species to a very intense insolation.

HEIGHT

The parameters estimates of the height growth curves by species and shade level, as well as the results of Test “t” comparing the values of parameters a and b of different shade levels in the same species are summarized in Table 1. The curves drawn with the values estimated by regression can be observed in Figure 1, where the observed values have not been plotted because of the large number of observations.

Table 1 shows a good fit of the curves, it can be observed that shading has influenced the exponential height growth rates of A. cearensis, T. avellaneade, and E. speciosa, resulting in growth curves with different forms, according to Figure 1. Z. tuberculosa did not show a response to shade level in its height growth rates. In A. cearensis, although the seedlings were initially higher at the shade levels of 0 and 41%, its growth rate was higher at 68 and 82% of shade, while in T. avellaneade the growth was faster at 68%.

In E. speciosa the height growth rate was lower only at 68% of shade, what does not look like being correlated to the factor shading or any other environmental condition, but to internal factors of the plants themselves. This species, together with Z. tuberculosa, did not
respond to the shade in relation to the height growth. Figure 2 shows the curves estimated by regression analysis for the final height of plants in relation to light relative intensity. It can be observed a negative linear response to the RKI (%) in *A. cearensis* and *T. avellanedae*, while in *E. speciosa* the relation was logarithmic positive, and in *Z. tuberculosa* there was no statistically significant regression.

![FIGURE 1](image)

**FIGURE 1.** Growth curves for height of plant cultivated at different shade levels. (1) *A. cearensis*; (2) *Z. tuberculosa*; (3) *T. avellanedae*; (4) *E. speciosa*. Values estimated by regression analysis.
TABLE II. Simple regression analysis for stem diameter growth (mm) at different shade levels as a function of age (days). Model: ln(y) = a + b ln(x). Species: (1) A. cearensis; (2) Z. tuberculosa; (3) T. avellanedae; (4) E. speciosa.

<table>
<thead>
<tr>
<th>Species</th>
<th>Shade Level (%)</th>
<th>N²</th>
<th>Parameter¹ a</th>
<th>Parameter¹ b</th>
<th>r²</th>
<th>F³</th>
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<td>0.6071 b</td>
<td>0.8540</td>
<td>1094.149**</td>
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</table>

(1) Parameters of the same species followed by the same letters are not statistically different at 5% level of probability.
(2) Number of observations.
(3) Values of F of regression analysis of variance significant at 1% of probability.

It can be noted also low values of r² (high dispersion of the observed data), although the regression analysis of variance have shown values for F highly significant in all cases.

STEM DIAMETER

The parameters estimates of the diameter growth curves by species and shade levels, as well as the results of the Test "t" for paired comparisons between the parameters of different shade levels and the same species are summarized in Table II. Figure 3 shows the curves traced with the values estimated by regression; the observed values were not plotted because of the large number of observations.

It can be observed a good fit of the curves to the model of eq. (2), with the exception of A. cearensis, where the lower values of r² are due to the higher percentage of failure.

For A. cearensis the higher diameter growth rates occurred at the seedlings raised under shade levels of 41 to 82%, showing that event the lower shade level was sufficient to stimulate the growth in this species, and further that at full daylight these plants pratically did not increase their diameter during the period studied.
The seedlings of *T. avellanedae* presented a faster growth under deeper shade levels (68 to 82%), being the level of 41% intermediate. On the other hand, *Z. tuberculosa* and *E. speciosa* have grown faster under shade levels up to 41%.

FIGURE 3. Growth curves for stem diameter (mm) of nursery plants cultivated at different shade levels. (1) *A. cearensis*; (2) *Z. tuberculosa*; (3) *T. avellanedae*; (4) *E. speciosa*. Values estimated by regression analysis.

Figure 4 shows the regression curves of final diameter as a function of light relative intensity (%), traced with estimated values. Although the low values of $r^2$, the regression analysis of variance present values for F highly significant, showing clearly a differential behaviour of species in response to shade.
As it can be observed, *A. cearensis* increases exponentially its diameter with the decrease of light intensity, but *T. avellanedae* can increase it up to 55-40% of relative light intensity, decreasing back its diameter with further decrease in light intensity. An opposite response was presented by *Z. tuberculosa* and *E. speciosa*, which have reached maximum values for diameters at full daylight and further exponential decrease with decreasing light intensity. This response is more obvious in *E. speciosa*; the pattern showed by *Z. tuberculosa* looks like being resulted from variations at the bark thickness and not in the diameter growth properly said.

**SHOOT DRY WEIGHT**

This paper deals only with shoot dry weight, because the results referring to root dry weight could not be evaluated. Meanwhile, this is considered valid to the objectives of the survey, since there is a relation between root biomass and stem diameter, as demonstrated by SOUZA (1981), and also the root growth keeps an interdependence relation with shoot growth (EVANS, 1973).

![Graph showing stem diameter vs. relative light intensity](image)

**FIGURE 4.** Influence of relative light intensity on stem diameter of nursery plants. Values estimated by regression analysis. Regression curves are: (1). In(y) = 2.2257 - 1.0101x, F = 13,803**; n = 77; (2). In(y) = 2.2747 + 0, 1105 In(x), F = 8, 149**, n = 104; (3). y = 9.7768 + 8.1746x -7.8365x^2, F = 4,084**, n = 108; (4). In(y) = 3.2670 + 0.1695 In (x), F = 31,289**, n = 108.
Figure 5 shows the curves obtained with data estimated by regression analysis, again showing observed low values for $r^2$, but values for F highly significant for all curves.

*Amburana cearensis* showed a sensible decrease of shoot weight with increase of relative light intensity, the same being valued for *Tabebuia avellanedae*, but the former at a lesser extent (lower values of b). On the contrary, the aerial biomass of *Erythrina speciosa* varied in an opposite way, with a maximal shoot dry weight being attained at full daylight. For *Zanthoxylum tuberculosa*, shoot a significant relation to light intensity, showing that this species adapts itself to a wide range of environmental luminosity.

Figure 5 shows that the relative light intensity of 60% is a critical point which determines the competitive capacity between *Tabebuia avellanedae* and *Erythrina speciosa*, under low levels of light intensity, as it could be found in forests, even *Amburana cearensis*, which has a few competitive life strategy, could show advantages in relation to *Erythrina speciosa* and also *Zanthoxylum tuberculosa*, in terms of cumulated shoot dry weight.

**LEAF AREA**

In Figure 6 it can be observed a negative logarithmic relation between leaf area and relative light intensity, or an exponential increase of shading, except for *Erythrina speciosa*.

The increase of leaf area with shade level is one way the plant increase its photosynthetic surface, thus assuring a better utilization of low light intensities (Boardman, 1977). This, according to Lugo (1970), is proper of shade tolerant species.
It is remarkable the great morphological plasticity of *A. cearensis*, which is capable of increasing up to 10 times its leaf area when cultivated under shade, in relation to plants grown at full light.

**ECOLOGICAL AND SILVICULTURAL IMPLICATIONS**

For the experimental conditions, *A. cearensis* showed to be a species which, besides being shade tolerant, is strongly favoured by shade levels above 68%, at least at the juvenile growth phase. It was also not able to adapt itself at full light, as was demonstrated by the high mortality showed by this species at this conditions. Besides, although it has a great morphological plasticity in response to shade its low metabolic and growth rhythms are characteristic of a typical shade tolerant species according to the concepts of BLACKMAN & NILSON (1951), GRIME (1982) and MARTINEZ-RAMOS (1985).

**FIGURE 6.** Influence of relative light intensity of leaf area. Values estimated by regression analysis. Regression curves are: (1) In(y) = 6.7950 - 3.6357x, F = 63.258**, n = 36; (2) In(y) = 7.5127 - 0.7397x, F = 6.059*, n = 47; (3) In(y) = 8.5884 - 1.0084x, F = 34.331 ***, n = 42.

It can be supposed then that in natural conditions, it would have better opportunity to regenerate under the canopy, supporting even very low light intensities resulting form a closed canopy. On the other way, it is known that it occurs naturally in a great variety of habitats, as the “caatinga” and “agreste” (scrubby savanna) at the Northeastern region in Brazil (DUCKE, 1959), rain forests and mesophytic forests (RIZZINI, 1971) from northeast to southeast and center – south of Brazil. In plant occurring at more xeric environments, it is possible to observe characteristics of xeromorphism, mainly at the leaves (VARBOSA, 1983), which contrast with the results obtained in this study. Other
results indicate even a better fit of *A. cearensis* seedlings to full daylight conditions (LUZ et alii, 1985). In face of so different results, it could be suggested the existence of several ecotypes, adapted to situations so contrastant as the “caatinga” and the forest understory. By means of a genetical divergence in a higher or lower degree, the phenotypic amplitude would have been restricted, but permitting the species to be adapted to a wider range of environmental conditions.

The response patterns of *Amburana cearensis* permit to consider it as belonging to the final stages of secondary succession, being adapted to regenerate and growth, although slowly, under the forest understory. Then, the seedlings production for this species should require an intense shade level to get a good survival and general vigour. Further, *A. cearensis* is not adequate for artificial regeneration systems in pure plantations, and should be planted under protection cover on in combination with more heliophyllous species. It has a good potential for enrichment planting in degrade forests, because of its favorable response to shade.

Nevertheless it is necessary a larger number of evidences to get more conclusive informations about this it.

*Zeyhera tuberculosa* has confirmed its capacity to adapt itself to a wide range of habitats, as told by LUZ & FERREIRA (1985), because of its ability of acclimatization to a wide range of light intensities, even full light up to 82% of shade, without any harm to its growth and development. By showing a low level of morphological differentiation in relation to shade, it could be considered a nomad species, according to MARTINEZ-RAMOS (1985), but being favoured in relation to its metabolic efficiency by higher light levels than *T. avellanedae*. It acts like a species of intermediate successional characteristics, being able to regenerate under the canopy cover as well as in open land. Thus, it fits to open land as well as to forest enrichment planting, as well as in agroforestry and mixed crop with more tolerant species.

For seedlings production, it must be considered the final utilization of the seedlings. For enrichment planting, the seedlings produced under a moderated shade level will present better condition to develop, by having or larger leaf area and then being capable to enlarge the light utilization.

Meanwhile, at very high shade levels this species looks to be etiolated because of a greater proportion of water in its tissues, which represents a search for more light, characteristic of competitive plants or nomads. Yet, to open sky plantings, the seedlings produced at full light will be more adequate, by presenting a larger stem diameter and probably a root system better developed, giving it an ability to better explore available soil water.

It should be considered also that this species, by its plasticity, shows a great silvicultural potential and for breeding programs by selecting genotypes with higher growth rates and better suited to specifics regeneration systems.

*Tabebuia avellanedae* revealed to be favoured by shade levels of 41 up to 82%, showing a very hight morphological plasticity in response to shade, characteristic of “nomade species”, according to the concept of MARTINEZ-RAMOS (1985) or “competitives”, as GRIME (1977, 1982).

This species has a satisfactory growth to full daylight but is able to quickly accelerate: growth rate when exposed to shade levels up to 68%, reaching higher height, stem diameter, leaf area and shoot dry weight. Such characteristics show that the species has a strategy of quick allocation of assimilates to the shoot when shaded, which permits to
overcome competing vegetation and to expose more favourably its photosynthetic surfaces to light. In natural conditions, this species would be favoured by small gaps in the forest canopy.

*T. avellanedae* then is better suited to plantings under cover and enrichments, when it might reach very high growth rates, in opposition to what have been registered for the species (CARVALHO, 1983). At moderate shade, it stands out for its quick initial growth, besides developing a better form and general vigour.

For seedlings production, the shading shows to be very favourable considering the quality of their aerial part.

If a very greater in balance between shoot and root seldom occurs, we might consider that the seedlings produced under shade will have better chances to succeed, even at full daylight.

The plants of *Erythrina speciosa* showed to be very intolerant to shade in it’s a juvenile growth phase, in relation to the parameters studied, having a better development at full daylight. *E. speciosa* is able to survive in shade, but suffers a decrease in its stem diameter growth, what might reflect a poorer developed root system, and a decrease in its shoot dry weight. The increase in leaf area with shade reflects a trend to enlarge the photosynthetic surface, but which is not sufficient to result in an increase in dry matter assimilation. By its characteristics of high seeds dormancy, high growth rates at full daylight and large proportion of water in its tissues, it is assumed that this species is adapted to grow in open lands, belonging to later phases of secondary succession and approaching to pioneer plants according the concepts of MARTINEZ-RAMOS, 1985. To these evidence, it can be added the capacity of forming a very dense root system, with well developed tap roots, and profuse rhizobacterias nodules, as has been observed, which might help in supplying water and nutrients to shoot and consequently adapting this species to grown in degraded lands.

*E. speciosa* is then adequate to open sky plantings, in degraded lands and in agroforestry systems. Its rapid growth and high rate of leaf renovation help the restablishment of soil organic cover. It might even be associated with shade tolerant species with a slower growth, as *A. cearensis*.

The seedlings production should be done at full light, when the species can reach it is full development with better quality. If the water is not limiting. It must be considered that it is necessary to study the survival of seedlings at field under different situations, to make more secure recommendations on this species.

Based to the parameters studied, it is possible to consider *E. speciosa* as typically belonging to the final stages of secondary succession, while *A. cearensis* occupy later ones and *Z. tuberculosa* and *T. avellanedae* being intermediate species. An increasing scale of shade tolerance can be established as follows: *E. speciosa* < *Z. tuberculosa* < *T. avellanedae* < *A. cearensis*.

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