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Competition within the root system of rubber seedlings (*Hevea brasiliensis*) studied by root pruning and blockage

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Abstract

The effects of taproot blocking and pruning on the development of the early secondary roots (ESR) of rubber seedlings were studied in root observation boxes under controlled conditions. During shoot flush, both the mean elongation rate and mean apical diameter of the ESR decreased regardless of treatments. Thereafter, the elongation rate of the ESR increased greatly when the taproot was blocked, slightly for the control and scarcely for the pruned systems in which fast growing regenerated roots developed. The differences between treatments were related to the proportion of ESR which ceased growing. Following shoot arrest, the apical diameter of ESR increased greatly for blocked seedlings and to a lesser extent for pruned seedlings. Branching density of the ESR and elongation of tertiary roots were also higher for seedlings without a growing taproot.

The dynamics of ESR response was not consistent with active inhibition of their development by the growing taproot. Moreover, this response was dependent on concurrent development of shoot and regenerating roots, hence competition processes were more likely to be determining. In such an hypothesis, root elongation can be limited by assimilate availability, but also by each root's maximum growth rate in non-limiting conditions, i.e. growth potential. Since the latter is related to apical diameter, a significant acceleration of elongation required a parallel increase in apical diameter and this may explain the relative inertia of ESR to taproot alteration. Conversely, regenerating roots could have a high growth potential because they were initiated in a favourable context, thus their development competed strongly with elongation of ESR.

Key words: *Hevea brasiliensis*, root system, development, growth potential, root diameter, competition.

Introduction

Within the root system the development of the different axes is co-ordinated. For example, growth of the main roots seems to regulate the development of their branches. Laterals are more numerous (Wightman and Thimann, 1980) or grow longer and faster when the main axis is prevented from elongating or removed (Riedacker *et al.*, 1982; Lamond *et al.*, 1983; Pagès *et al.*, 1992). Such behaviour has been interpreted as an inhibitory effect exerted by the apical meristem of the growing root on the development of its laterals (Wightman and Thimann, 1980), or by (and sometimes interacting with) competition for growth factors originating from the shoot. The inhibitory substances are thought to be cytokinins produced in the root apex (Torrey, 1976; Wightman *et al.*, 1980) whereas the promoting factors could be hormones, such as auxins, moving basipetally from the growing shoots (Scott, 1972; Wightman *et al.*, 1980) and carbohydrates required as a substrate for energy production and as a source of carbon skeleton (Bingham and Stevenson, 1993; Atzmon *et al.*, 1994). The influence of carbon allocation patterns on the growth and branching of roots has recently been emphasized (review by Aguirrezabal *et al.*, 1993; Bingham and Stevenson, 1993; Atzmon *et al.*, 1994). Allocation of resources between competing axes is thought to depend on their sink strength, namely their potential capacity to accumulate the resource related to their growth potential, i.e. maximum growth rate in non-limiting conditions (Wareing and Patrick, 1975; Ho, 1988). Rubber tree roots show a gradient for growth potential: taproots (first order) have indefinite rapid growth and dense ramification, unlike tertiary roots (third order) which have short and

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Abbreviation: ESR: early secondary roots.

slow growth with very few branches, secondary roots (second order) being split between many intermediate cases depending on their inception date and location (Le Roux and Pagès, 1994). Therefore, if the taproot, representing the main root sink and the presumed source of inhibitory substances, is removed or prevented from growing, the development responses of different secondary roots will provide helpful indications on the growth correlations within the root system.

The purpose of the work was to determine the effects of such manipulations of the taproot on the development of a particular type of secondary roots: the early secondary roots (ESR). These ramifications form a whorl at the base of the taproot, they are preformed during embryogenesis (Premakumari and Sobhana, 1995) and emerge 1–2 d after the emergence of the hypocotyl-radicle axis (Le Roux and Pagès, 1994). All these roots (12 on an average) develop in the same context, namely the same location, origin and inception date, hence they can be considered as an homogeneous sample. Typically, most of these roots show a rapid decline in both elongation rate and diameter and stop growing during the first flush of shoot growth, but some of them continue to grow thereafter (Le Roux and Pagès, 1994; Thaler and Pagès, 1996a). This decrease has been interpreted in terms of enhanced competition for carbohydrates (originating from the seed) induced by the growth of the shoot (Thaler and Pagès, 1996a). According to this hypothesis, a decrease in the number of roots competing for carbohydrates during this development stage is likely to increase carbohydrate (and auxin) availability to the remaining axes and to limit their growth decline. However, it has also been proposed that the elongation rate of a root could be limited by the properties of its meristem and vascular pathways, indicated by the diameter of the apex (Hackett, 1969; Thaler and Pagès, 1996b). Consequently, the observed decrease in elongation rate may result from meristem properties and would not be influenced by the rapid decrease in the number of competing sinks. However, since it is known that the apical diameter itself is apt to vary (Thaler and Pagès, 1996b), it was necessary to investigate its evolution. On the other hand, if the growth of the ESR is considered to be inhibited by substances produced in the apex of the growing taproot, alteration of the latter will certainly induce rapid changes in the development patterns of the ESR.

In order to test these hypotheses, the experiment was carried out in root observation boxes, so that the growth and branching dynamics of individual roots, together with their apical diameter could be recorded over several weeks.

Materials and methods

Plant material

Seeds of *Hevea brasiliensis* Müll. Arg. were collected in Gabon. The seed coats were removed and the seeds were treated with

0.5 g l⁻¹ benomyl and 0.025 g l⁻¹ furalaxyl, and placed in moist vermiculite at 30 °C to germinate.

Treatments

Different surgical treatments were applied 3–4 d after germination and the seedlings were placed in the root observation boxes. The mean length of the taproots was about 4 cm. They bore a mean of 12 ESR. Some seedlings bore an additional ESR whorl just behind the first one, and therefore bore up to 20 ESR. The length of the ESR ranged from 1.0 to 8.1 cm. The taproots were pruned 1 cm below the ESR (pruned treatment, -T) or inserted into small plastic cones in order not only to stop their elongation but also to prevent regeneration of new taproots (blocked treatment, bT). Some ESR were removed too in order to perform the following treatments:

- +T12 (control): taproot + approximately 12 ESR (range 11–20)
 - +T6: taproot + 6 ESR
 - T12: pruned taproot + approximately 12 ESR (range 11–13)
 - T6: pruned taproot + 6 ESR
 - bT12: blocked taproot + approximately 12 ESR (range 10–13)
 - bT6: blocked taproot + 6 ESR
- Each treatment was replicated 3–4 times.

Root observation boxes and growing conditions

The root observation boxes were similar to those described by Neufeld *et al.* (1989). They were 49 cm high × 28 cm broad × 5 mm wide (internal dimensions) PVC boxes. The back and sides were made of opaque PVC. The front pane was 2 mm thick transparent PVC.

The root boxes were filled with fine vermiculite, with a maximum grain diameter of 2 mm. A nylon mesh (30 µm) was stretched between the substrate and the front pane. The root system could thus develop in a plane between the transparent front pane and the nylon mesh. It was entirely visible through the pane, since the roots were prevented from penetrating the substrate. The boxes were placed in a container to keep the roots in darkness. The plants were grown in a growth chamber from May to June, 1995. Each seedling was observed for 36–37 d. The air temperature was 28 ± 1 °C during the day and 22 ± 1 °C during the night, the relative humidity 70 ± 10% and the photoperiod 12 h. The photosynthetically active radiation (PAR) was 600 µmol m⁻² s⁻¹ (HQI lamps, 400 W, Mazda, Belgium). The plants were watered every 2 d with one-tenth Hoagland's solution up to free drainage.

Root and shoot development

The development of both the shoot and root system was observed every 2 d. The stem length, from cotyledonary node to the apex, and the length of the main leaflet of each leaf were measured. On other seedlings, grown in pots in the same growth chamber, a linear relationship was established between the length of the main leaflet and the leaf area.

Root emergence and growth were recorded by tracing the new growth increments with waterproof coloured pens on a transparent plastic sheet placed over the front pane. A new colour was used for each observation date.

The apical diameter was measured on a sample of 6 ESR on each plant. The diameter was measured 0.5 mm behind the tip of the root, to an accuracy of 0.02 mm, through the transparent front pane using a portable monocular microscope (magnification × 50) fitted with an ocular micrometer.

Data inputting and analysis

Root development data were inputted according to the method described in detail by Colin-Belgrand *et al.* (1989). The

information on the transparent sheet was digitized with a tablet connected to a computer, using in-house software (Colin-Belgrand *et al.*, 1989). With this software and the pointer buttons, the space (coordinates of the growth segments), structure (connections), and time information (observation dates) could be inputted. A set of programs calculated root development data (position of a root along its mother root, emergence date, length increment) from the original data.

In order to compare the time-course evolution of studied parameters, within-treatment average data could be used since the first growth flush was synchronized between plants. Statistical tests were not used because the number of independent units (the seedlings) was too low (3–4 per treatment). In addition, data obtained by periodic recording of root length cannot be considered as independent. Thus, the analyses are mainly exploratory, relying on graphs showing both average and individual time-dependent patterns. The dominant trends in scatter plots were fitted by 'lowess' algorithm (Chambers *et al.*, 1983).

Results

Elongation of the ESR

Figure 1 shows the inter-seedling mean elongation rate of the ESR for the control (+T), taproot pruning treatment (-T), and taproot blocking treatment (bT). From the beginning of the experiment to the end of the first flush of shoot growth (20–25 d after emergence), the growth pattern of these roots was independent of the treatment applied to the taproot. Following a short phase of increase, the mean elongation rate of the ESR showed a decrease from a maximum value of 7.2 to 8.1 cm d⁻¹ per seedling to a minimum one. The minimum value reached by the control (2.4 cm d⁻¹) was slightly lower than that for the -T and bT treatments (3.1 cm d⁻¹ and 3.0 cm d⁻¹, respectively). When the shoot ceased growing, the mean growth rate for the control increased slightly

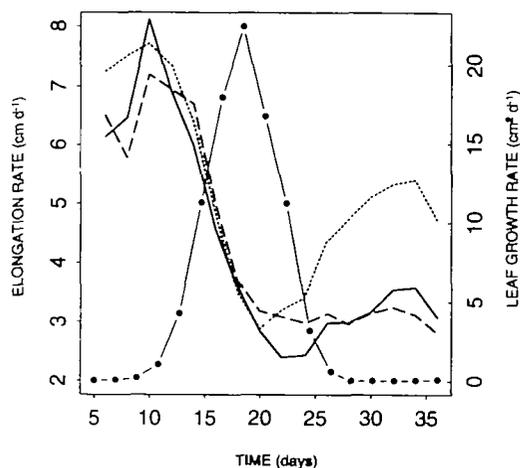


Fig. 1. Variations in the mean cumulated elongation rate of the early secondary roots (ESR) for the control (+T, —), pruned taproot (-T, - -) and blocked taproot (bT, ···) seedlings. Each line is the mean for 6–7 seedlings. Each seedling bore 6–20 ESR. Mean leaf growth rate for all seedlings is also shown (-·-·).

whereas the mean growth rate for -T seedlings was stabilized, hence both treatments reached similar values. However, the ESR for bT seedlings revealed a substantial increase in their mean elongation rate (up to 5.4 cm d⁻¹) following shoot growth.

Growth rate patterns for individual ESR were generally consistent with this average pattern, except that a number of ESR ceased growing, mainly during the shoot growth period. As shown in Fig. 2, some roots stopped growing during the shoot growth period while others continued to grow, more or less regularly. The proportion of ESR that maintained their growth was highly variable and did not appear to depend on the number of ESR allowed to grow. When the taproot was prevented from growing, but not pruned (bT), a larger proportion (62–90%) of ESR continued to grow compared to the control (0–64%) and the pruned seedlings (0–67%) (Fig. 3). The duration of growth was dependent on the initial growth rates, within a seedling the roots with higher initial growth rates were likely to grow longer than the roots with lower initial growth rates (Fig. 2). The number of ESR had no substantial influence on the distribution of the final length reached by these roots.

Regeneration of new roots

All the pruned taproots regenerated new roots which developed and emerged at the wound site or just above (Fig. 4B). The first regenerated roots appeared 8–16 d after the excision of the taproot (Fig. 5A). Some regenerated roots continued to appear subsequently and the data

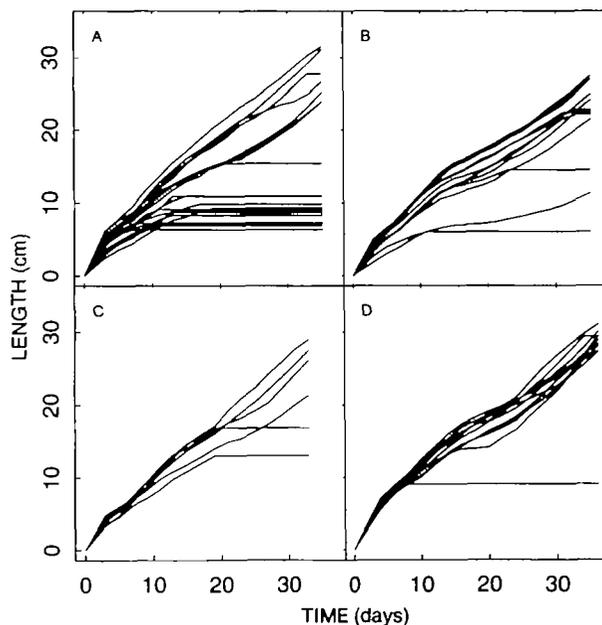


Fig. 2. Growth curves of individual early secondary roots (ESR) for a control seedling with 20 ESR (A), a pruned taproot seedling with 12 ESR (B), a pruned taproot seedling with 6 ESR (C) and a blocked taproot seedling with 12 ESR (D). Each line represents an ESR.

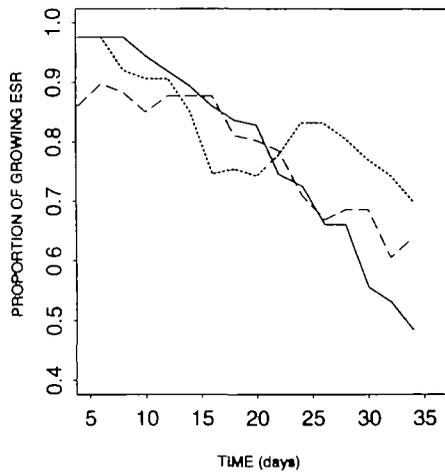


Fig. 3. Evolution of the proportion of growing early secondary roots (number of growing ESR divided by the initial number of ESR), for the control (+T, —), pruned taproot (-T, - -) and blocked taproot (bT, ···) seedlings. Each line is the mean for 6–7 seedlings

were unclear whether this process had stopped at the end of the experiment (33 d after taproot pruning). Three to seven regenerated roots were observed for each seedling. As shown in Fig. 5A and B, the elongation rate of the regenerated roots was higher than that of the ESR (up to 1.2 cm d^{-1}), but lower than the initial values for taproots (*c.* 2 cm d^{-1} , data not shown). Although some of them emerged and grew during the shoot growth phase, the elongation rates of the different regenerated roots seemed constant throughout the experiment. Moreover, the cumulated elongation rate of the ESR declined when new regenerated roots began to grow (Fig. 5B) and consequently, some regenerated roots quickly became longer than all the ESR (Figs 4B, 5A).

No roots regenerated from blocked taproots (Fig. 4C).

Branching

Table 1 shows the branching density (number of tertiary roots divided by the total length of the ESR) for each

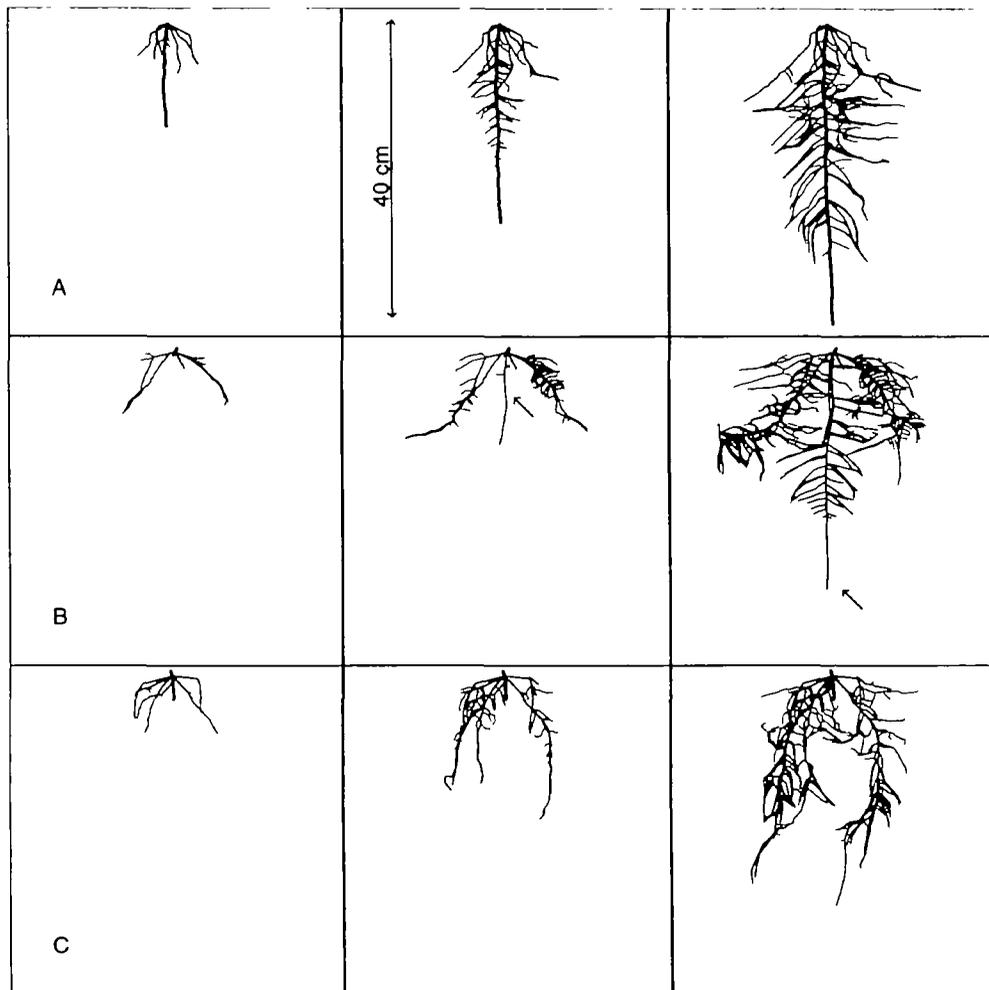


Fig. 4. Evolution of typical root systems for a control (A), a pruned taproot (B) and a blocked taproot (C) seedling. The first column shows 10-d-old, the second column 20-d-old and the third column 36-d-old systems. Arrows indicate the regenerated roots which appeared at the wound site for the pruned taproot. A whorl of 5–6 early secondary roots (ESR) developed on each system.

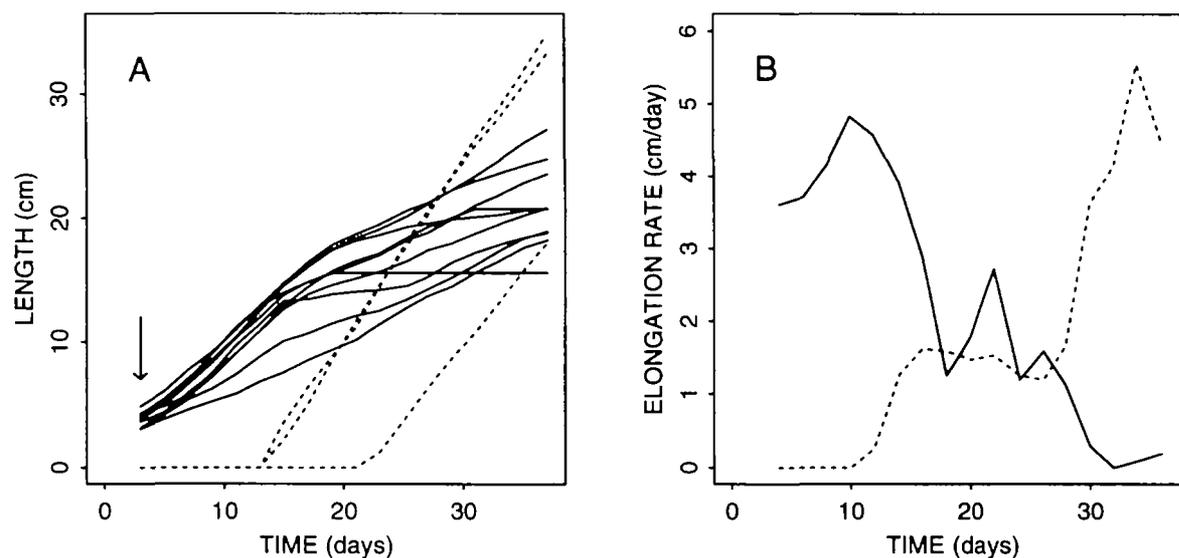


Fig. 5. Growth curves (A) for the individual ESR (—) and regenerated roots (---) and variations in cumulated elongation rate (B) for early secondary roots (ESR, —) and regenerated roots (---) and for a pruned (–T) seedling.

Table 1. Branching density and distribution of the lengths, at day 37, of the tertiary roots on the early secondary roots (ESR) for the control (+T), pruned taproot (–T) and blocked taproot (bT)

Branching density was calculated as the total number of tertiary roots divided by the total length of ESR per seedling.

	Control +T	Pruned taproot –T	Blocked taproot bT
Branching density (root cm ⁻¹)			
Mean	0.57	0.93	0.80
Range	0.18–0.80	0.53–1.51	0.66–1.07
Percentage of roots per length category (cm)			
<2	68.8	50.6	49.5
2–4	25.0	32.5	28.3
4–6	5.0	11.8	14.8
>6	1.3	5.0	7.4

treatment. The branching density for the –T seedlings (0.93 root cm⁻¹) and the bT seedlings (0.80 root cm⁻¹) was higher than for the control (0.57 root cm⁻¹).

Elongation of the tertiary roots

As shown in Fig. 6, the mean elongation rate per seedling for the tertiary roots borne by the ESR was higher for –T and bT seedlings than for the control. The latter remained low (< 5 cm d⁻¹) until the end of the flush of shoot growth and reached a maximum value of 13 cm d⁻¹ thereafter. The growth rate of the tertiary roots of the –T and the bT seedlings revealed an initial peak before the period of high leaf growth, declined during this period and resumed thereafter, reaching a maximum value of 25 cm d⁻¹ for the pruned treatment and 35 cm d⁻¹ for the blocked treatment.

As a consequence of branching and elongation processes, the tertiary roots developed on the ESR growing without a taproot (–T and bT) were more numerous and longer (Fig. 4; Table 1). Half of the tertiary roots

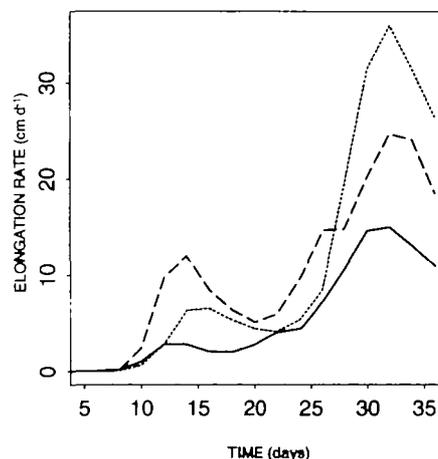


Fig. 6. Variations in the mean cumulated elongation rate of the tertiary roots borne by the ESR for control (+T, —), pruned taproot (–T, - -) and blocked taproot (bT, ···) seedlings. Each line is the mean for 6–7 seedlings.

borne by the ESR were shorter than 2 cm for -T and bT compared to two-thirds for the control; 16.8% and 22.2% of tertiary roots were longer than 4 cm for -T and bT, respectively, and only 6.3% for the control (Table 1).

Apical diameter

The mean apical diameter of ESR varied in the same way as their mean elongation rate—it was depressed during leaf growth and resumed thereafter (Fig. 7)—and this was also the case for individual roots (Fig. 8). But the magnitude of these variations was different with regard to the treatment applied to the taproot (Fig. 7). The minimum mean apical diameter was lower for the control (0.34 mm) than for both -T and bT treatments (0.44 mm). Following shoot growth, all treatments showed an increase in their mean apical diameter, but this was much more substantial for bT than for -T and the control. The maximum mean apical diameter for ESR developed with a blocked taproot was 1.00 mm, whereas the maximum values for -T and the control were 0.66 and 0.56 mm, respectively. Thus, at the end of the experiment, the apical diameter of ESR grown without taproot and without regenerated roots (bT) was considerably larger than at the time of emergence. The maximum diameter for individual roots was 1.54, 1.14 and 0.80 mm for bT, -T and +T, respectively. The diameter was recorded for five regenerated roots. For these roots, apical diameter ranged from 0.70 to 1.34 mm the day after emergence and subsequently fluctuated between 0.80 and 1.40 mm.

Relationship between apical diameter and elongation rate

Apical diameter and elongation rate revealed clear similar temporal variations for individual roots (Fig. 8), but these variations were not proportional. Therefore, the overall relation (considering all measured ESR, for all

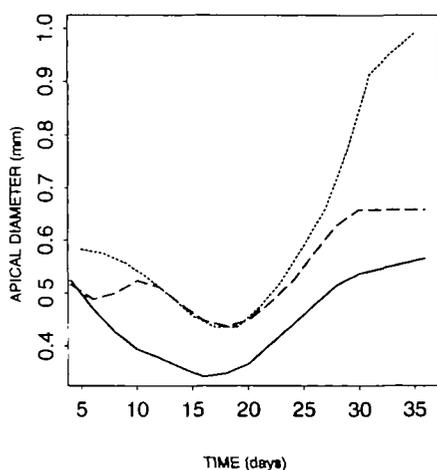


Fig. 7. Variations in the mean apical diameter of the early secondary roots (ESR) for control (+T, —), pruned taproot (-T, --) and blocked taproot (bT, ...) seedlings. Each line is the mean for 6–7 seedlings.

seedlings at each measurement date) between elongation rate and diameter was not very close (data not shown). During the first phase (shoot growth), apical diameters did not exceed 0.80 mm regardless of the treatments and the maximum elongation rate for a given diameter increased with this diameter. However, only a few roots reached this maximum growth. For control, the relationship and the range of diameters remained the same throughout the experiment (data not shown). On the other hand, during shoot rest, it was possible to look at the relation for a larger range of diameters concerning -T and bT. Figure 9 shows the relation between the two parameters for all measured ESR at each measurement date following shoot growth for -T and bT. The smoothed curves representing the trends revealed an increase in elongation rate when apical diameter increased from 0.20 to 0.60 mm, for -T. The relation was similar for bT, but the minimum diameter was 0.40 mm. Above 0.60 mm, the relationships were different depending on treatments. For bT the trend continued to increase, but slightly, and reached a maximum at about 1.20 mm. For -T seedlings, the trend indicated that the elongation rate did not increase further, while apical diameter increased from 0.60 to 1.14 mm. Accordingly, for a given apical diameter in this range of variation, the ESR which grew without a taproot but in the presence of regenerated roots (-T) reached lower elongation rates than those which grew without regenerated roots (bT). Such altered relationships between diameter and elongation occurred for the ESR which continued to grow following the shoot growth flush.

Discussion

Pruning or blocking the taproot 3–4 d after its emergence had significant consequences for the development of the laterals that were already present, i.e. the early secondary roots (ESR).

Following the period of shoot growth, the elongation rate of the ESR for blocked taproot (bT) seedlings reach higher mean values than for the pruned taproot (-T) and control. The overall elongation rate of tertiary roots for seedlings without a growing taproot (bT and -T) was also higher than for the control. This was related to the higher branching density recorded on ESR for these treatments. Elongation duration was also affected, the proportion of ESR which stopped growing during the experiment was larger for the control than for seedlings without a growing taproot. Taproot manipulation also had a substantial effect on the apical diameter of the ESR. For both -T and bT, the diameters of the roots which grew longer were larger than those recorded for the control or for secondary roots in previous studies (Thaler and Pagès, 1996b). The highest values recorded for ESR were similar to the diameters of normal taproots.

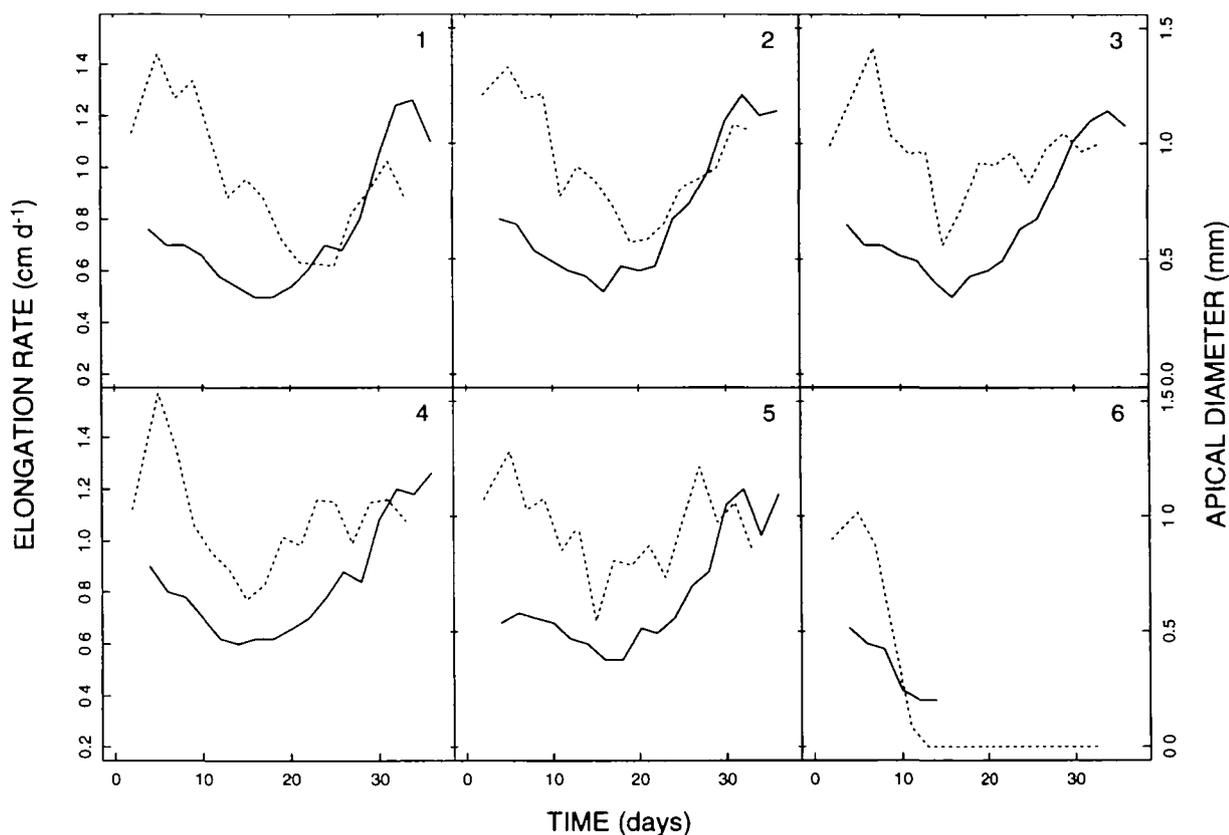


Fig. 8. Variations in the apical diameter (—) and elongation rate (---) for the individual early secondary roots (ESR, numbered from 1 to 6) for a typical blocked taproot seedling.

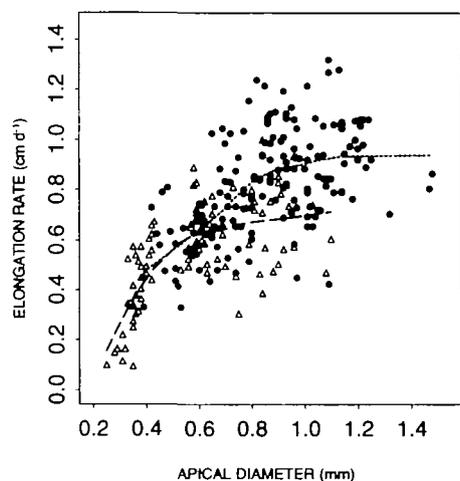


Fig. 9. Relationship between the elongation rate and apical diameter following the shoot growth period. The points represent data for the early secondary roots for all the pruned taproot (pT, Δ ---) and all the blocked taproot (bT, \bullet ---) seedlings. Trends were fitted by a 'lowess' algorithm (Chambers *et al.*, 1982)

first 20 d following taproot alteration, which corresponded to the development of the first shoot growth unit. During, this period, both the mean elongation rate and mean apical diameter of the ESR continued to decrease regardless of the treatment. Moreover, the subsequent increase in ESR elongation rate and apical diameter was less important for the pruned treatment, for which new roots regenerated at the wound site, than for the blocked treatment, for which ESR were the only roots allowed to grow. These results, in accordance with previous work on the secondary roots of oak trees (Riedacker *et al.*, 1982; Lamond *et al.*, 1983; Pagès *et al.*, 1992), indicated that the elongation pattern of a growing secondary root cannot quickly be altered by sudden modifications in the development of the main axis of the root system.

The delay between taproot alteration and response of the ESR is not consistent with the hypothesis that the meristem of the taproot actively inhibits the development of lateral roots (by the action of hormones). In this hypothesis, a quick-acting enhancement of ESR elongation rate would be expected following removal of the taproot and consequent breaking of the inhibition. Moreover, the observed synchronism between the end of shoot growth and the acceleration of ESR elongation is

However, the induced changes were delayed and seemed to depend on the correlative context, i.e. the state of development of the other parts of the plant. In particular, there were few differences between treatments during the

hardly explained by active control of lateral root growth by a factor originating from the taproot apex.

On the contrary, these observations reinforce the hypothesis that root growth is controlled by competition for a factor originating from the shoot, probably carbohydrates. This can be inferred from the observed relation between the development of the ESR and the level of demand from the other sinks of the system. ESR elongation was obviously depleted during shoot development (Fig. 1), but also related to the elongation of regenerating roots for the pruned treatment (Fig. 5). Previous work has shown that developing shoots are stronger sinks for carbohydrates than roots (Head, 1967; Bevington and Castle, 1985; Thaler and Pagès, 1996a). The results of Riedacker *et al.* (1982) and Amin *et al.* (1987) on oak indicated that regenerating roots also compete with already growing secondary roots and prevent a possible increase in the elongation of the latter.

When shoot growth demand stopped, the elongation rate of the ESR for the blocked taproot increased, but progressively (Fig. 1). The apparent inertia of ESR elongation and the differences between ESR and regenerating roots can be interpreted considering that root growth is regulated by competition for assimilates governed by each root's growth potential, i.e. maximum growth rate when the considered resource is not limiting. In this hypothesis, current elongation of a root can be limited by the level of assimilate at the time, but also by its own maximum growth rate. This growth potential had been shown to be closely related to the diameter of the apex (Thaler and Pagès, 1996b) which reflects the volume of the meristem and quiescent centre and thereby the number of meristematic cells (Torrey and Feldman, 1977; Clowes, 1984). In order for the elongation rate of an already growing root to accelerate markedly, an increase in its growth potential, thus in the size of its meristem, is required. Such an increase in both elongation rate and apical width was actually observed in the experiment (Fig. 7) and has been reported in experiments on cultured roots: when supplied with a high sucrose concentration, roots develop more rapidly but also present a higher number of cell files than roots grown on a sucrose-poor medium (Barlow and Adam, 1989). These previous or simultaneous changes in the structure of the root apex can partly explain the dynamics of ESR elongation response to taproot removal or blocking. At the end of the period of shoot growth, apical diameter in all treatments was low, hence an increase in assimilate availability allowed by shoot rest and taproot blocking could not quickly result in a high elongation rate for ESR, before the meristem of the latter had recovered an appropriate size. Moreover, for the control, the diameter of many ESR became lower than 0.2–0.3 mm, which has been shown to be a threshold under which elongation definitely stops (Thaler and Pagès, 1996b). Consequently, in the

presence of a growing taproot, a larger proportion of ESR became unable to respond to a possibly more favourable context. Conversely, the apical diameter remained greater than 0.3 mm for a large number of ESR in both bT and –T treatments thereby preserving their ability to grow further. The behaviour of the ESR when the taproot is prevented from growing demonstrates the possibility of describing the effects of competition on root development as two-step regulation: short-term changes will determine the proportion of the growth potential currently achieved and long-term changes will affect the growth potential itself.

Changes in ESR growth rate seemed to be prevented when regenerating roots emerged following taproot pruning. According to a review by Coutts (1987), regenerating roots that develop at the wound site when the tip of a main axis is removed have large meristems from the primordium stage. This can result from a favourable developmental context, since the main root sink had been removed, thus initial growth of regenerating primordia could be enhanced by carbohydrate availability or by increased deposition of auxins at the wound site. The histological origins could also determine the differences between regenerating roots and laterals (Reihman and Rost, 1990). Such initial larger dimensions of the meristem for regenerating roots are likely to provide them with a higher growth potential (Hackett, 1969). Consequently, ESR for pruned taproot seedling had to compete with strong sinks when regenerating roots emerged, and could not realise the growth potential allowed by their apical diameter. This reinforces the hypothesis that the long-term growth pattern of the ESR depends on the competition between roots.

The data obtained in this work underline the importance of the type of treatment applied in order to prevent the taproot from growing in studies of competition between roots. Taproot pruning which results in neomorphogenesis of large roots obviously has different consequences from taproot blocking. Moreover, the relation with shoot growth indicates that the shoot development stage is also important in regulating root response to local alterations. The rhythmic growth of rubber tree shoot provides periodic variations in assimilate supply and demand, that are proved to be helpful for the study of competition patterns within the root system.

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