Cell Cycle Duration in the Root Meristem of Sonoran Desert Cactaceae as Estimated by Cell-flow and Rate-of-cell-production Methods

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Slow rates of cactus growth in the Sonoran Desert and high productivity of some Cactaceae under cultivation suggest that relatively low growth rates are not the consequence of a long cell division cycle but of short optimal periods for growth and adverse environmental factors. To verify this hypothesis, the duration of the cell division cycle (T) in the root apical meristem of seedlings of three sympatric species from the Sonoran Desert [Ferocactus peninsulae (F. A. C. Weber) Britton & Rose 'Townsendianus' (Britton & Rose) N. P. Taylor, stat. nov., Stenocereus gummosus (Engelm.) Gibson & Horak and Pachycereus pringlei (S. Watson) Britton & Rose] was estimated with the rate-of-cell-production (RCP) and the cell-flow (colchicine) methods. Both methods were applied during the steady-state growth phase, which was relatively short in the first two species because of the determinate pattern of root growth. The RCP method permitted estimation of T in each root individually. Durations of the cell division cycle were inversely proportional to the rate of root growth (r² ranged from 0.42 to 0.88, P < 0.05). T, determined by the cell-flow method, ranged from 14.4 to 19.3 h in these species and was within the same range as T determined by the RCP method. The average T determined by the RCP method was 67 to 75% of that determined by the cell-flow method. Results obtained with both methods are compared and analysed. The proposed hypothesis appears to be correct, indicating that these species can be more productive under cultivation than in the wild due to the relatively short duration of the cell division cycle. Adaptive features of these findings are also considered.

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Key words: Cactaceae, cell division cycle, root growth, root meristem, Sonoran Desert.

INTRODUCTION

In arid and semiarid environments, rates of cactus growth are very low: Carnegiea gigantea and Stenocereus thurberi in Arizona showed annual stem length increments of 10 and 8 cm, respectively (Shreve, 1935); certain specimens of Coryphanta and Mamillaria grew less than 1 mm in height per annum (Nobel, 1988); Cephalocereus columna-trajani (Karwinski ex. Pfeiffer) Schumann growing in semiarid central Mexico showed stem growth increments from 3 to 11 mm per year (Zavala-Hurtado and Díaz-Solís, 1995). However, some cultivated cactus species have productivity comparable to that of highly productive agricultural crops. For example, prickly pear, Opuntia ficus-indica, produced 2 kg d. wt (m² ground area)⁻¹ year⁻¹ (Nobel, 1988, 1996). Similar productivity was reported for cultivated Ferocactus peruvianus introduced into the Negev Desert of Israel (Nerd, Raveh and Mizrahi, 1993).

Factors contributing to high productivity of agave and cactus species include: (1) the potential for year-round growth; and (2) Crassulacean acid metabolism leading to high net CO₂ uptake per unit of water transpired (Nobel, 1988). Productivity is closely related to growth, and growth is related to a combination of processes of cell division and cell growth. The duration of the cell division cycle must be considered as a possible internal factor permitting or limiting high productivity. Because of the known high productivity of certain cactus species under cultivation, we hypothesize that the slow growth of cacti in natural environments is not caused by long cell division cycles but by drastic pressure of a stressful environment and short optimal periods for growth. To test this hypothesis was one of our objectives.

In the root apical meristem of Stenocereus gummosus the duration of the cell division cycle (T) determined by the cell-flow method was shown to be relatively short (Dubrovsky, 1997a). To the best of our knowledge, there are no other reports on T in cactus apical meristems (Grif and Ivanov, 1975, 1980, 1995). Knowledge of T is important for a better understanding of the drought-adaptive features of this interesting family of succulent plants. Stem and root growth are usually correlated in plants. T in shoot and root apical meristems in a species is usually close, even though there are cases when T in the shoot apical meristem is longer than in the root apical meristem (Ivanov, 1983). Due to the more simple structural organization of the root, our estimations of T were made in a seedling root apical meristem under optimal conditions of growth. Estimation of T in the root apical meristem, our second objective, will allow us to understand better how the root meristem functions and how it is adapted to the arid environment.

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Our third objective was the comparison of the rate-of-cell-production (RCP) method (Ivanov and Dubrovsky, 1997) with the accepted cell-flow method for estimation of $T$. The RCP method, which until now has not had wide use, is particularly useful for field studies. Furthermore, the use of more than one method for the estimation of $T$ will also increase the validity of data obtained.

The species selected for this study are sympatric Cactaceae from the Sonoran Desert. They are characterized by determinate (Stenocereus gummosus and Ferocactus peninsulae, Dubrovsky 1997a, b) and indeterminate (Pachycereus pringlei) primary-root growth of their seedlings. S. gummosus (‘Pitaya agria’) produces edible fruit and can be cultivated (León de la Luz et al., 1995). F. peninsulae (‘Biznaga’) is a species endemic to Baja California (Wiggins, 1980) and is used for candy production. All species are widely distributed in the Sonoran Desert (Turner, Bowers and Burgess, 1995) and are important resources for reforestation.

MATERIALS AND METHODS

Plant material and seed germination

Fruit of Ferocactus peninsulae (F. A. C. Weber) Britton & Rose, ‘Townsendianus’ (Britton & Rose) N. P. Taylor, stat. nov., Stenocereus gummosus (Engelm.) Gibson & Horak, and Pachycereus pringlei (S. Watson) Britton & Rose was collected from plants growing near La Paz, Baja California Sur, Mexico. Seeds were washed free of pulp and air-dried at room temperature. The seeds were surface sterilized for 5 min in 20 ml of an aqueous solution containing 5-25% sodium hypochlorite and 20 µl 10% Triton X-100, then thoroughly washed with distilled water. Seeds were germinated in 140 mm Petri dishes on filter paper (Whatman No. 1) moistened with 20 ml 20% Hoagland mineral solution (Hoagland and Arnon, 1938). Plates were maintained in an 18 to 20° inclined position in a temperature-controlled room at 29±1 °C under light (38 µmol m⁻² s⁻¹) for a 12 h day/night photoperiod. For determination of the root-growth pattern, seeds with broken testas were selected at day 0 after the start of radicle protrusion (ASRP) and arranged on filter paper in a line 2–3 cm from the edge of the Hoagland mineral solution in inclined Petri dishes and maintained under the same conditions as germinating seeds. Root length was measured daily. If a root had slow or no growth, the seedlings were discarded.

$T$ was determined in roots during the period of steady-state growth. In F. peninsulae and S. gummosus, $T$ was determined during day 2 ASRP, and in P. pringlei during day 3 ASRP. Cell-flow and rate-of-cell-production (RCP) methods for determination of $T$ were always used simultaneously on seedlings from the same population. The starting time for both determinations was the same (i.e. the time of root length measurements in the RCP method and the time when roots were submerged in colchicine solution in the cell-flow method).

Cell-flow method

For all three species, the cell-flow method was the colchicine method based on the accumulation of cells in metaphases (Webster and MacLeod, 1980). Seedling roots were incubated in 0.025% colchicine in 20% Hoagland mineral solution for 1 or 3 h (treatments) and for 3 h in 20% Hoagland mineral solution (control). Roots 1–2 mm long were incubated in inclined Petri dishes on filter paper moistened with the solutions in such a way that their 1-mm root tips were submerged in the solutions. After incubation, seedlings were fixed in 96% ethyl alcohol: glacial acetic acid, 3:1 (acetic alcohol).

Each treatment and control was performed in triplicate. Five to 15 roots per replicate were fixed and Feulgen stained (Berlyn and Mikesche, 1976). Permanent squash preparations were made with a 0.5% solution of gelatin and 0.02% of Alcian Blue 8GX (Dubrovsky and Contreras-Burciaga, 1998), then dehydrated and mounted in Canada Balsam. In each replicate, not less than 700 cells for S. gummosus and 1000 cells for the other two species were scored. The duration of the cell division cycle was calculated, assuming an exponential character of the increase in number of cells in the meristem, using the equation $T = \ln 2 k^{-1}$, where $k$ is the relative rate of accumulation of metaphases (Webster and MacLeod, 1980). $k$ was estimated by taking into consideration restitution nuclei, explaining why $k$ was termed cell birth rate by Barlow and Woodiwiss (1992). $k$ was estimated as follows: $\frac{[(M+R) - (M_t + R_t)]}{t}$, where $M_t$ and $R_t$ are indices of metaphases and restitution nuclei, respectively.

The rate-of-cell-production method

The theory behind the RCP method in the root apical meristem has been analysed in detail (Ivanov and Dubrovsky, 1997). In practice, roots of the same size as those taken for the colchicine method were selected and numbered and their precise root length measured using an OLYMPUS BX-50 microscope with an ocular micrometer (Olympus America Inc., Miami, Florida). The time of the first measurement was taken as $t_0$. At this time, five to ten seedlings were fixed in acetic alcohol for subsequent determination of the number of meristematic cells in the root apical meristem ($N_m$ at $t_0$). Live seedlings were arranged in the same manner as germinating seeds i.e. 2–3 cm from the edge of the 20% Hoagland mineral solution in inclined Petri dishes. After 24 or less hours ($t_1$), the primary-root length was measured again. Afterwards, seedling roots were infiltrated with water under a slight vacuum, stained with 0.1% Toluidine blue 0 and the length of the fully elongated epidermal cells was measured with the microscope within the region of new growth that occurred between $t_0$ and $t_1$. These roots were then fixed in acetic alcohol and washed in alcohol. These roots and those fixed at $t_0$ were Feulgen stained and mounted (in total) in Canada Balsam.

The number of meristematic epidermal cells in a cell file was determined in roots stained by Feulgen and fixed at $t_0$ and $t_1$. The meristem extension for the epidermis was determined in the apical root portion by the presence of cells.
with the interval between neighbouring cells in a cell file approximately equal to or less than the diameter of the nuclei. \( T \) was calculated for each individual root using the equation: \( T = \left( \ln 2 \times N_m \times l_i \right) V^{-1} \), where \( N_m \) is the average number of meristematic cells in one file of the epidermis at \( t_0 \) and \( t_1 \) (\( N_m \) at \( t_0 \) was taken as the average number of meristematic cells in the epidermis of five to ten roots), \( l_i \) is the average length of ten fully elongated epidermal cells measured in two to three cell files of a root, and \( V \) is the rate of growth of an individual root, calculated as \( \mu \text{m h}^{-1} \) (Ivanov and Dubrovsky, 1997). The average \( T \) was calculated for 11 individual roots of each species.

**RESULTS**

**Pattern of root growth**

Primary roots of *S. gummosus* and *F. peninsulare* only grew for 2 d after the start of radicle protrusion (Fig. 1). There were no statistical differences in root lengths of these species at 3 d or subsequently (\( P > 0.05 \)). A similar root growth pattern had previously been observed in these species and was defined as determinate growth (Dubrovsky 1997a, b). *P. pringlei* had indeterminate primary root growth (Fig. 1). The steady-state phase of root growth for the first two species was maintained during day 2 ASRP only. Because of this growth pattern, \( T \) was determined only during this period for these two species, and during day 3 for *P. pringlei*.

**Cell-flow method**

The concentration of colchicine used did not have a significant effect on the number of cells entering mitosis (Table 1), except in *F. peninsulare*. The percentage of prophase in roots of this species incubated for 3 h in colchicine was 1.4% less than in untreated roots. This difference was statistically significant (\( P < 0.05 \), Student’s \( t \)-test). In all other cases, the percentage of prophase in control and colchicine-treated roots was the same. The colchicine solution used was sufficient to produce the accumulation of cells in metaphase and to block the anaphase separation of chromatids; the percentage of anaphase and telophase was, in most cases, zero (Table 1). The cell birth rate, \( k \), and \( T \) estimated as cell doubling time, are presented in Table 1. For comparison purposes, \( T \) determined previously for *S. gummosus* is also included in Table 1 because neither the percentage of cells in different stages of mitosis, nor \( k \), were reported (Dubrovsky, 1997a).

**Rate-of-cell-production method**

Data on the rate of root growth, the length of fully elongated cells, the average number of cells in the meristem, and calculated \( T \) are presented in Table 2. The apical meristems of the species studied were relatively small and were (minimum to maximum) seven to 20, 16 to 24 and 13 to 25 epidermal cells in a cell file in *S. gummosus*, *F. peninsulare* and *P. pringlei*, respectively. The CV of average \( N_m \) (mean of average \( N_m \) at \( t_0 \) and \( N_m \) at an individual root at \( t_1 \)) did not exceed 6%. Due to the determinate pattern of root growth, \( N_m \) at \( t_0 \) and \( t_1 \) in *S. gummosus* was different (\( P < 0.001 \)) being, on average, 14.6 ± 0.1 (mean ± s.e., \( n = 14 \)) and 9.5 ± 0.3 (\( n = 11 \)) cells, respectively. The time between \( t_0 \) and \( t_1 \) was 24 h. To decrease the difference between \( N_m \) at \( t_0 \) and \( t_1 \) in the experiment with *F. peninsulare*, which is also characterized by determinate growth (Fig. 1), the time between \( t_0 \) and \( t_1 \) was decreased to 5 and 9 h for two subsamples of a sample compared with the colchicine method. This resulted in a similar \( N_m \) at \( t_0 \) and \( t_1 \) in *F. peninsulare* (\( P > 0.05 \)). In *P. pringlei* there were no differences in \( N_m \) (\( P > 0.05 \)) over 24 h.

\( T \) was determined by the RCP method for each individual root. The CV of the length of fully elongated cells and of the average number of cells in the meristem file was 5 to 10%, whereas the CV of the rates of root growth and the calculated \( T \) were much higher (Table 2). Because of this variation and for comparison of data obtained by alternate methods, values of \( T \) for each individual root were plotted against the rate of root growth (Fig. 2). Rates of root growth were inversely proportional to the \( T \) calculated.

Correlations between the rate of root growth and the duration of the cell division cycle were significant (\( P < 0.05 \); Fig. 2). No correlations were found (\( r^2 = 0.14, P > 0.27 \)) between (a) the rate of root growth and the length of fully elongated cells; (b) the rate of root growth and the number of cells in the meristem (except for *S. gummosus*; \( r^2 = 0.43, P = 0.03 \)); or (c) the length of fully elongated cells and the number of cells in the meristem.

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**Fig. 1.** Primary root length in *Stenocereus thurberi*, *Ferocactus peninsulare* and *Pachycereus pringlei* over time after the start of radicle protrusion. Data are means ± s.e. \( n = 12, 13 \) and 20 roots in each species, respectively.
In these two species, **P. pringlei** was most affected by colchicine treatment. This was observed in terms of the duration of metaphase and the number of cells in the meristematic and elongation zones. The epidermal cells in the meristem also showed a decrease in the rate of cell division. In **S. gummosus**, the number of meristematic cells decreases after 36 h ASRP, and is constant in **F. peninsulae** until 24 h ASRP (Dubrovsky, 1997b). In **P. pringlei**, the number of epidermal cells in the meristem did not change during first 24 h ASRP. Thus, when the roots were incubated in the colchicine solution (24 to 27 h ASRP), they maintained steady (**S. gummosus** and **P. pringlei**) or nearly steady (**F. peninsulae**) growth.

Restitution nuclei were present in **S. gummosus** and **P. pringlei** incubated for 1 h in colchicine solution. The duration of metaphase (**t_m**) can be estimated by the equation **t_m = (T x I_m) 100°**, where **I_m** is the metaphase index (Barlow and Woodiwiss, 1992). In these two species, **t_m** was estimated as 0.14 h for 1 h and 0.42 h. The presence of restitution nuclei after incubation for 1 h in colchicine showed these cactus species were probably relatively insensitive to colchicine. The species most affected by colchicine treatment was **F. peninsulae** which had no restitution nuclei after 1 h of incubation and the prophase index after incubation for 3 h was significantly decreased (Table 1). Nevertheless, **T** obtained by the cell-flow method is within the range of **T** obtained by the RCP method (compare Table 1 and Fig. 2).

Meristems of the species studied are relatively small (Table 2). As a result the exact excision of the meristem for squash preparation was not possible. Cell counts will

<table>
<thead>
<tr>
<th>Species</th>
<th>Hours in colchicine</th>
<th>Prophases</th>
<th>Metaphases</th>
<th>Restitution nuclei</th>
<th>Ana- and telophases</th>
<th>k</th>
<th>T (h)</th>
</tr>
</thead>
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<td><strong>S. gummosus</strong></td>
<td>0</td>
<td>2.6 ± 0.4</td>
<td>10 ± 0.2</td>
<td>0</td>
<td>12 ± 0.3</td>
<td>0.048</td>
<td>144</td>
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<tr>
<td></td>
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<td>2.1 ± 0.0</td>
<td>53 ± 0.3</td>
<td>0.2 ± 0.1</td>
<td>0.1 ± 0.1</td>
<td>0.042</td>
<td>16.5</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>32 ± 0.3</td>
<td>142 ± 0.9</td>
<td>0.9 ± 0.1</td>
<td>0</td>
<td>0.036</td>
<td>19.3</td>
</tr>
<tr>
<td><strong>F. peninsulae</strong></td>
<td>0</td>
<td>5.1 ± 0.4</td>
<td>23 ± 0.5</td>
<td>0</td>
<td>14 ± 0.1</td>
<td>0.048</td>
<td>144</td>
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<tr>
<td></td>
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<td>59 ± 0.3</td>
<td>0</td>
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<td>0.042</td>
<td>16.5</td>
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<tr>
<td></td>
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<td>37 ± 0.1</td>
<td>131 ± 0.2</td>
<td>1.2 ± 0.2</td>
<td>0</td>
<td>0.036</td>
<td>19.3</td>
</tr>
<tr>
<td><strong>P. pringlei</strong></td>
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<td>3.3 ± 0.2</td>
<td>22 ± 0.3</td>
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<td>14 ± 0.1</td>
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<td>0</td>
<td>0.036</td>
<td>19.3</td>
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</table>

**DISCUSSION**

In steadily growing roots, the root-growth rate and the number of cells in the meristem and in the elongation zone are maintained nearly constant (Brown, 1951; Ivanov, 1981, 1994). Roots of species with a determinate pattern of root growth (**S. gummosus** and **F. peninsulae**) have a very short period of steady-state growth, as reported earlier (Dubrovsky 1997a, b); they grow linearly and with the same rate during day 2 ASRP. In **S. gummosus**, the number of meristematic cells decreases after 36 h ASRP, and is constant in **F. peninsulae** until 24 h ASRP (Dubrovsky, 1997b). In **P. pringlei**, the number of epidermal cells in the meristem did not change during first 24 h ASRP. Thus, when the roots were incubated in the colchicine solution (24 to 27 h ASRP), they maintained steady (**S. gummosus**, **P. pringlei**) or nearly steady (**F. peninsulae**) growth.

FIG. 2. Correlation between rate of root growth and the estimated duration of the cell division cycle in individual roots of three cactus species by the rate-of-cell-production method. **Stenocereus gummosus**: \( y = 1669 - 7.6 \times, r^2 = 0.88, P < 0.001; \) **Ferocactus peninsulae**: \( y = 223.3 - 9.6 \times, r^2 = 0.82, P < 0.001; \) **Parodia pringlei**: \( y = 288.2 - 7.6 \times, r^2 = 0.42, P < 0.05. \)
therefore include both meristematic and non-meristematic cells. To avoid this problem the counterstain Alcian Blue 8GX was used as a cell wall stain (Beneš, 1968), permitting the recognition of cell shapes (Dubrovsky and Contreras-Burciaga, 1998) and thus meristematic and non-meristematic cells (because meristematic cells have a higher ratio of nucleus to whole cell volume compared to non-meristematic cells). However, it is possible that some cells which had ceased division and were at the beginning of the elongation phase were also scored. This may introduce error into the cell-flow method and explain why the average $T$ determined by the cell-flow method was 133 to 148% of that determined by the RCP method. The RCP method is based on the assumption that all cells are proliferatively active and the growth fraction is equal to one (Ivanov, 1994; Ivanov and Dubrovsky, 1997). Thus, results of the RCP method always give the lower limit of $T$.

Detailed analysis of root growth in a population of seedlings of *S. gummosus* and *F. peninsulare* showed there are roots that do not grow longer than 2 mm (Dubrovsky, 1997b). Seedlings with 1–2 mm long roots were selected for the cell-flow method, thus the sample may contain roots that terminated their growth and had low or no meristematic activity. In this case, $T$, as calculated, may be overestimated. This also explains slight differences in the results obtained by these methods.

The rate of root growth ($V$) is a complex parameter because both cell division and cell growth contribute to it; this explains the relatively high variability of $V$ we obtained (Table 2). Because $V$ is a parameter used in the calculation of $T$ by the RCP method, the relatively high variation of $V$ explains the variability of $T$ (Table 2). One of the advantages of the RCP method is that $T$ can be estimated for each root individually. The distribution of roots by their rate of growth in a population under the same conditions is a common phenomenon (Pilet, 1996). As a result of the relatively short incubation period (3 h) in the cell-flow method, fast- and slow-growing roots at the moment of fixation could not be recognized and all roots were combined together. However, because of the absence of sliding growth of cells in a root (Sinnott and Bloch, 1939; Brumfield, 1942), the same population of meristematic cells cannot contain significant amounts of both fast- and slow-dividing cells. The RCP method helped to prevent this problem. Rapidly growing roots had a shorter $T$, and roots growing slowly had a longer $T$ (Fig. 2). Comparison showed the results obtained by the cell-flow method are within the range of $T$ obtained by the RCP method (compare results of Table 1 and Fig. 2).

In *S. gummosus*, the RCP method was applied to roots in which the number of meristematic cells was not constant, though constancy is assumed by this method. That is why the average $N_w$ (at the beginning and at the end of root-length measurements) was used to calculate $T$. An average $T$ equal to 9.7 h (Table 2) is probably an underestimation. Interestingly, the approach based on the dynamics of meristem exhaustion during determinate growth showed the duration of the cell division cycle is supposed to be 14 h (Dubrovsky, 1997b). This is close to that determined by the cell-flow method.

In *F. peninsulare*, the number of meristematic cells was constant during the 5 and 9 h of root-length measurements and gave an average $T$, by the RCP method, of 12 h. Based on the dynamics of meristem exhaustion during determinate growth, the duration of the cell division cycle was deduced to be 16 h in this species (Dubrovsky, 1997b). This result was close to that determined by the cell-flow method (Table 1).

General analysis showed the duration of the cell division cycle determined by the two methods used in this study was similar, close to that estimated by analysis of the dynamics of meristem exhaustion (Dubrovsky, 1997a,b), and was relatively short. The root meristem is programmed to determinate development in some Cactaceae of the Sonoran desert, and only a few cell division cycles are permitted (Dubrovsky, 1997b). This research confirmed this conclusion. Determinate growth was proposed as a physiological root-tip decapitation, a mechanism important for rapid lateral-root formation (Dubrovsky 1997a,b). In this respect, a relatively short cell division cycle in the apical meristem is an essential condition for both primary and lateral root growth and for rapid seedling establishment during the short optimal growth periods in the desert. In desert plants with both a determinate and an indeterminate growth pattern (such as *P. pringlei*), water and mineral absorption after a drought and during a wet period can be facilitated by new apical growth and by rapid formation of new roots, particularly, ephemeral (‘rain’) roots (Nobel, 1988; Nobel and Huang, 1992; North and Nobel, 1995; Nobel and North, 1996). A relatively short $T$ is an essential condition for rapid root-system development. The relatively short cell division cycle in the Cactaceae studied therefore has an important adaptive significance.

The hypothesis that slow growth of cacti in a natural environment is not caused by long cell division cycles but by the drastic pressure of a stressful environment and short optimal periods for growth appears correct. Correlation between winter precipitation levels in southern Arizona and interannual variation in stem growth rates of *Stenocereus thurberi* and *Lophocereus schottii* (Parker, 1988) are in agreement with the hypothesis proposed. Theoretically, for species characterized by slow rates of growth, it is possible to develop some techniques that decrease the pressure of desert environments and improve biomass production. This is especially important for reforestation and for the agricultural introduction of some wild desert species of potential economic importance in the Americas, such as *S. gummosus* (León de la Luz et al., 1995) and *Stenocereus queretaroensis* (Weber) Buxbaum (Pimienta-Barrios and Nobel, 1994; Nobel and Pimienta-Barrios, 1995) as well as for their introduction to old world agriculture (Nerd, Raveh and Mizrahi, 1993; Raveh et al., 1993; Weiss, Nerd and Mizrahi, 1993).

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