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Clonal Analysis Provides Evidence for Transient Initial Cells in Shoot Apical Meristems of Seed Plants

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Abstract

Drift of mutated sectors in sectorial or mericlinal plant chimeras has been interpreted as indirect evidence of initial impermanence at the apex. However, the same effect may result from mutation in noninitial cells positioned close to the vertex of the apical dome. Clonal analysis of the cell packets present in the superficial layer of spruce and magnolia apices provided the library of patterns suggesting that the position and the number of initial cells, and in some cases also the meristem axis inclination, may change over time. Multicellular clones originating from a single cell have been found in the geometric center of some apices, whereas in other apices the cellular center (where three or four clonal borders meet) did not correspond to the geometric center of the apex. Such effects may result only from initial impermanence.

Introduction

The progressive character of the shoot apical meristem is the increasing number of initial cells. In seed plants these cells are positioned in one or more layers at the vertex of the apical dome axis. They are difficult to discern because, unlike in lower land plants, they do not differ morphologically from their nearest derivatives. The question of how many initials are at the apex and whether these initials are permanent (Rogers and Bonnett 1989; Stewart and Dermen 1970) or functional (Klekowski 1988; Klekowski; Kazarinowa-Fukshansky 1984 and Soma and Ball 1963) remains unsolved.

One possibility for determining the position and the number of initial cells at the apex is to observe the mutated sector widths in shoots of the sectorial or mericlinal chimeras (Tilney-Bassett 1986). Results suggest the presence of two, three, or four initials in each layer (Lyndon 1998; Rogers and Bonnett 1989; Romberger and others 1993; Stewart and Dermen 1970). Such evidence, however, is indirect, and the conclusions might be affected by the following facts:

1. In sectorial and mericlinal chimeras the mutated sector often either expands or shrinks, ultimately drifting away from the apex. This is due either to the selection of new initials in the stochastic meristems, as postulated by Klekowski (1988), or to the mutation occurring in the cell positioned near the vertex, but not being an initial cell, as proposed by Puławska (1986).

2. The contribution of the initial cells to apex (and shoot) circumference is not necessarily equal. The ratio of meridinal and equatorial divisions in the derivatives of the initial cells may vary in sectors produced by different initials as demonstrated by Puławska (1986) in her reconstruction of cellular

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clones (each produced by a separate initial cell) in the outermost tunica layer of an *Actinidia arguta* meristem: clones of the same age were of different width. With a special computer program we have also recently shown that the contribution of each cell to apex circumference depends to some extent on its original shape (Zagórska-Marek and Karwowski, unpublished data).

Another approach to the problem of initial cell identification in apical meristems is the tedious analysis of twin cell packets, forming on the surface of the apex. This analysis is particularly suitable for solving the dilemma of initial impermanence. As already mentioned, drift of the mutated sectors itself does not prove the stochastic character of the meristems, although the evolutionary advantage of stochasticity is obvious. It is so because a mutation in the nearest derivative of the initial cell produces an almost indistinguishable effect. If, indeed, the initials are impermanent, the record of this fact should be visible in the cellular patterns of the apical meristem. As long as the same cells function as initials, the clonal borders between the sectors, to which the derivatives of these initial cells belong, should meet at the geometric center of the apex (that is, at the vertex). The continuity of the borders should become disrupted after new cells become initials. We have tested these assumptions in this study.

The problem of initial impermanence itself was not as interesting to us as its possible consequences. The phenomenon of ontogenetic transformations of phyllotaxis, studied in our lab for more than a decade (Gola 1996, 1997; Kwiatkowska 1995, 1997; Zagórska-Marek 1985, 1987, 1994, 1999a,b), shows that pattern change arises mainly by dislocations—imperfections in the phyllotactic lattice analogous to the defects present in crystal lattices. The sectorial character of dislocations in phyllotactic patterns suggest that they may result from the local instability of apex circumferential growth. This in turn might be, according to our hypothesis, an outcome of changes in initial number and position at the summit of the apex.

Materials and Methods

Magnolia acuminata L. floral apices and *Picea abies* (L.) Karsten vegetative apices were selected for study because they are distinguished by preformed organs. These species form organ primordia in the organogenic region of the enlarged apex in the season preceding the season of elongation. Before winter, the apices transform into embryonic shoots (Romberger and others 1993) and become dormant within the buds until spring. Spruce meristems were collected in winter from trees more than 15 years old in various forest stands of Lower Silesia. Magnolia floral apices were collected in early summer from trees about 50 years old in the Botanical Garden of Wrocław University. In a spruce apex, after needle primordia for the next season are formed, a small portion of the distal apex is always left unused. From the remaining cells, a shoot meristem much smaller in diameter is renewed. The meristem enlarges and becomes active again in the early summer of the next growing season. In magnolia, the distal part of the generative shoot meristem ultimately transforms into the last, uppermost carpel primordium. These apices had to be collected before organogenesis of the embryonic shoot was completed. Thus, the apices of both species had sufficient numbers of young primordia to determine phyllotaxy and calculate the apex center on the basis of primordia position. Above the primordia, the apices still had a surface sufficient for analysis of the apical dome's cellular pattern (Figure 1).

The main reason for selecting these two genera was the difference in their phyllotaxy. In coniferous vegetative shoots, ontogenetic transformations of phyllotaxy, accomplished through dislocations, are infrequent, whereas in magnolia they are so common that they contribute greatly to the extremely rich and diverse phyllotaxis of generative shoots (Zagórska-Marek 1987, 1994, 1999a). As already mentioned, dislocations, or defects in the regular phyllotactic lattice, are circumferentially localized. We do not know why dislocations are more frequent in some plants than in others. One reason may be the instability of shoot apex geometry. The degree of instability could be unequal in cases differing to such an extent as spruce and magnolia. We hoped that the instability would be reflected in surface-viewed cell division patterns of apices.

Scanning electron microscopy (SEM) images of epoxy replicas of the apices did not prove particularly useful in our analysis. They did not provide reliable and sufficient information on the thickness of cell walls, which is necessary in clonal analysis. Clonal borders on SEM images of apices appeared thicker or thinner (furrows between the replicated cells being respectively deeper or shallower), depending on the orientation of the specimen in the column of the microscope. Therefore, we turned to the classical methods of fixing and staining. Shoot apices were fixed in FAA, cleared in sodium hypochlorite (Bierhorst 1977), and stained with a 0.1% solution of nigrosine in 95% ethanol (Charlton and others 1989).

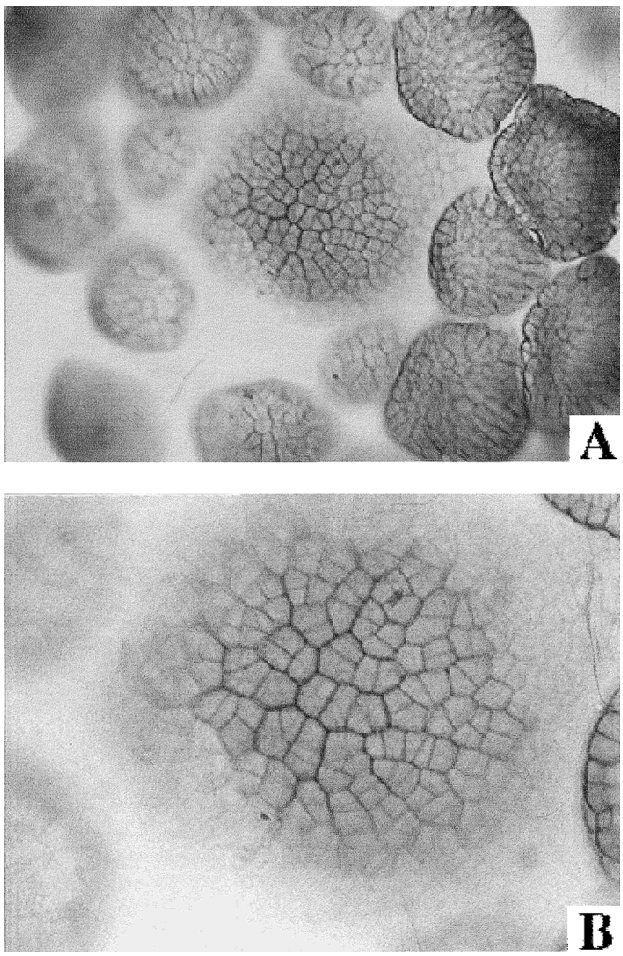

Figure 1. *Picea abies*—the apex with needle primordia **(A)** arranged in spiral *5z:8s* phyllotactic system with clear cellular structure of the surface **(B).** The surface is made of four cellular clones. The main clonal borders run at right angles to one another.

The strictly vertical position of each apex on each slide was very important. It was estimated under a light microscope, at low magnification, on the basis of even distribution of primordia along the circumference. Even slightly tilted apices had visibly less primordia on one side because the cutting surface was not at a right angle to their axes. Such apices were not considered for further study. The shoot apex geometric center was initially determined with the use of computer programs described in our earlier work (Matkowski and others 1998). This method, however, did not appear good enough for our purpose because, as we demonstrated in the article quoted previously, the center of the apex, determined on the basis of primordia position, usually oscillates. Later, we found that the most useful criterion for determining the most recent center of the apical dome, rising above the uppermost primordia,

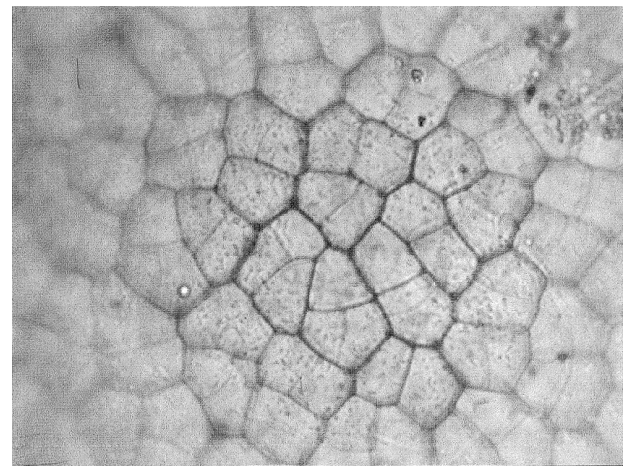

Figure 2. *Magnolia acuminata*—clonal tetrads of cells on top of the apex. They are radially symmetric because they develop in a condition of growth isotropy.

was the concentric arrangement of the youngest cell wall partitions in the cells surrounding the center. These partitions run perpendicularly to the main trajectories of growth (Hejnowicz 1984), which radiate in all directions away from the geometric center. Cellular patterns were then analyzed. Special attention was paid to the points where the clonal borders intersect. A library of various patterns was created and stored on SGI Workstation INDY (Silicon Graphics, Mountain View, CA) connected to an Olympus BX50 microscope (Olympus Optical CO., LTD, Tokyo, Japan). In some cases, particularly when a larger area of the apex surface had to be mapped, reconstruction of the cellular pattern was done on the basis of sequential photos taken with the focus changing gradually. These reconstructions were mapped and are presented here in the form of drawings.

Results

Twin cellular clones or packets that develop at the surface of the apex consist of twin cells and twin subclones of the same lineage. They can be easily identified because a thicker wall belonging to the ancestral cell surrounds each clone. The younger the walls within the clone, the thinner they are. At the summit of the apical meristem, surface growth is more or less isotropic. Thus, as shown in Figure 2, the clones are isodiametric with a predominantly fourfold radial symmetry: the cell walls of consecutive divisions are at right angles to one another in accordance with the minimum energy principle (Errera 1888, Schüepp 1966). On the lateral side of the apical dome, where growth becomes polarized and

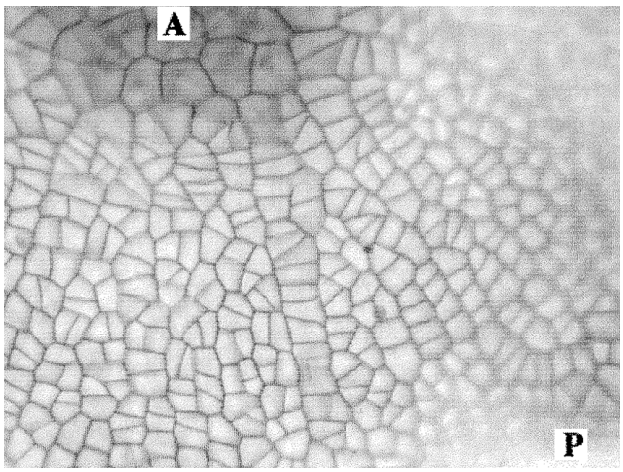

Figure 3. *Picea abies*—elongated clones on the lateral surface of the apex. Growth here is polarized. *A*, apex; *P*, primordium.

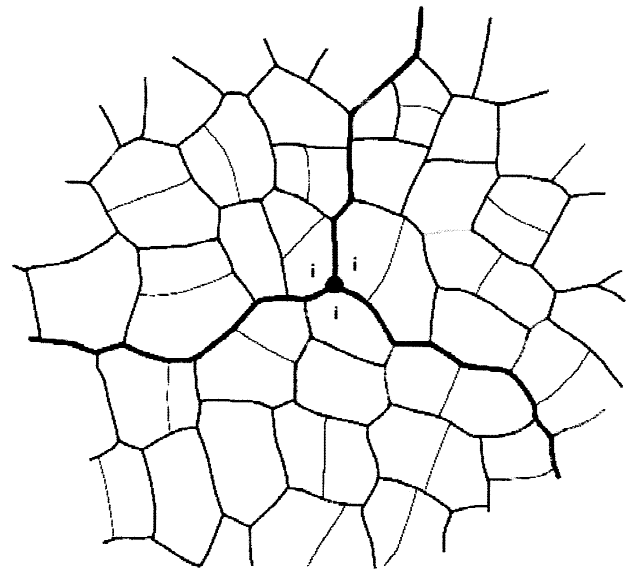

Figure 4. *Magnolia acuminata*—map of the *triad* of clones produced by three initials (*i*). Three clonal borders meeting at the geometric center of the apex run characteristically at 120 degrees to one another. Bar length here and on other drawings is 30 μm.

the meridinal component of growth prevails because of elongation, clones are oblong (Figure 3). Consecutive cell walls in the clones are parallel to each other and positioned at a right angle to the direction of growth. Their surface is again minimal in such a configuration.

Surface observations of the apical meristems led, in the first place, to the identification of clonal sectors and clonal borders. This was done under the assumption that every sector is comprised of cells that are the descendants of one self-renewing initial, positioned nearest the apical vertex. The clonal borders were identified as continuous lines, composed of cell walls distinctively thick, thicker than any other, younger partition within the clone. It was immediately noticed that in both species the intersection point of clonal borders was rarely found exactly at the geometric center of the apex.

Although in most cases surface-viewed apical cellular patterns were complicated and not easy to interpret, several types of patterns were recognized repeatedly in both species. Neither pattern type was species-specific. In the first type, three initials were present and three clonal borders separating their derivatives met at the geometric center of the apex (Figures 4, 5). The borders run in this case at approximately 120 degrees to one another. In the second type, the situation was similar except that four instead of three initials generated the pattern and the clonal borders were more or less perpendicular (Figures 1, 6, 7).

In many apices the intersection point of clonal borders—the cellular center of the apex—was positioned off-center (that is, shifted from the geometric center to the side of the apical dome) (Figures 8, 9). The most interesting finding, however, was the discovery of the young tetrad of subclones, clearly developing from a single cell, which, in some shoot meristems, occupied the summit of the apex. Such tetrads were found both in spruce and in magnolia apices (Figures 10, 11). Their development varied because they were composed of a few or of many cells. The two last types of patterns were most important because they provided proof for apex stochasticity.

It is worth mentioning here that a triad of clones should be very stable, geometrically, when the vertex of the shoot meristem axis is positioned exactly where the three initials meet. The isotropic growth of the surface at this point guarantees the stability of this configuration. Nevertheless, the situation shown in Figures 8 and 9 proves that even when, theoretically, the same three cells could function as initials indefinitely, a shift of the axial vertex may select only one cell for a new initial. The shift means tilting of the meristem axis. This tilt introduces a new relationship between the cells in the apex and the pattern of the main trajectories of growth.

Surprisingly, on the very top of a few apices of spruce, strange multicellular clones were found, in which the partitions of all consecutive divisions

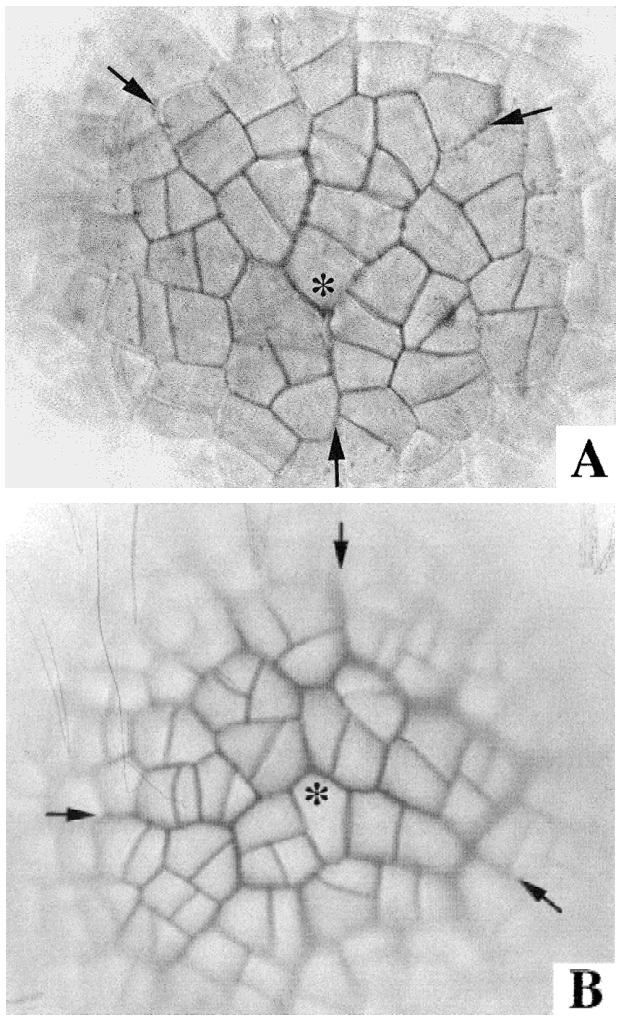

Figure 5. *Picea abies*—microphotographs of the surface view of two different apices (**A** and **B**) with a *triad*-type cellular pattern. Clonal borders are indicated with arrows. The point where they intersect is shown with an asterisk. The concentric arrangement of the youngest cell walls shows that this point is positioned in the present geometric center of the apex.

were parallel (Figure 12). They were very similar to clones typical for the lateral surface of apices found well below the summit (Figure 3). They usually consisted of four or five cells. In one exceptional apex, however, the whole surface seemed to be composed of such clones (Figure 13). Their presence suggests that the expansion of the meristem surface, even in the most distal part of the apex, may sometimes be oriented. As the phyllotaxy of these meristems was spiral, although not bijugate, we cannot attribute this polarization to the formation of primordia in pairs—opposing each other, as it was of *Vinca,* a plant with decussate phyllotaxy (Green 1985).

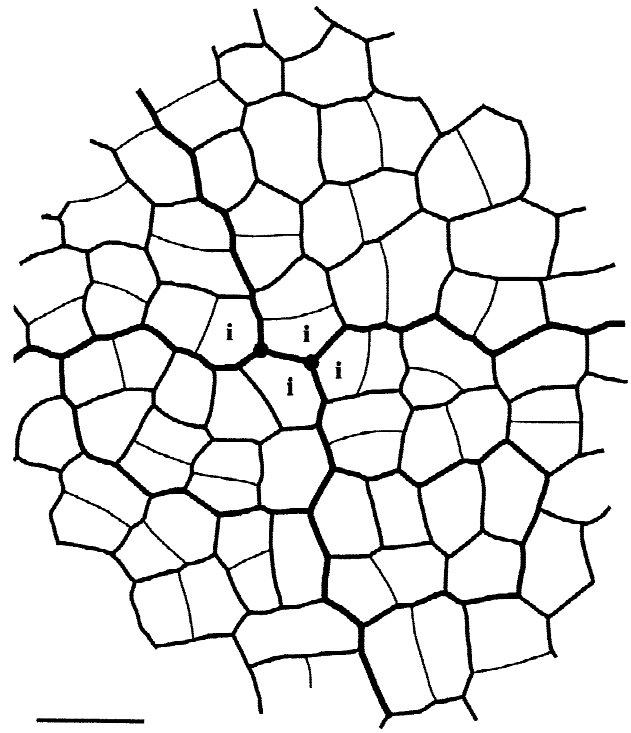

Figure 6. *Magnolia acuminata*—drawn reconstruction of the cellular pattern in which four initials (*i*) produced a *tetrad* of clones. Four clonal borders run toward the geometric center of the apex at approximately right angles to one another.

Discussion

The triads of clones on the surface of shoot apices were shown earlier in young spruce seedlings (Nakielski and Zagórska-Marek 1995). Also, the pictures of sequentially made epoxy replicas of the same growing apex of *Anagallis,* published by Green and others (1991) in their most elegant study on the displacement of cells at the summit of the shoot apex, traced in three consecutive platochrons, show the existence of three cellular clones. The fourth clone, initially very close to the central point of the apex, evidently drifts away. As we have mentioned earlier, the triad of initials should be very stable geometrically but sometimes, as shown on Figures 8 and 9, it is not. It is our first proof of the stochastic character of the apex.

The conclusion from Puławska's work on the apex of *Actinidia arguta* is that only four to eight divisions of permanent (during the time of these divisions) four initial cells are sufficient to produce the entire area of the meristem surface above the youngest primordia. During that time the edge be-

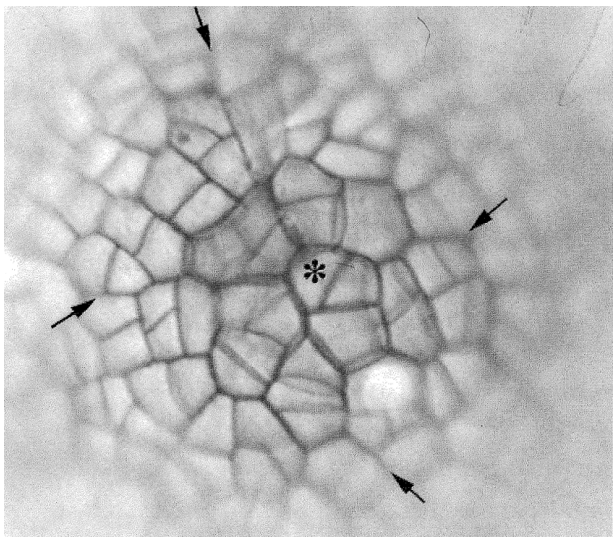

Figure 7. *Picea abies*—microphotograph of the apex, the surface of which is made of four clones. The borders between them are indicated with arrows. The intersection point in the geometric center of the apex is shown with an asterisk. Note, that two of four initials belonging to opposite quadrants (upper right and lower left) are separated by the short wall, which connects the remaining two initials.

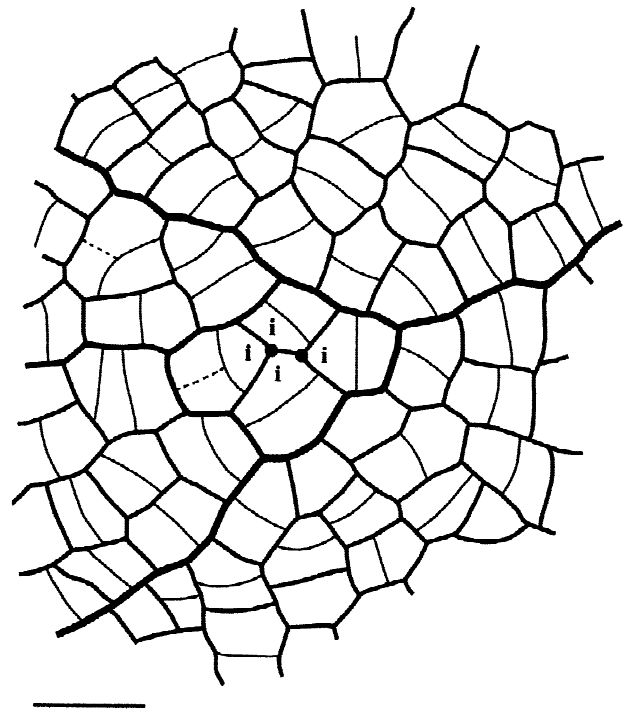

Figure 8. *Picea abies*—map of the cellular pattern, in which one cell, recently positioned in the present geometric center of the apex, formed a young, radially symmetric tetrad. The previous cellular center, where clonal borders of three sectors produced by three former initials meet, is already shifted toward the side of the meristem. The position of the present geometric center of the apex is clearly indicted by the concentric arrangement of the youngest cell walls on the periphery of the meristem. Initials presently functioning in the apex are labeled with letter *i* (from Zagórska-Marek 1999b with permission).

tween opposite quadrant initials does not elongate very much. This finding is consistent with the presence of patterns characterized by four clonal sectors in spruce and in magnolia. However, very young tetrads, originating evidently from one cell, positioned on the top of the apices of old trees, not of seedlings, documented in our work, prove that the situation described for *Actinidia* may not last indefinitely. These tetrads represent the second solid piece of evidence for the impermanence of initials in shoot apical meristems.

To summarize, we think that the results of our clonal analysis on meristems of selected representatives of seed plants provide the first *in situ* evidence for the transient status of initial cells. All the patterns described in this work are understandable and logically connected to one another in the context of the following scenario of changes in clonal structure and number of initials in a growing apex:

1. A single initial cell (*i*) positioned at the vertex of a shoot apical meristem expands evenly in all directions because the surface growth of the apex is isotropic at this point (Figure 14A). The center of the cell and the center of the apex overlap.

2. The first division of this cell (Figure 14B) runs through the center of the apex; it is randomly oriented because of growth isotropy and produces two initial cells (i_1 and i_2).

3. Subsequent divisions of these two cells (second-generation divisions) transform the two-celled clone into a tetrad of initials (i_1, i_2, i_3, i_4). Newly formed cell walls, which are perpendicular to the wall of the first-generation division, are offset from one another, and as a result cells i_1 and i_3 are no longer in physical contact (Figure 14C). For that very reason the tetrad, in contrast to the triad, cannot be a stable pattern.

4. The expansion of the tetrad inevitably increases the distance between initials i_1 and i_3, as well as between the subclones deriving from them. As they drift apart, the wall between initials i_2 and i_4 elongates (Figure 14D, Figure 15); the division of either i_2 or i_4, the partition of which is perpendicular to that wall, creates two cells (Figures 14E, Figure 15). Now there are two possibilities:

The vertex of the apex axis stays where it was—two subclones, originating from i_1 and i_3, drift away

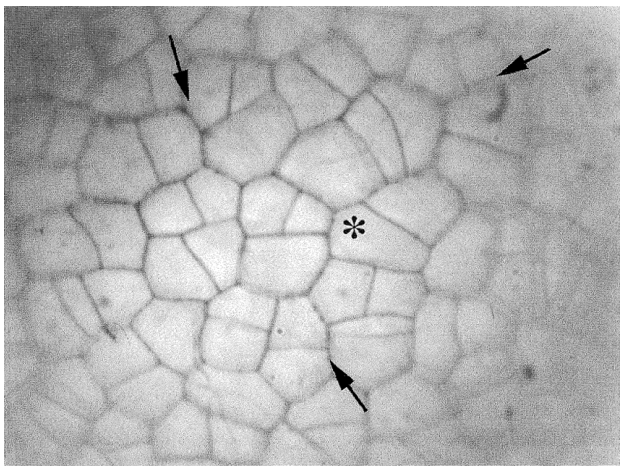

Figure 9. *Picea abies*—microphotograph of another apex, where the cellular center is shifted to the side of the meristem. The point of intersection of the three clonal borders is shown with an asterisk. The geometric center, indicated by orientation of the youngest cell walls, is in the light central area of the photograph. This means that other cells are taking over as functioning initials.

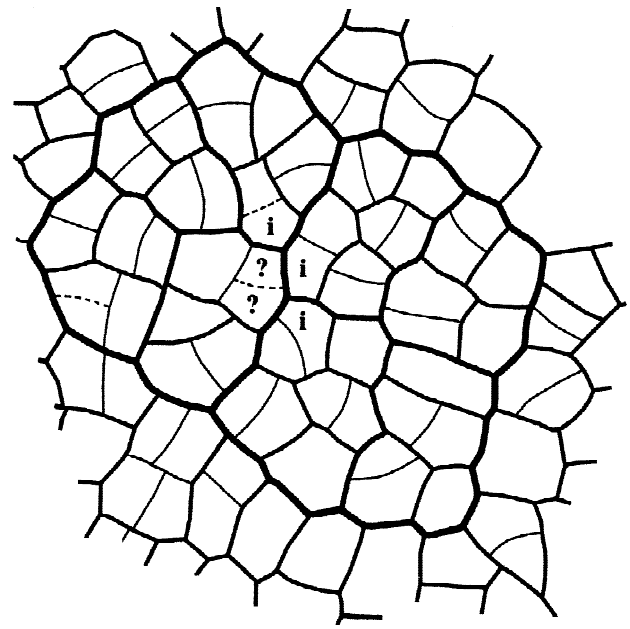

Figure 10. *Magnolia acuminata*—map of the surface-viewed situation, where, in the geometric center of the apex, a clear, well-developed, multicellular tetrad is present. The ultimate separation of two, opposite, noncontacting initials takes place in the tetrad when cell division (cell partition marked with a broken line) introduces two cells (question marks) separating the noncontacting initials. Questions marks indicate cells that may become initials.

from the apex; only the cells originating from i_2 or i_4 may become initials; these will always be the cells, either two or three, neighboring the vertex; as a consequence, the clonal organization of the apex will change: if i_4 became earlier mutated, it contributed initially to one-fourth of the apex circumference, with i_1 and i_3 disappearing, the mutated sector will increase depending on the ultimate number of acting initials either to one-third (one initial of i_4 origin, two of i_2), to one-half (one initial of i_4, one of i_2) or to two-thirds of the apex circumference (two initials of i_4 origin, one of i_2)

The vertex moves—according to the principle of the self-renewing initial, only one of the sister cells becomes an initial, and the other, a derivative; with the selection of either one of the two twin descendant cells labeled on Figure 14E with question marks for an initial, the tetrad of initials is replaced by a triad; in this case the meristem axis tilts; as a result, only one of the clonal sectors of the original tetrad starts drifting away from the summit of the apex; this would be either the upper left quadrant clone or the lower right quadrant clone on Figure 14E; the direction and the extent of the vertex shift are probably undetermined; thus there is a possibility that as a result of the shift again a single cell will start functioning as a new initial in a new center of the meristem. The scenario is reiterated.

The second pathway is extremely interesting to us—it is associated with a necessary change in the position of the vertex, thus with a tilt of the axis. As already stated, such an event must bring a change in the position of all cells in the meristem with respect to the trajectories of growth existing until now. This in turn might create irregularities in the circumferential growth of the apex that accommodate dislocations in phyllotactic patterns. Whether such irregularities associated with dislocations are detectable in plant meristems remains to be seen.

Does the tilt of the axis occur in meristems at all? Observation of patterns such as those seen in Figures 8 and 9 allow us to answer yes. The triads, once formed, should be very stable as long as the cellular and geometric center overlap. Only the shift of the geometric center and a tilt of the axis may trigger reorganization of the apex.

Although we did not find any qualitative difference in the types of cellular patterns between spruce and magnolia meristems, the more frequent movement of the vertex in magnolia than in spruce still cannot be excluded. Solving this would require more precise, quantitative studies.

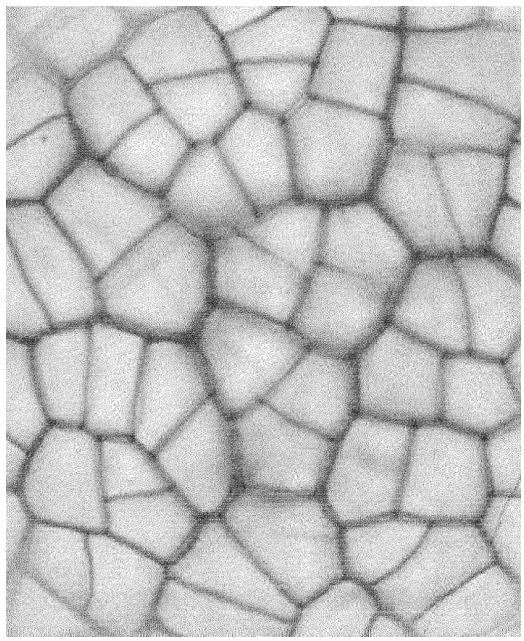

Figure 11. *Picea abies*—microphotograph of an apex with a young tetrad positioned exactly on the top. Geometric center of the apex is indicated by orientation of the newly formed cell walls.

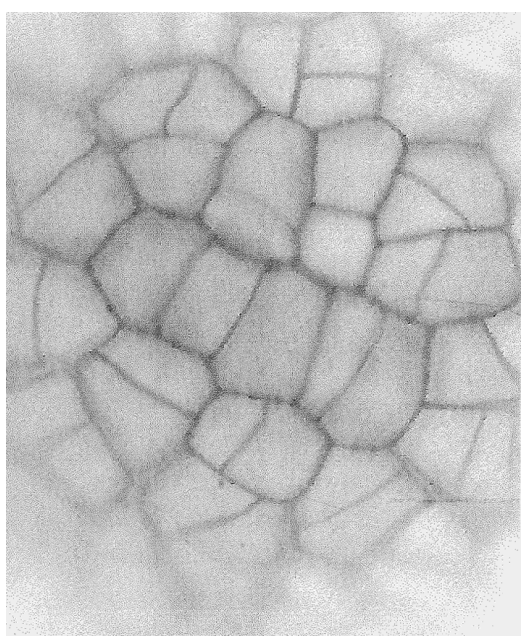

Figure 12. *Picea abies*—microphotograph of the distal portal of the apex, where a clone expanding in one direction only, is present.

Our proposal seems to reconcile opposing views of structured versus stochastic shoot apex character: an apex can be structured at one time and stochastic

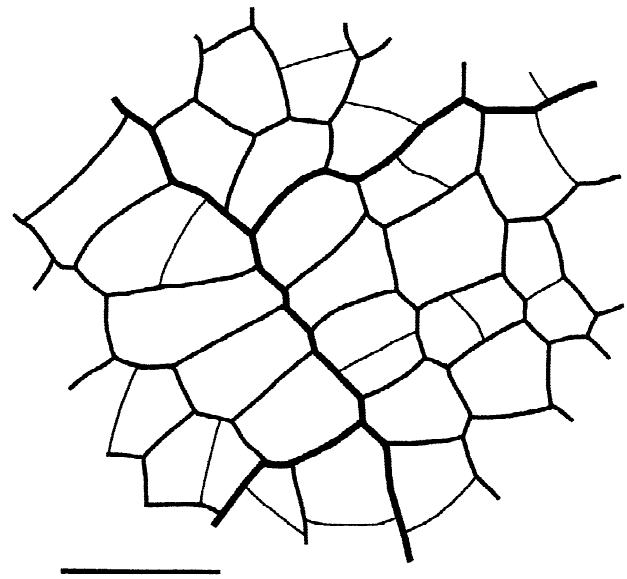

Figure 13. *Picea abies*—pattern of new cell walls paralleling each other in two separate lines of cells suggests that the growth of this apex surface has been recently oriented. It means that even at the vertex of the apical dome the surface expansion is not always isometric but can be temporarily polarized (from Zagórska-Marek 1999b with permission)

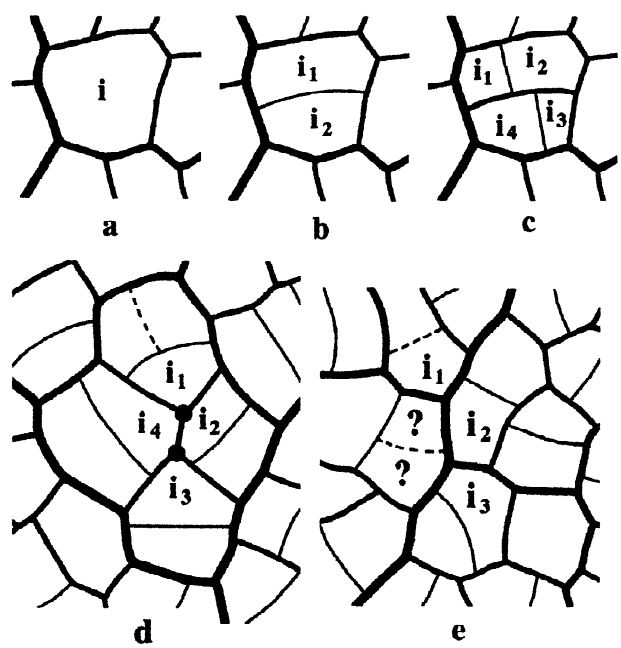

Figure 14. A scheme of a clonal tetrad gradually developing from a single cell positioned on the top of an apex. The consequences are discussed in the text.

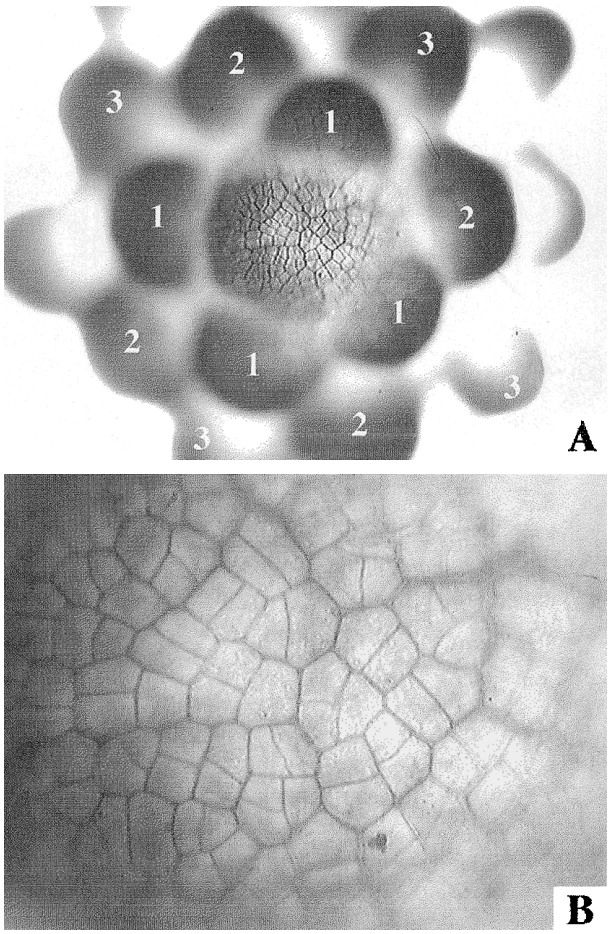

Figure 15. *Magnolia acuminata*—apex with tetrajugate pattern of phyllotaxy **(A):** carpel primordia are in whorls of four, each subsequent whorl from three to one is initiated to one another at the angle 137.5° or ~34.4° apart from one another; on the apex surface **(B)** the opposite subclones of the initial tetrad are clearly separated by the long edge wall and both drift away from the geometric center of the apex. The apex is slightly tilted to the right.

at another, and vice versa. Our theory also explains why, in sectorial or mericlinal chimeras, the stable sectors are 180 or 120 degrees in angular width. It shows that the drift of the sectors, observed in chimeras, does not have to be associated with the shift of the meristem center. It makes the presence of tetrads on the top of the meristems understandable and explains why intersection points of clonal borders are often positioned off-center. However, the most important conclusion of this analysis is that permanent initials may exist only when the position of geometric center of the shoot apex is steady but steady center, retaining the same spatial place, does not necessarily mean the permanence of initials.

To some extent, Schüepp (1926) had foreseen our results in his early work on meristems, in which he produced a scheme in which a clonal multicellular tetrad developed from a cell positioned initially on the top of the apical meristem but slightly off-center. He assumed, in the scheme, that the center of the apex is steady (that is, it is not displaced during growth) and that the partition of the first division does not run through that center. Consequently, only one cell of the clone inherits the initial status—the others have to drift away with time as the apex grows. Shüepps' theoretical predictions have been confirmed in our work—they correspond to the situations described previously.

There are many possible pathways of cell reorganization in the distal part of the apex. Certainly even the most complicated patterns can be interpreted once we know the general principles of this process. Our intent is to point out the necessity of the continuous flow of "streaming" cells, which, including initials, constantly change their position within the apex during its growth.

The impermanence of initials in seed plants is, in the light of our findings, an unavoidable effect of evolutionary change in their number and morphology combined with the condition of isotropic growth of the meristem surface and with the minimal energy principle observed by dividing cells.

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