ASYMMETRIC CELL DIVISION: BINOMIAL IDENTITIES FOR AGE ANALYSIS OF MORTAL VS. IMMORTAL TREES

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INTRODUCTION

The generalized Fibonacci numbers arise in models of growth and death [15], with interesting applications in medical sciences and statistics, such as dose escalation strategies in clinical drug trials [21]. Bronchial airway segments follow a Fibonacci pattern of bifurcation [7]. Experimental growth of tumor nodules can follow Fibonacci ratios related to dynamics of intratumoral pressure [20]. The associations of plant phyllotaxis and patterns of invertebrate growth with the Fibonacci series remain charming but puzzling connections to biology. Mechanistically, dislodgement, diffusion, and contact pressure models can be successfully applied to describe macroscopic growth patterns [17,23], but specific cellular rationales for such recursive patternings have been wanting.

In kinetic analysis of cell growth, the assumption is usually made that cell division yields two daughter cells symmetrically. The essence of the semi-conservative replication of chromosomal DNA implies complete identity between daughter cells. Nonetheless, in bacteria, yeast, insects, nematodes, and plants, cell division is regularly asymmetric, with spatial and functional differences between the two products of division [16]. The binary bud-scar growth of *Saccharomyces* occurs with regular asymmetric surface marker evidence, enabling modeling of events of the lifespan [11]. Mechanisms of asymmetric division include cytoplasmic and membrane localization of specific proteins or of messenger RNA, differential methylation of the two strands of DNA in a chromosome, asymmetric segregation of centrioles and mitochondria, and bipolar differences in the spindle apparatus in mitosis.
Asymmetric binary cell division can be described by the generalized Fibonacci numbers \( \{G_n\} \), \( G_n = G_{n-1} + G_{n-c} \) with starting conditions \( G_0 = 0, \ G_1 = G_2 = \cdots = G_{c-1} = 1, \ c \geq 2 \). In the limiting case of \( c = 2 \), immortal and mortal identity asymmetric binary trees may be represented as in Fig. 1, in which the filled symbols are replicating or stem cells \( (S_n) \) and open symbols are immature, non-replicating cells.

\[
G_n
\]

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Figure 1. Immortal and mortal identity trees: above, the Fibonacci case. Below, the interchange of vertices that creates the \( G_n \) identity.

The symbols denote different generations. One of the products of division is parent-like and the other, daughter-like. An identity between immortal and mortal \( G_n \) sequences results from the operation of decreasing the lag period for maturation by one cell cycle unit of time, from \( c - 1 \) in immortal division to the mortal lag of \( c - 2 \), and setting the lifespan (with death of parent in childbirth) as \( L = 2c - 2 \); \( L \) is equal to \( 2(c - 2) \) degree two vertices plus 2 degree three vertices. In Fig. 1, at \( G_n = c = 2 \), the degree two vertex has been exchanged with the degree three vertex, by rearrangement in the skeletonized subtrees as shown in Fig. 1. Mature cells of mortal identity trees show continuous binary production of daughter cells for \( c \) consecutive cell cycles, \( L = c + (c - 2) \). These rules preserve the distribution and sum of the degrees of the vertices, so that a bijection exists between the immortal asymmetric binary tree and the mortal asymmetric binary tree, \( c \geq 2, \ n \geq 1 \).
Thus, in the Fig. 1 example, both trees have 6 leaves, 2 degree two vertices, and 4 degree three vertices. Note that the Fig. 1 mortal Fibonacci tree is all stem cells: we define stem or $S_n$ cells as replicating cells, i.e., the progenitor or potential parent of another cell. For a given tree of size $G_n$ it is immediately apparent that the number of degree one vertices is $G_n + 1$, the number of degree three vertices is $G_n - 1$, and since the sum of all vertices is equal to $G_n + c - 1$, the number of degree two vertices is $G_n + c - 2G_n - 1$.

$G_n$ values over time $n$ are not only the population sums, but also represent the number of paths from root vertex at $n = 0$ to leaves of these ordered trees. $G_0$ begins with the $(k - 1)$st entry of 1 (represented by the dotted line, Fig. 1) for the mortal tree, vs. $k$th for the immortal tree, which normalizes $n = 1$ at $G_n = 2$. Among positive integers, the $c = 2$ Fibonacci mortal series is unique among the mortal identity trees in having no maturation lag, and for which $S_n = G_n$. Our convention in tree display is that sequential generations are alternated left and right.

**IMMORTAL TREES 1. GENERATION AND AGE ANALYSES OF IMMORTAL ASYMMETRIC BINARY TREES BY $G_n = G_{n-1} + G_{n-c}$**

$$G_n = G_{n-1} + G_{n-c}, \ c = 4$$

![Immortal Trees Diagram](image-url)

**Figure 2.** Immortal $G_n = G_{n-1} + G_{n-4}$. 
Binomial coefficients are conveniently \( c \)-adjusted to give horizontal rows of entries to describe \( G_n = G_{n-1} + G_{n-c} \). For example, for \( c = 4 \), the number array and tree are shown in fig. 2. For each \( k \) and \( (n,k) = (ck - c + 1, k) \) the entry is 1, that is there is a \( c \)-step displacement downward. This gives horizontal inventory of all cells at time \( n \), in population \( G_n \) by \( k \)th generation.

Traditionally, the \( G_n = G_{n-1} + G_{n-c} \) recursion is associated with slants of Pascal's triangle, for which there is an extensive number theoretic literature [3, 5, 6, 9, 12-14], but here the rising diagonals are converted to horizontal rows. We set \( n = 1 \) at \( G_n = 2 \), which normalizes the start of population growth to \( G_n = 2 \) for variable \( c \); more thorough accounting of starting condition values could set \( n = 0 \) at the top of the zeroth column (as in the \( T_m \) case, below), or at \( k = -1 \) (in which case, however, the rather unbiological \( G_n \) values 1, 0, 0... occur).

It is readily shown that

\[
G_n = G_{n-1} + G_{n-c} = \sum_{k=0}^{n+c-1} \binom{n-(c-1)(k-1)}{k} \tag{1}
\]

Spreadsheet labeling of all age groups of these immortal trees by maturation and replicative status is obtained by \( c \) repetitions of \( k \) columns in double left-justified array, as in \( d = 1, 2, 3 \) for \( c = 3 \) in Table 1, which presents a comparison between single-column, generation sums and the stem-cell array for \( G_n = G_{n-1} + G_{n-3} \).

An expression for the stem cell array is:

\[
G_n = \sum_{k=0}^{n} \sum_{d=1}^{c} \binom{n-k(c-1)-d+1}{k} \tag{2}
\]
Table 1
Immortal c-Adjusted Arrays

<table>
<thead>
<tr>
<th>Generational Sums</th>
<th>Stem Cell Array</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Single Columns)</td>
<td>(c-Column Repeats)</td>
</tr>
<tr>
<td>k</td>
<td>0</td>
</tr>
<tr>
<td>n</td>
<td>G_n</td>
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<tr>
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</table>

Table 1. Age analysis of immortal asymmetric binary trees. **Left,** immortal $G_n$ single column array for $c = 3$ in which entries are the total for each $k$th generation for a given cell cycle time, $n$, by (1). **Right,** $c$-column-repeat horizontal distribution of cells by maturational age, by (2). The right-most column entry within each $(k+1)$th generation is the number of stem or replicating cells $(S_n)$, with the number of youngest, newborn cells in the left-most entry within a given $k$th generation. For example, for $G_n = 19$, the 7 first generation cells include 1 newborn, 1 adolescent, and 5 $S_n$ cells, and the 10 second generation cells include 4 newborn, 3 adolescent, and 3 $S_n$ cells.

2. MATRIX AGE ANALYSIS OF IMMORTAL BINARY TREES

We recently described combinatoric identities of $c \times c$ matrices whose elements obey the $G_n = G_{n-1} + G_{n-c}$ generalized Fibonacci recursion equation [1]. Matrices of order $c$ give a facile approach to age analysis of the immortal asymmetric binary tree. For example, for $c = 4$, 

The Pascal-triangle-like construction is apparent with \((r, s) = (r, s - 1) + (r - 1, s), r > 1; (1, s) = (1, s - 1) + (4, s - 1)\). Many identities exist in these arrays [1]. Each entry \(G_n\) is the sum of the horizontal row entries, beginning with \(s = 0\), ending in the \((r - 1)\)th entry just above \(G_n\). The circled \((s, r) = (0, 1)\) entry is set to 1, for combinatorial convenience; thus the bottom row contains sums from \((r, 0)\) to \((r, s)\), with the sum of the elements in the bottom row equal to the \((1, s + 1)\) entry at the top of the next column. There is also a “column sum” rule; each entry \(G_n\) is the sum of \(c\) consecutive column entries beginning with \(G_n(c - 2)\) and ending with \(G_n(c - 1)\). Thus, \(G_n = 131\) cells at time \(n\) of asymmetric immortal division by \(G_n = G_{n - 1} + G_{n - 4}\) is comprised of \(19 + 26 + 36 + 50\) cells, in order, from oldest to youngest non-replicating age, except for 50 \((G_{n - c + 1})\) which is the number of replicating cells since this is the sum of all prior entries up to \(G_{n - 2c + 1}\).

The organism \(C.\) elegans is a small nematode with more than a thousand somatic cells in initial development to adulthood, of which exactly 131 cells are regularly programmed for death [22]. Thus, one could conjecture that these 131 cells are comprised of 50 stem cells, 36 newborn, 26 youngster, and 19 juvenile cells, in the immortal \(G_n = G_{n - 1} + G_{n - 4}\) model. In the mortal identity array for \(c = 4\), below, these would be 58 stem, 42 newborn, and 31 juvenile cells, which numbers are conceivably relevant for subpopulations [22]. The immortal model may be most applicable to budding yeast populations [11] and plant cells. The asymmetrical division of bacterial species is typically associated with non-reproductive sporulation [16].

3. **GENERATION AND AGE ANALYSES OF MORTALITY IDENTITIES ASYMMETRIC BINARY TREES BY** \(G_n = G_{n - 1} + G_{n - c}\).

In most normal cells, a programmed, discrete lifespan exists in \textit{vitro}. Several intracellular proteins, such as p53, control both the lag before cell cycling and the lifespan [10].
Mutations in such genes can shorten lag and concurrently block programmed cell death (also known as apoptosis, after the Greek word for dying leaves falling from trees), which helps immortalize cells, such as malignant transformation of mammalian cells. Thus, those mortal asymmetric trees with unperturbed growth curves \( G_n \) vs. \( n \) that are typically identical to the immortal case enable statements about the relative contributions of lag vis-a-vis lifespan \( c \) vs. \( L \) on growth. In plant cells, however, although apoptosis can occur after toxic stress [4], an immortal model of asymmetric binary division, or mortal models with very long lifespan, combined with parastichy behaviour are more relevant for pursuing clues in Fibonacci/Lucas phyllotaxis [17].

Figure 3 shows the \( G_n = G_{n-1} + G_{n-c} \) mortal identity asymmetric binary tree for \( c = 4, L = 2c - 2 = 6 \), with maturation lag \( c - 2 = 2 \), and the associated stem cells \( S_n \) and dying cells \( D_n \).

![Diagram](image)

Figure 3. \( G_n = G_{n-1} + G_{n-4} \) mortal \((L = 6)\) asymmetric tree in which \( G_n = S_n + S_{n-1} + S_{n-2} \).

The number of stem cells is obtained from the starting conditions \( S_n = 0 \) at \( n = -1 \), \( S_n = 1 \) at \( n = 0, 1, \) and \( 2 \) and summation of \( c - 1 \) consecutive \( S_n \) terms. Thus, \( G_n = G_{n-1} + G_{n-4} = S_n + S_{n-1} + S_{n-2} \).

\( S_i \) sequences also describe other age groupings (e.g., \( D_n = S_{n-2c+2} \)) adjusted according to starting points for that given age, similar to the assumptions of [15]. Since the stem cells of the mortal identity trees include the terminal vertex degree-two dying cells, \( S_n - D_n = G_{n-c+1} \).

A natural partitioning or sectioning of mortal trees into age units based on lifespan \((2c - 2)\) units is a fundamental difference, of course, from immortal trees. Table 2 is the spreadsheet array for mortal \( G_n = G_{n-1} + G_{n-3} \). \( L = 4 \), and four age grouping-columns.
repeat to describe all ages by cycle or \( n \) values.

Equation (3) describes the Table 2 array of \( L \)-partitioned mortal cells for \( c = 3 \), with \( k \) representing the generation identifier. Ages \( d \) from 1 to \( 2c - 2 \) all apply to the same generation. Since lag is \( c - 2 = 1 \), entries in the \( d = 1 \) columns are newborn, non-dividing offspring, and \( d \geq 2 \) are all \( S_n \) cells of increasing age to the right.

\[
G_n = \sum_{k \geq 1}^{[n/(c-1)]} \sum_{d=1}^{2c-2} (-1)^d \binom{k}{j} \binom{n-(k-1)(c-1)-cj+k-d-1}{k-1}
\]

Table 2
Lifespan-Partitioning of Mortal Identity \( G_n = G_{n-1} + G_{n-3} \)

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Table 2. Partitioning of \( L = 2c - 2 = 4 \), of \( G_n = G_{n-1} + G_{n-3} \) mortal identity asymmetric binary tree array. The number of column repeats is equal to \( L \). The spreadsheet rule for formation is that \( c \) vertical entries are entered \( L \) steps to the right and \( c - 1 \) steps down from the top of the summed entries. From left to right within each \( k \) generation, there are \( c - 2 \) columns(s) of immature cells, plus \( c \) columns of \( S_n \) cells of increasing age. Entries in \( d = L \) columns are \( D_n \) cells.

Table 3 presents a single column per generation array, and a stem cell \( (c - 1) \)-column-repeat array for spreadsheet display of asymmetric mortal identity \( G_n = G_{n-1} + G_{n-c} \), \( c = 4 \).
As in the immortal case given in Eq. (2) and Table 1, \( d \) represents the column repeats, from 1 to \((c - 2)\), for newborn cells up to the oldest immature age then \( c \) ages for \( S_n \) cells. Sums for \( d = 1 \) to \( 2c - 2 \) in Eq. (3) at a given \( k \) give the single-column entries of the mortal array in Table 3.

\[
G_n = G_{n-1} + G_{n-4}
\]

**Mortal Identity Arrays**

<table>
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</table>

Table 3. Age analysis of mortal identity asymmetric binary trees, by maturation age to replicative status \( S_n \). **Left**, single column array for mortal identity tree \((c = 4)\); entries are generation sums. The spreadsheet rule for formation is that \( c \) vertical entries of a \( k \)th generation are summed and entered \( c - 1 \) steps lower in the \((k + 1)\)st generation. The number of vertical 1s in the \( k \)th generation is equal to \( L \). **Right**, \( c - 1 \) column-repeat array for mortal identity trees. Column entries form a left lower diagonal array. The spreadsheet rule of formation is that \( c \) vertical entries are entered \( c - 1 \) steps down and \( c - 1 \) steps to the right. The maturational age distribution of cells reads horizontally from left to right for newborn plus maturing from 1 to \( c - 2 \) and \( S_n \) cells. \( S_n \) cells are summed without regard to age, in the rightmost column \( (\sum) \) within each generation.

The stem cell, lower diagonal array of the mortal identity asymmetric binary tree in Table 3 is obtained from the lifespan-partitioned, upper diagonal array (such as the example in Table 2, where \( c = 3 \)) by summation of the rightward \( c \) columns within each \( k \) generation.
A likely more familiar, combinatorial interpretation of (3), for the $j$ value sums is that entries are the number of compositions of $n$ into $k$ parts [8].

4. $T_m$ OR TRIBONACCI-TYPE ARRAYS AND TIME-SYMMETRIC MORTAL TREES

Equations related to familiar $T_m$ arrays [2, 3, 6, 19] may be used to vary $L$ and $c$ independently and keep the convention that columns of $c$-adjusted spreadsheet arrays represent generations. In contrast to the identity trees and arrays, here the arrays present the initial conditions for determination of the behaviour of the trees vs. the rules of tree formation determining the number arrays, above. Time-symmetric, but spatially asymmetric, binary division with no maturation lag ($c = 1$) of mortal trees may be described using $T_m$ or Tribonacci-type equations of the form $G_n = G_{n-c} + G_{n-c-1} + \cdots + G_{n-(c+m-1)}$ where $m$ is the order of the array of coefficients in the expansion of $(1 + x + x^2 + \cdots + x^{m-1})^r$ for $m, n \geq 0$. In our arrays such as Figure 4, label units of downward column displacement between successive increasing $k$ generations as $c$ (with tree maturation lag as $c-1$), and let the order $m$ of the array be equal to lifespan $L$ to write

$$G_n = \sum_{k} \sum_{j} (-1)^j \binom{k+1}{j} \binom{n-k(c-1)-Lj}{k}$$

Figure 4 illustrates a $T_m$ array and mortal binary tree for $T_6$ with $L = 6$ and $c = 3$. To preserve $k$ as the generation identifier, $c \geq 2$, one solution is to have the offspring of a dying cell show no maturation lag and produce self-generation for $c-1$ divisions, here two consecutive divisions (starred). This may be viewed as a mutational event, with temporary loss of maturation to the next generation. Such a hyperproliferation parameter could represent "crisis" periods in aged normal fibroblast populations, in which subpopulations fail to differentiate to programmed cell death. When $c = 1$ (no maturation lag), Eq. (5) results, which then represents time-symmetric, but spatially asymmetric binary division, with $L \geq 2$ as the only variable:

$$G_n = \sum_{k} \sum_{j} (-1)^j \binom{k+1}{j} \binom{n-Lj}{k}$$

When $L = 2$, the Fig. 1 mortal Fibonacci tree results, and $L = 3$ gives the ersatz 'Treebonacci' case [5].
\[ G_n = G_{n-c} + G_{n-c-1} + \cdots + G_{n-(c+L-1)} = G_{n-3} + G_{n-4} + \cdots + G_{n-8} \]

\[ \begin{array}{cccc} n & 0 & 1 & 2 & 3 & 4 \\ k & 0 & 1 & 2 & 3 & 4 \\ G_n & 1 & 1 & 1 & 1 \\ 31 & 4 & 1 & 5 \\ 7 & 5 & 3 & 8 \\ 8 & 6 & 6 & 12 \\ 9 & 10 & 1 & 16 \\ 10 & 15 & 4 & 23 \\ 11 & 21 & 10 & 34 \\ 12 & 25 & 20 & 48 \\ 13 & 27 & 35 & 5 & 68 \end{array} \]

Figure 4. Tribonacci-, or \( T_m \)-type, array and binary mortal tree for \( T_6 \), or \( L = 6 \), and \( c = 3 \).

To preserve \( k \) = generation, \( c \geq 2 \), one solution is to have the offspring of a dying parent cell show no maturation lag and produce self-generation for \( c-1 \) divisions, here 2 consecutive divisions (starred).

In Figure 5, taking \( c = 2 \) and \( L = 2 \), the resulting \( G_k = G_{k-c} + G_{k-(c+L-1)} = G_{k-2} + G_{k-3} \) are column sums of the classic Mann-Shanks array [18], described by Eq. (6):

\[ G_n = \sum_k \sum_j (-1)^j \binom{k+1}{j} \binom{n-k-2j}{k} \]  \hspace{1cm} (6)

which of course is (4) with \( c = 2 \), \( L = 2 \). A \( T_m \)-type tree for this case, in which maturation lag is \( c-1 \) for the first daughter cell (and thus the second daughter, produced at 'death in childbirth,' 'back-mutates' just once \((c-1)\) and has no maturation lag), is shown in Fig. 5, \( n \) and \( k \) according to [18].
Figure 5. **Left**, $T_2$ array for the Mann-Shank series. The spreadsheet rule for formation of entries $n \geq 2$ is that $c = 2$ vertical entries are summed to be entered one step to the right and $c = 2$ steps down; $n$ and $k$ are labeled in conformity with [2], so that when $k$ is prime, all entries for that row are evenly divided by their $n$ values. **Right**, a Mann-Shanks tree, $L = 2$, $c = 2$, lag $= c - 1$, terminal (2nd) offspring maturation lag $= 0$ with $c - 1$ 'back mutations' production of self-generation. There are four different types of cells per generation, as exemplified by generation $\Delta$. Each type of cell is described by the same sequence, $\{\ldots 1, 0, 1, 1, 2, 2, 3, \ldots\}$, i.e., $S_k = S_{k-2} + S_{k-3}$.

The occurrence of unequal dichotomies in plants, such as in *Fucus spiralis* [17] could result from asymmetric binary cell division with consequences on a macroscopic scale. Although a physical representation of our tree structures is only implicit, the spatial relationships among a given population may echo the temporal patterns, such as by secretion of products that provide structural scaffolding. From Jean [17, p. 142], “The botanist Church (1904) frequently insists on $\ldots$ the periodic sequence of ones and twos $\ldots$ for the explanation of rising phyllotaxis, analogous to the phenomenon of cell division.” Is regular asymmetric cell division, temporal or spatial, the fundamental mechanism of plant phyllotaxis? Is it the unifying theme behind mathematical patterning in animals, and if so, could it relate to combinatoric homeostatic mechanisms that compensate apoptotic losses with gain of form and function?
Binary cell division is regularly asymmetric in most species. Growth by asymmetric binary division may be represented by the generalized Fibonacci equation, $G_n = G_{n-1} + G_{n-c}$. Mortal-immortal identities are of interest for study of influences of checkpoint genes with dual functions for control of programmed cell death vs. lag period before cycling. The mortal and immortal growth models presented give predictions of percentages of cells by age after birth and by generation. Our models, for the first time at the single cell level, provide rational bases for the occurrence of Fibonacci and other recursive mathematical phyllotaxis and patterning in biology, founded on the occurrence of regular asymmetry of binary division.

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REFERENCES


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