Rubus spectabilis, salmonberry, is a dominant understory shrub in the Pacific Northwest. It reproduces sexually by producing fruits, and asexually through underground rhizomes and aerial shoots. Ramet demography can be considered in a four-stage matrix model that includes seedlings, small ramets, medium ramets, and large ramets. (Ramet size class is determined by the basal stem diameter.) Reproductive rates, mortality rates, and transition probabilities (e.g., probability of a small ramet becoming a medium ramet) were estimated from five years of repeated observations of marked individuals. Consider the following data (all are on a per year basis).

1% of seedlings produced a small ramet the following year; the others died.
30% of small ramets remained small ramets, 25% became medium ramets, and the others died.
33% of medium ramets remained medium ramets, 27% became large ramets, and the others died.
60% of large ramets remained large ramets, and the remainder died.

Only the large ramets reproduced. An average of 11 seedlings were produced in year \( t+1 \) per large ramet in year \( t \). An average of 1.7 small ramets were produced (via aerial shoots) in year \( t+1 \) per large ramet in year \( t \). An average of 0.4 medium ramets were produced (via rhizomes) in year \( t+1 \) per large ramet in year \( t \).

1. Construct a life-cycle path diagram for this population of Rubus ramets. Label the life-stages as "seedling", "small ramet", "medium ramet", and "large ramet". Denote all meaningful paths with arrows and indicate the transition coefficients associated with each path.

2. Construct the corresponding transition matrix \( A \).

3. The study site has recently been disturbed by selective logging. A post-disturbance census indicated 42 seedlings, 110 small ramets, 85 medium ramets, and 370 large ramets. Construct the matrix \( n_0 \) to represent this stage distribution.

4. Assuming that the transition probabilities have remained unchanged, project the number of individuals in each stage class in the next year (\( t+1 \)). Write out the equation that you use to calculate the abundance of each stage class.

\[
N_{t+1} = \begin{align*}
&\text{seedlings:} \\
&\text{small ramets:} \\
&\text{medium ramets:} \\
&\text{large ramets:}
\end{align*}
\]

Equation
5. What is $\lambda$, the realized rate of population growth, for the time interval from $t=0$ to $t=1$. ____________

6. Use a spreadsheet to project the stage structure for each year from $t=0$ to $t=10$. For each year in the 10-year projection, calculate:
   - the number individuals in each stage class
   - the total number of individuals in the population
   - the rate of population growth ($\lambda$) from $t=i$ to $t=i+1$
   - the percent of individuals in each stage class
   - the stage-specific growth rates ($\lambda$), i.e., proportional change in seedlings from $t=0$ to $t=1$, etc.
   (attach a copy of your spreadsheet to show the results)

7. Bears feed on salmonberries, dispersing and fertilizing the seeds. The demographic data for *Rubus* was collected from a system that included bears. It has been estimated that with the loss of bears from the community, the average number of seedlings produced per large ramet per year declines from 11 to 1. What is the effect of losing bears on: (1) population growth rate, (2) stable stage distribution, and (3) the relative value of plant investments into sexual vs asexual reproduction.

Deer browse on the medium size class of *Rubus* ramets. How much deer browsing produces an effect on *Rubus* population growth that is comparable to the effect of bear removal?

To multiply two matrices using the MMULT function in Excel; e.g, $A \cdot n_0$:
1. select range for output; e.g, select d12:d15
2. enter "=MMULT(range for A, range for n_0)"; e.g., "=MMULT(c5:f8,c12:c15)"
3. press Ctrl-Shift-ENTER (i.e., hold down control and shift keys while pressing ENTER). In a Macintosh, use APPLE+ENTER; (i.e., hold down Apple command key while pressing ENTER)

MMULT works with both relative and absolute references. For example:
   - Select d12:d15
   - Enter "=MMULT($c$5:$f$8,c12:c15)"
   - Press Ctrl+Shift+Enter (Windows) or APPLE+ENTER (Macintosh).
   - Copy the formulas in d12:d15 to right to project population sizes through subsequent time steps
   - Note that with each iteration, the equation should reference the same $A$ matrix, but the last $n$ matrix.

To edit array equations, select the range over which the matrix result is output, edit the equation, press Ctrl-Shift-ENTER