RESEARCH PROBLEMS:

In this department DYNAMICA presents problems that have the potential to stimulate research involving the system dynamics perspective. Articles may address real-world dynamic problems that could be approached fruitfully using system dynamics, or methodological problems affecting the field. A submitted paper should concisely motivate and define a problem and start a process of conceptualization or formulation that can open the way for further studies. Manuscripts, not exceeding 2,000 words, should be sent to George P. Richardson, Wheaton College, Norton,, Massachusetts, 02766.

Entrained Oscillations in Pinon Pine

Problem submitted by Mary E. Floyd and George P. Richardson, Wheaton College, Norton, Massachusetts, U.S.A.

1. INTRODUCTION

In the southwestern United States a hardy tree known as the pinon pine exhibits a remarkable oscillatory phenomenon that is not well understood. Every four to seven years piñon pines produce massive numbers of cones, far more than can be harvested by the natural consumers of the succulent piñon pine nuts the cones contain. In the intervening years, the trees produce very few cones. Further, the natural oscillations exhibited by individual trees entrain: all the piñon pines in a given geographical area covering many square miles overproduce and underproduce precisely together.

The pinon-juniper ecosystem occupies a belt of 1350-2500 meter elevation throughout the southwestern United States and northern Mexico. Within the United States, *Pinus edulis*, the Colorado piñon is, along with several species of *Juniper*, the dominant tree of this ecosystem. Information available on the ecology of this ecosystem is summarised in Floyd[1] and Lanner[2].

There are three on-going areas of investigation to which modeling studies of piñon pine dynamics might contribute. First, what are the most plausible theories responsible for the oscillatory pattern that an individual tree exhibits? Second, what can most accurately account for the entrainment of oscillations in entire stands of piñones? And finally, to what extent can the dynamics of piñon pines be shown to be the result of the evolution of a "clever" reproductive strategy for the species in its harsh environment?

2. PLANT REPRODUCTION

We may view any plant as a system with competing components, each vying for internal resources. Photosynthates – stored carbohydrates – are required for both growth and reproduction, and each process necessarily takes resources from the other. Tree growth rings in the ponderosa pine, for example, show a marked decrease in size when a large reproductive effort has occurred[3]. Similarly, large seed crops in birch trees are followed by dwarfed folliage and die-back[4]. Thus, plant physiologists hypothesize that the distribution of resources within an individual may change to suit the appropriate life process. To some extent, the reproductive load may be offset by the degree to which flowers and fruits are photosynthetic[5]. Since piñon cones are green until the seeds are shed (and therefore photosynthetic), it is conceivable that they provide part of the energy for their own seed production.

Theoretically, an individual plant can reproduce when it has a sufficient carbohydrate reserve. The reproductive process is influenced by the presence of certain hormones (e.g., giberellins promote male flowers, cytokinins promote female flowers[6]). But what might control the timing of reproductive effort in a long-lived plant such as a tree? Several theories have been presented, including 1) surpassing of a critical threshold of stored photosynthates in the roots, 2) presence of specific environmental conditions, such as photoperiod, temperature, or moisture which "trigger" the proper growth

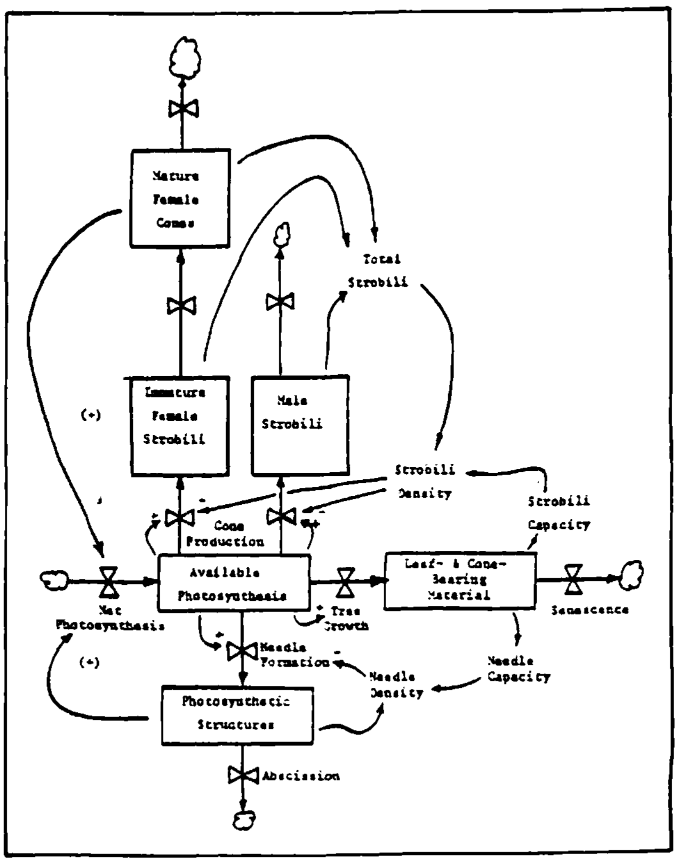

Figure 1: Trade offs in growth and reproduction processes underlying oscillations in an individual pinon pine.

regulating hormones[7], 3) the likelihood that the costs of reproduction will be great, decreasing the chance of surviving beyond the reproductive event[8]. Figure 1 sketches the hypothesized flow of photosynthates in the growth and reproductive processes in an individual piñon tree. Only a few of the feedback effects that influence growth, leaf production, and reproduction are shown. We hypothesize that a model exhibiting the 3-to-5 year oscillatory pattern could begin with such a structure.

3. ENTRAINMENT

Plants do not exist alone, however, and a more interesting question involves the population of trees and the timing of the reproductive effort of the entire stand. Let us assume individual trees reproduce whenever their internal resources are sufficient. The result of such independence would be seed production in any given year by some tree(s) in the stand. This is not the case in piñon pine populations or in many temperate forest trees[9]. Instead, mast fruiting, in which the majority of the trees in a given geographic area are synchronized in the reproductive effort, is common. In piñon pines, reproductive synchrony occurs regardless of the age or health of individuals in the population. This oscillation at the population level has been cited in the piñon pines by foresters[10] and biologists[11] to have a periodicity of 4-7 years; some say one-to-three large crops in a 10 year span. In most estimates the geographic area over which piñon cone production is entrained ranges from 3,000 – 80,000 acres.

Possible theories of entrainment include various means by which the trees of a population communicate with each other, and hence "know" when conditions are best to reproduce. Communication might occur via root grafts which are known to occur in gymnosperms. Recently attention has focused on pheromonal communication between trees through the production of volatile terpenes, "indicating" the presence of insect pathogens to as yet uninfected trees. Finally, trees of all ages and physiological readiness might respond similarly to some environmental cue (moisture availability or temperature?) and as a result become physiologically ready for reproduction[9,11]. Here the notion of probabalistic entrainment is potentially significant. Graham[12] showed that two oscillating systems with slightly different periods could become entrained if they were both affected by identically the same random influence. Are naturally varying environmental influences such as weather sufficient to induce entrainment among all the piñon in a given area?

4. EVOLUTION OF THE OSCILLATORY PATTERN

Just as plants do not exist alone, plant populations do not occur in a vacuum. They have evolved with, for example, avian and mammalian populations. Now we must change our time frame from the recent past to a geologic one. The reproduction of piñon pines has been viewed as an evolutionary adaptation to interactions with piñon jays and other birds, deer mice and other mammals including native americans, and can be described as a clever survival strategy for a tree in an inhospitable environment. Piñon seeds are very large, nutritious, and quite expensive for the plant to produce. Large seeds are common in arid habitats, and are presumably adapted for germination where water may not be readily available. They are also attractive to birds, insects, and mammals as food sources. Were the piñon pine foolish enough to produce a few seeds every year, those seeds would be quickly devoured, leaving none for germination. If however, the reproductive event is delayed and synchronized, reproduction when it occurs will be sufficient to "flood the market" and satiate predators as well as produce an excess of seeds for them to store. Unretrieved caches provide good sites for germination and establishment of piñon seeds and seedlings. Data are available for the caching of seeds by piñon jays and Clark's nutcrackers when excesses are present[13], for the depletion of seeds from stores by small mammals[14], and for the use of piñones by native americans[15]. Forcella[16] proposes that the timing of piñon reproductive effort has coevolved with insect predation.

This information raises the possibility of two simulation studies in an evolutionary time frame. The first study would produce a simulation model describing two types of piñon trees interacting with predators: Type 1 would have no entrained oscillations, while Type 2 would show the 4-7 year entrained oscillations noted in todays populations. What reasonable assumptions in a simulation model are necessary or sufficient to produce a tendency for Type 2 trees to dominate?

The second evolutionary study involves evidence that the typically monoecious (producing both male and female cones on the same individual) piñon pine may become temporarily dioecious (either male or female) when under different types of stress, e.g., when very young or when mature and under moisture stress[17]. Can a model-based study help to determine when a dioecious, rather than a monoecious, strategy is in the best interest of the pinon individual?

5. SIGNIFICANCE OF THESE STUDIES

A large group of plant ecologists focus on the evolution of reproductive systems[8]. They are interested in questions relating to reproductive effort in variable and stable environments, and when the timing and method of reproduction is an adaptive response. The system dynamics studies proposed here would be of significance especially because they deal with a long-lived organism (piñon pines typically reach 400 years) which occupies a harsh, variable environment. Experimental studies designed to unravel questions about reproductive adaptations generally involve short-lived herbaceous or at best perenniel shrubs[18] since the lift cycles of most trees preclude experimental manipulation.

What is proposed here is two sets of modeling studies, each of which would assist the plant population biologist in attempts to unravel the significance of the reproductive strategies seen at any one time in a long-lived organism. The first set focuses on the individual tree and the possibility that internal physiology is entrained across populations. The second set approaches reproduction in the population over evolutionary time and might elucidate the aspects of reproduction which are in fact evolutionary adaptations.

The studies suggested here also raise several methodological issues within the field of system dynamics. First is the issue of competing explanations of the same dynamic phenomenon. The several existing hypotheses for the same dynamic patterns of piñon pines provide an opportunity to explore the extent to which simulation modeling can help swing the balance of evidence toward one particular hypothesis. Second, the studies suggested here could expand our understanding of the phenomenon of entrainment. Piñon pine trees might eventually help us identify the mechanisms by which oscillations in economic sectors, or menstrual cycles among college roommates, can become entrained. Third, there is the issue of evolution as a dynamic phenomenon. Is there a way of capturing in a simulation model the structure of arguments that derive short-term oscillatory patterns from long-term evolutionary processes?

REFERENCES

1. FLOYD, M.E., (1981), Reproductive strategies of two species of piñon pine in the southwestern United States and northern Mexico. PhD dissertation. University of Colorado. Boulder, Co.

2. LANNER, R.M., (1981), The piñon pine: A natural and cultural history, Univ. of Nev. Press, Reno, Nevada.

3. LINHART, Y.B., MITTON, J.B., BOWMAN, D.M., and STURGEON, K.B., (1979), Genetic aspects of fertility differentials in ponderosa pine. Genet. Res. Camb. 33: 237-242.

4. GROSS, H.L., (1972), Crown deterioration and reduced growth associated with excessive seed production by birch. Can. J. Bot. 50: 2431-2437.

5. BAZZAZ, F.A., CARLSON, R.W., and HARPER, J.L., (1979), Contribution to reproductive effort by photosynthesis of flowers and fruits. Nature 279: 554-555.

6. CHAILAKHYAN, M. Kh., (1979), Genetic and hormonal regulation of growth, flowering, and sex expression in plants. Amer. J. Botany 66: 717-736.

7. WOLGAST, L.J., and ZEIDE, B, (1983), Reproduction of trees in a variable environment. Bot. Gaz 144: 260-262.

8. WILLSON, M.F., (1983), Plant Reproductive Ecology. John Wiley and Sons. New York.

9. SILVERTOWN, J.W., (1980), The evolutionary ecology of mast seedling in trees. Biol. J. Linn. Soc. 14: 235-250.

10. LITTLE, E.L., (1940-1947), Estimates of the 1940-1947 piñon nut crop on National Forests of New Mexico and Arizona. USDA Forest Service Research Notes # 87, 92, 108, 109, 112, 113, 114. Southwest Forest and Range Experiment Station, Tucson, Arizona.

11. FORCELLA, F., (1981), Ovulate cone production in pinyon:negative exponential relationship with late summer temperature. Ecology. 62: 488-490.

12. GRAHAM, A.K., (1977), Principles on the relationship between structure and behaviour of dynamic systems. PhD dissertation. Massachusetts Institute of Technology. Cambridge, MA.

13. VANDER WALL, S.B., and BALDA, R.B., (1977), Co-adaptation of the Clarks nutcracker and piñon pine for efficient seed harvest and dispersal. Ecol. Mongr. 47: 89-111.

14. FLOYD, M.E., (1982), The interaction of piñon pine and gambel oak in sucession near Dolores, Colorado. Southwestern Naturalist. 27: 143-147.

15. THOMAS, D.H., (1972), Western Shoshone Ecology: settlement patterns and beyond. In "Great Basin Cultural Ecology: A symposium" Desert Research Institute for the Social Sciences 8. Reno and Las Vegas.

16. FORCELLA, F., (1980), Cone predation by pinyon cone beetle *(Conopthorus edulis:* Scolytidae) Dependence on frequency and magnitude of cone production. Amer. Nat. 116: 594-598.

17. FLOYD, M.E., (1983), Dioecy in five *Pinus edulis* stands in the southwestern United States. The American Midland Naturalist. 110: 405-411.

18. MCARTHUR, E.D., (1977), Environmentally induced changes of sex expression in *Atriplex canescens.* Heredity. 38: 97-103.