

A reprint from
American Scientist
the magazine of Sigma Xi, The Scientific Research Society

This reprint is provided for personal and noncommercial use. For any other use, please send a request to Permissions, American Scientist, P.O. Box 13975, Research Triangle Park, NC, 27709, U.S.A., or by electronic mail to perms@amsci.org. ©Sigma Xi, The Scientific Research Society and other rightsholders

The Mystery of Masting in Trees

Some trees reproduce synchronously over large areas, with widespread ecological effects, but how and why?

Walter D. Koenig and Johannes M. H. Knops

This autumn, the vast hardwood forests of North America could be chock full of acorns, a pulse of resources that will cascade through the ecosystem, affecting mice, birds and other wildlife for years to come. Over far-flung areas virtually all the oaks of the same species, and perhaps more than one species, are already gearing up to produce the seed crop of the decade. Or not. In fact, there may be almost no acorns, and a substantial proportion of the wildlife will starve or have to eat something else.

Such highly variable and synchronized reproduction is known as “mast-fruited” or “masting.” The term comes from the Old English word, *mæst*, for nuts of forest trees that have accumulated on the ground, especially for those used as food for fattening swine. Evolutionarily, a significant selective benefit of masting is “predator satiation.” The idea is that large crops satiate seed eaters so that some seeds escape being eaten, particularly in “mast” years with bumper crops. To reinforce this effect, small crops keep seed-predator populations so low that there are too few animals to eat all the seed produced during good years. Thus, a higher proportion of seeds overall ultimately escape predation.

Walter D. Koenig received his Ph.D. in zoology in 1978 from the University of California, Berkeley, where he is currently an adjunct professor in the Department of Integrative Biology and a research zoologist at the Museum of Vertebrate Zoology. His research interests include social behavior of birds, reproductive traits of forest trees and patterns of spatial synchrony in nature. Johannes M. H. Knops received his Ph.D. in botany in 1994 from Arizona State University and is currently an associate professor in the School of Biological Sciences at the University of Nebraska. He studies ecosystem nutrient cycling and how biodiversity relates to ecosystem function. Address for Koenig: Hastings Natural History Reservation, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924. Internet: wicker@berkeley.edu

People have witnessed masting since time immemorial; after all, it's pretty obvious when you're tripping over nuts strewn all over the path some years and you find barely one or two in others. In agrarian communities, farmers would have been especially aware of the boom and bust cycle because they fed acorns to livestock. Although records are sparse, historical economic data have been used to infer the size of acorn crops from as far back as the mid-17th century. Only recently, however, have scientists begun to recognize the geographic scope and ecological consequences of masting and attempt to explain how this remarkable phenomenon is achieved. So how do all those millions of trees do it?

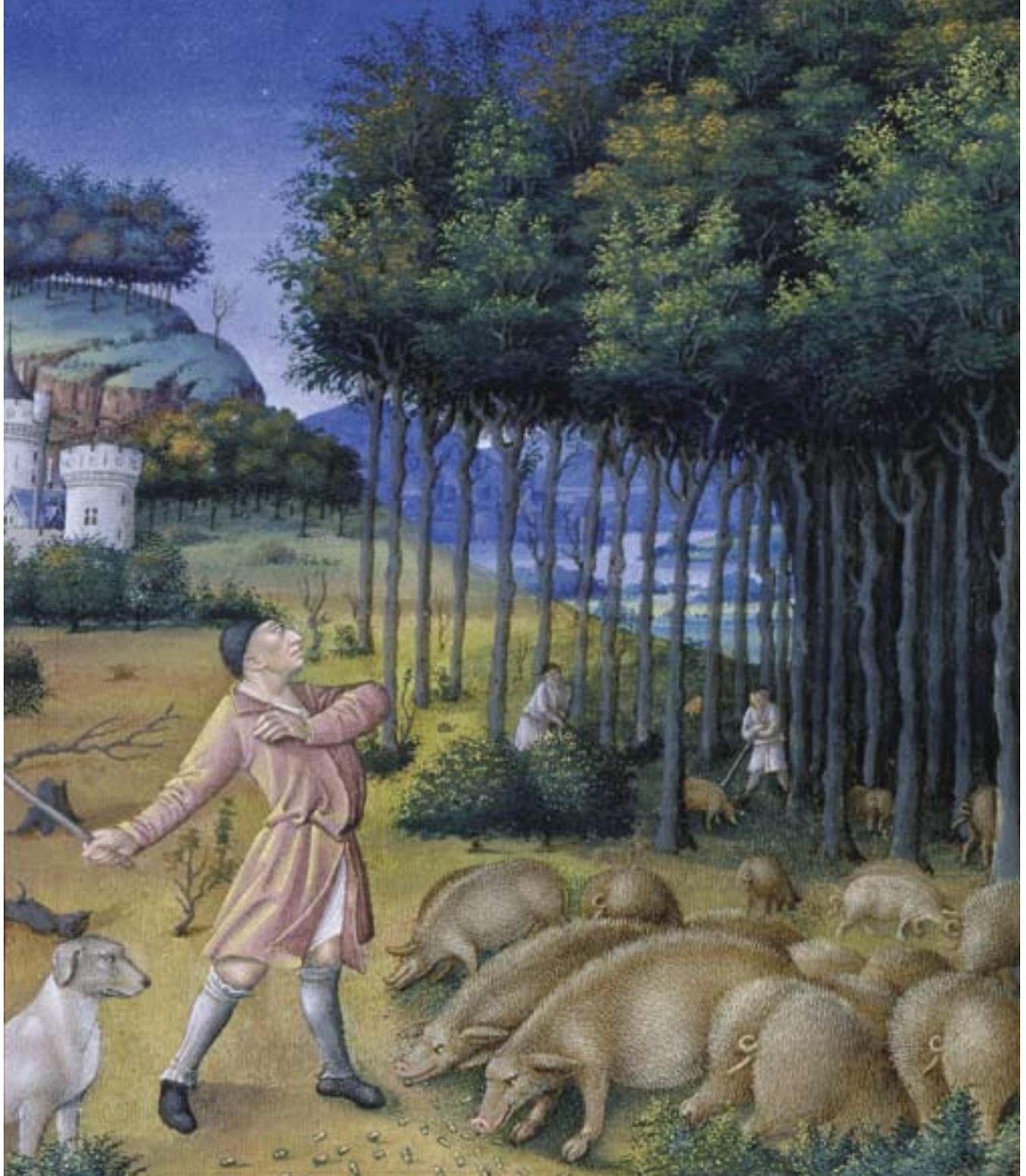
In this article, we describe the ecological and economic consequences of masting and discuss what causes seed production to vary so widely. This leads us to review the latest research into proposed mechanisms that govern the synchronous production of seed across wide geographic areas. Finally, we speculate on the admittedly uncertain effects of global climate change on ecosystems in which masting plays a crucial role.

Mighty Ecosystems from Little Acorns

Mast crops produce resource pulses that can broadly affect the local ecosystem in which they happen. Along the West Coast of North America, variable acorn crops may be the primary determinant of increases and decreases in the populations of certain birds. For example, acorn woodpeckers (*Melanerpes formicivorus*) depend almost entirely on acorns for food. Uniquely among birds, acorn woodpeckers store acorns, often by the thousands, in holes they drill in special “storage trees” or “granaries” located in their territory. In years of bumper crops, acorn woodpeckers survive well during the winter. Moreover, they tend to

begin reproducing in the fall—one of a handful of temperate resident species that will sometimes breed then—and resume the following spring. In poor years, by contrast, birds may be forced to abandon their territories in order to search for food elsewhere. The associated risk of moving into unfamiliar areas and consequent starvation results in severe population crashes.

Direct effects of the variable acorn crop are only the beginning. At the Institute of Ecosystem Studies in New York, Richard S. Ostfeld and Clive G. Jones have unraveled a series of ecosystem-wide domino effects caused by masting. In eastern North America, where hardwood forests dominate, large acorn crops increase populations of mice and deer, two major acorn predators. In turn, populations of ticks, major ectoparasites of mice and deer, increase. And again, since ticks cause Lyme disease, the incidence of Lyme disease in human populations rises, as reported by Ostfeld in *American Scientist* (July–August 1997). Mice also plunder the nests of local bird species, particularly those that nest on or near the ground, and high numbers of them correlate with decreases in populations of species such as the veery (*Catharus fuscescens*) and several species of warblers, typically two years following mast events. But the effects of big acorn crops are not all bad. High mouse densities following large acorn crops tend to keep populations of their major food items in check. Among the most commercially important is the gypsy moth (*Lymantria dispar*). This pest defoliates a wide variety of valuable species, costing an average \$30 million yearly, according to the USDA Forest Service. In short, the pulse of resources dumped into the ecosystem during a mast year leads to a “trophic cascade” in which masting affects the numbers of organisms in various levels



Réunion des Musées Nationaux/Art Resource

Figure 1. Oak trees have long provided sustenance for people and their livestock. During a mast year, entire populations of oaks produce huge crops of acorns, and farmers have taken advantage of this bounty since at least medieval times. Painted in 1416, this picture for November from the calendar section of the *Très Riches Heures*, by the Limbourg brothers from Flanders, shows a peasant throwing a stick to knock down acorns on which his pigs are feeding. Only recently have scientists begun to understand the ecological significance and underlying biology of masting.

of the food chain. The resulting ripple effect can influence community composition for years following the event.

Top Seed

Ostfeld and Jones's studies demonstrate that highly variable seed crops have important and long-lasting effects within their communities. Parallel to

this research, recent work has investigated mast-fruiting in plants at both the individual and population levels. Individual plants do not mast. Masting is a group phenomenon that results when plants within a population synchronize their reproductive activity. Thus, masting takes place as a result of two separate but related features of reproducing

trees: variability and synchrony. That is, trees must synchronize the quantity and timing of seed production. In this way, by mechanisms that remain poorly understood, the masting trees apparently come to a consensus as to how bountiful a crop to produce in a particular year. Let's look at some ideas of how this might come about.



Figure 2. Blue oaks (*Quercus douglasii*) are classic masting species, producing a highly variable seed crop from one year to the next that is synchronized among individuals over a wide area. In a mast year, a mature blue oak may produce more than 100,000 acorns—more than 10 times the annual average—and is likely to produce few or no acorns in a poor year. (Except where noted, all photographs courtesy of the authors.)

First, what might cause variability in seed crops? One idea is the “resource tracking” hypothesis. This mechanism requires that the number of seeds produced each year varies in direct response to the amount of resources available to the tree. For example, warm, wet years might provide trees more resources to grow seeds by enhancing photosynthesis and increasing the availability of soil nutrients. In contrast, cold, dry years would result in less photosynthesis and lower nutrient availability, resulting in meager seed crops. Resource tracking could also account for the geographic synchrony of seed production observed in masting species, since rainfall and temperature tend to fluctuate in the same direction from one year to the next over large areas. Most important, if resource tracking can account for masting behavior, then evolutionary explanations for masting would not be necessary. Instead, masting could merely be a side effect of resources that vary from year to year.

However, the evidence does not support a simple view of resource tracking as a cause of masting. For example, annual fluctuations in rainfall and temperature are smaller in magnitude than those of crop sizes of masting species, although resource tracking predicts they should be at least as great. Moreover, yearly variation in these environmental quantities usually exhibits statistical characteristics distinctly different from those of mast crop sizes. Specifically, annual rainfall and temperature tend to be distributed normally, following a bell

curve, whereas the annual size of the seed crop is not. Also, rainfall one year provides no clue as to how much rainfall there will be in any subsequent year. That is, environmental variables usually show no consistent patterns of temporal autocorrelation, when later measures in a time series are correlated with earlier measures.

In contrast, Victoria Sork, now at the University of California, Los Angeles, and her colleagues have shown that seed production by individual oak trees in Missouri is highly autocorrelated over time; a good crop one year is generally followed by a relatively poor crop the next, a pattern found in several oak species. Thus, knowing the size of a tree’s crop this year gives you information about how many acorns it is likely to produce in subsequent years. This finding suggests that masting trees put so much energy into producing a good seed crop that they are forced to forgo reproduction in at least one subsequent year.

The growth-reproduction tradeoff is a second line of evidence that masting cannot be fully explained by resource tracking. To evaluate trade-offs more precisely we have measured annual growth and reproduction in blue oaks (*Quercus douglasii*) at Hastings Reservation in central coastal California. To quantify growth we use dendrometers, which are stainless-steel bands placed around the trunk. Yearly acorn counts have provided estimates of reproductive effort. The data show that trees tend to grow slowly the year that they produce a large acorn crop, but usually grow well the next year, after which they will again grow relatively poorly.

Producing a large seed crop during a masting episode apparently takes a lot of resources and has long-term consequences for growth and subsequent reproduction by individual trees. That is, the trees shunt an inordinate amount of resources into flower and seed production during mast years, while shifting resources back into growth during poor seed-crop years. Such switching of resources proves that masting must be an adaptation—an evolutionary response by trees to some environmental challenge.

Among the most severe selective pressures a plant faces is having its seeds eaten. An adaptation that minimizes such consumption will be strongly favored by natural selection because it directly improves reproductive success. As men-

tioned earlier, predator satiation is an effective way a tree can keep predators from eating all its seeds. Predator satiation is an example of “economy of scale,” to use the terminology of David A. Norton and Dave Kelly of the University of Canterbury in New Zealand. The idea is that big investments (large seed crops) are more efficient than small crops because each seed has a higher probability of escaping predation. Thus, it’s more economical for the tree over the long run to produce an occasional bumper crop than to produce the same size crop each year, even though in the other years it produces few or no seeds that survive.

Another challenge for trees is to maximize pollination efficiency. This is especially true for wind-pollinated trees that are primarily outcrossing (rather than self-fertilizing), such as oaks, pines and the majority of tree species in the temperate and boreal regions of the Northern Hemisphere. This consideration contrasts wind-pollinated species with animal-pollinated species, as the latter risk lowering their reproductive success by satiating their pollinators if too many flowers are produced at once. Consequently, masting is expected to be more widespread among wind-pollinated species. From an evolutionary standpoint, a tree should not produce huge quantities of pollen or flowers that go to waste. By flowering at the same time, trees maximize their chances of pollination and minimize waste.

The extent to which masting succeeds at enhancing pollination is not entirely clear. Pollen is frequently limited in



Figure 3. The acorn woodpeckers (*Melanerpes formicivorus*) is one of many wildlife species whose population dynamics are affected by the size of the acorn crop.

animal-pollinated species, but scientists have generally thought that pollen was for all practical purposes unlimited in wind-pollinated species. From this, it was assumed that increased pollination efficiency was unlikely to play an important role in natural selection for masting. However, this premise has been overturned in the last several years. Evidence that wind-pollinated species are indeed pollen-limited has begun to accumulate from field experiments. These data are consistent with conclusions from wind-pollination models. Theoretical work, largely by Akiko Satake and Yoh Iwasa of Kyushu University in Japan, demonstrates that *pollen coupling*, the dependence of individual trees on pollen from members of the same species, can be sufficient to drive the highly variable seed production that is characteristic of masting species.

Going to Seed

But how do trees synchronize flowering, and hence their production of seeds? It is one thing for trees to produce more seeds some years than others, but how do they manage to coordinate their activities, given that masting involves switching resources between growth and reproduction? For that matter, how many trees are involved, and over how large an area?

Answering the last question requires accumulating data on a large geographic scale over many years, so it's not surprising that no one has attempted to address it until recently. Our own work has approached the problem in two ways. First, we have analyzed data extracted from the literature, and second, we have collected field data from California oaks.

The literature search involved lots of

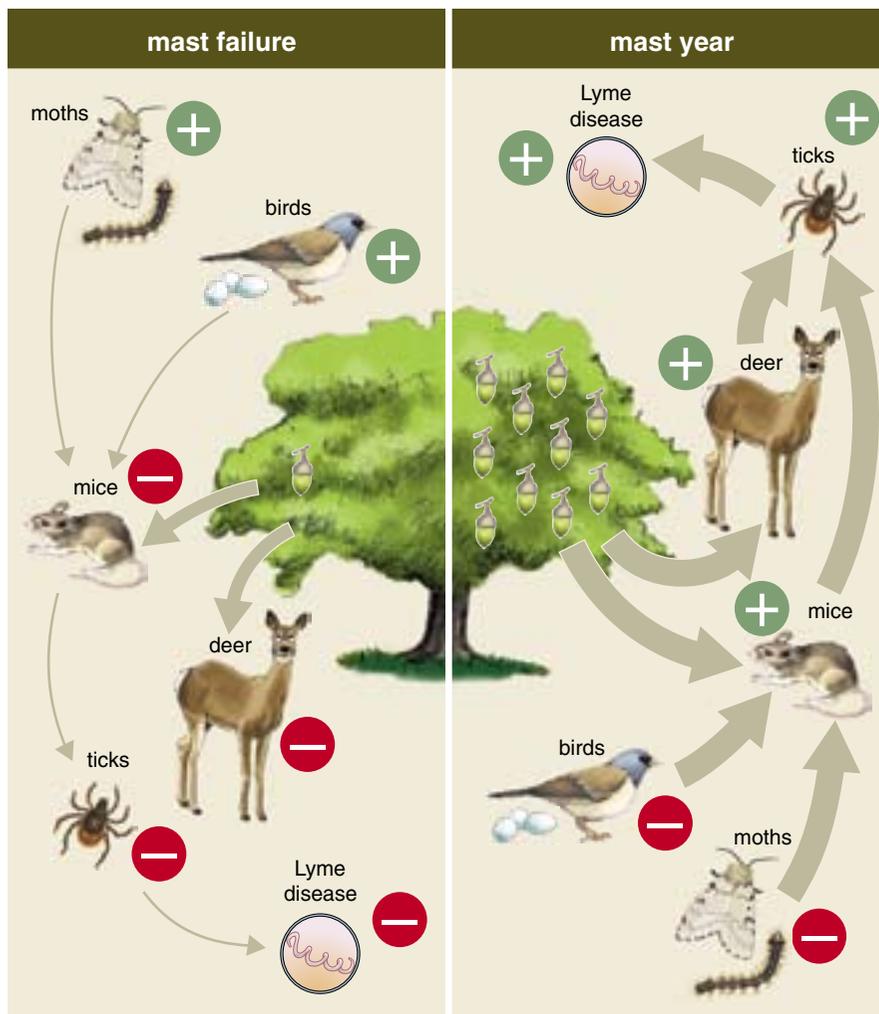


Figure 4. Multiple ecological interactions between species in a model Eastern deciduous forest result in a trophic cascade in which the effects of acorn crop size ripple through the food web, setting off a chain of events that cause animal populations to change. Large amounts of energy (arrows) flow through the system during a mast year (right) when a large acorn crop is produced by an oak (center), causing populations of deer, mice and ticks to increase and raising the incidence of tick-borne Lyme disease (+). Populations of ground-nesting birds and gypsy moths decrease (-) owing to predation by mice. During a mast failure (left) effects of an acorn shortage on the food web are negative for acorn-eaters and their predators and positive for birds and moths, whose eggs and larvae are eaten by mice.

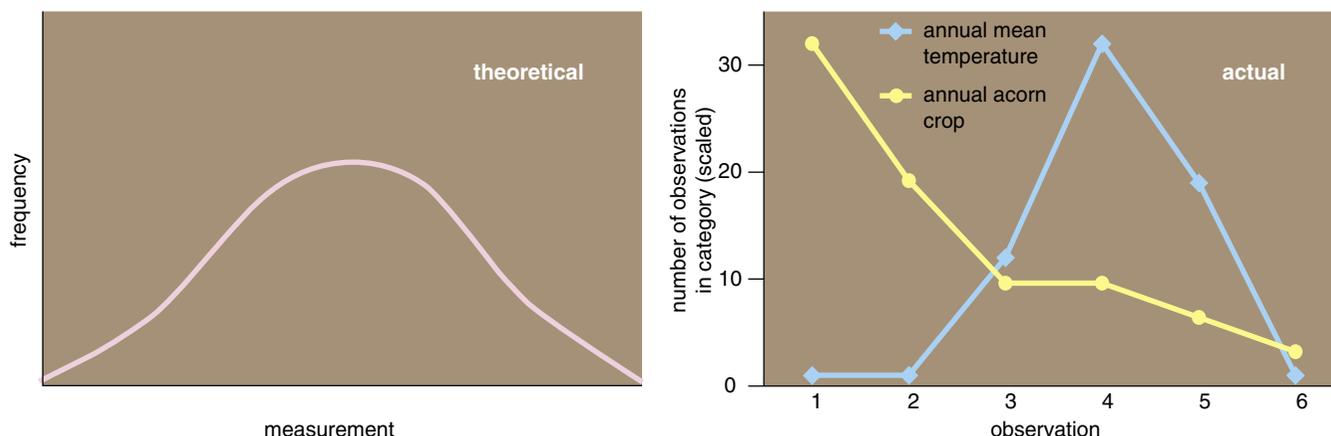


Figure 5. According to the resource tracking hypothesis, environmental fluctuations cause seed crops to vary. If these fluctuations account for masting, theoretical frequency distributions for environmental measures and crop size are both expected to be normal, following a bell curve (left). Actual data (right) for environmental fluctuations (annual mean temperature) are distributed this way. Crop-size data (annual acorn crop) are not. The difference implies that resource tracking alone cannot account for variation in seed production and that other factors initiate and regulate masting.



Figure 6. Newly emerged catkins of valley oak will soon begin to shed pollen. Pollination efficiency increases during a good acorn year, offering a selective advantage for masting in addition to predator satiation—when so many acorns are produced that some escape being eaten.



Figure 7. Dendrometers, such as this one on a blue oak, facilitate precise measurement of a tree's radial growth. A stainless steel band held together by a spring expands along with the tree. The expansion is measured using notches on the band.

library time, but yielded results much faster. We found more than 400 relevant publications on various tree species, including hardwoods such as oaks and beeches, and conifers such as firs,

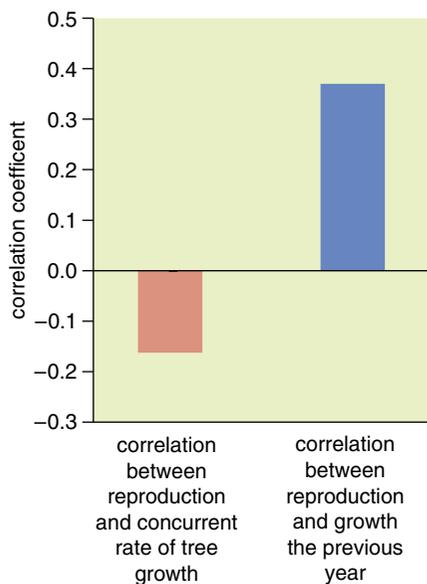


Figure 8. Correlation between reproduction (measured by annual acorn surveys) and concurrent growth in blue oaks is negative, reflecting the trade-off between these two biological imperatives. That is, when the resources invested in reproduction are significant, growth tends to be small, and vice versa. Interestingly, if one compares reproduction in one year with growth in the previous year and calculates a correlation coefficient using observations from all the survey years for which such pairings are available, a positive value results, indicating that these trees tend to switch between masting and growing from one year to the next.

spruces and pines. The data set represents 72 Northern Hemisphere sites and includes more than 5,000 data points. Each point corresponds to one species' seed crop from one site for a particular year. We crunched the numbers and found strong evidence for spatial synchrony in seed production among sites. Results of the meta-analysis indicate that conifer genera at sites as far as 2,500 kilometers apart spatially synchronize their seed production. This implies that trees are synchronizing reproductive activities over an area of at least six million square kilometers. Even the switching of resources between reproduction and growth appears to be coordinated over this vast area—crop sizes and radial growth are inversely correlated over distances of up to 1,000 kilometers. (Reproduction was inferred with the data from our literature search, and radial growth was measured by tree-ring chronologies of conifers obtained from the International Tree-ring Databank.)

A longer-term undertaking has been the gathering of field data on the spatial synchrony of seed production. To accomplish this, we initiated the California Acorn Survey in 1994. Each September we spend ten days counting acorns and driving 3,500 kilometers around the state. To quantify the acorn crops, we scan the crowns of each marked tree, counting as many acorns as possible for 30 seconds. Since a larger crop will result in a higher density of acorns, this method is an efficient way to sample relative crop sizes, rather than attempting to count every acorn

or to get total acorn weights. Because the estimate includes acorns in the crown, this technique also minimizes under-sampling caused by not counting acorns that are eaten by arboreal seed eaters. Such bias is a significant source of error in counts from traps that catch fallen acorns.

From 19 sites scattered throughout California, our data currently encompass more than a thousand trees divided among 50 populations of nine oak species (eight *Quercus* species and the tanbark oak, *Lithocarpus densiflorus*). After 11 years we're at last getting a picture of the extent to which California oaks synchronize their reproductive activities.

The results vary among species but clearly show considerable synchrony. Consider blue oaks, which are one of the most extensively distributed trees in California. They grow in foothill regions around the Central Valley over an area of some 20,000 square kilometers, about five percent of the state's total land area. Eleven years of data from 10 sites between 80 and 700 kilometers apart demonstrate strong synchrony between sites. In the absence of synchrony, we would expect the average pairwise correlation in the mean acorn crop between sites, r , to approach zero; with perfect synchrony, it would approach 1. In our data, r averages about 0.6. It decreases slightly as sites get farther apart but remains well above zero even between the sites farthest apart. In other words, synchrony in acorn production extends to pretty much every blue oak, a population of 100 to 200 million individuals.

Tree's Company

Scientists recognize at least three possible mechanisms by which trees synchronize seed production: chemical signaling, response to environmental cues and pollen coupling. In the first case, a chemical signal could transmit the necessary information from one tree to the next. Molecules might travel via a physical connection or through the air. Herbivory is known to induce chemical signals in some plants. Combined root and fungus structures share fungal filaments, or *mycelia*, that pass nutrients from one tree to the next, providing a potential signaling mechanism. However, both mycelial connections and airborne chemicals would facilitate synchrony only among trees that were in close proximity, and it's unlikely they could work effectively across a large area. These mechanisms are especially implausible given that many individuals are in fragmented populations, and therefore out of contact with trees in other parts of the range.

If chemical signaling is inadequate to explain masting, how could masting be mediated by an environmental factor such as rainfall, mean spring temperature, or perhaps even sunspot activity? This may sound rather like a reworking of the discredited resource tracking hypothesis, but the basic idea is different. In this instance, the amount of resources devoted to reproduction does not depend on metabolic processes limited by the environment, but rather on the trees' use of the environment as a stimulus that provides information about how they will allocate resources. To the extent

that the environmental cue is spatially synchronous, the trees would then be synchronized as well.

The principle of synchronization of population dynamics by environmental fluctuations is termed the "Moran effect," from work in the 1950s by Patrick Moran, an Australian statistician. Moran showed that an external factor, such as weather, that acts across separated populations with similar ecophysiology would tend to produce correlated changes in their abundance and hence synchronize their population cycles. The Moran effect has since been shown to generate spatial synchrony in the population dynamics of a wide variety of organisms. Well-established examples include human viral pathogens, sheep on the St. Kilda archipelago and caribou in Greenland. The Moran effect is behind spatial synchrony in many bird populations, and there are good reasons to suspect it plays a crucial role in synchronizing masting behavior as well.

Several weather phenomena have effects on wide geographic scales; some approach the global level. The best-known is the El Niño (more properly called the El Niño/Southern Oscillation, ENSO). This climatic anomaly starts with unusually warm temperatures in the central and equatorial eastern Pacific Ocean that cause changes in ocean current direction, precipitation and air temperatures across a significant proportion of the globe.

But spatial synchrony is not limited to sporadic patterns; even everyday temperature and rainfall can be spatially

synchronous on large geographic scales. Synchrony does decline with distance but remains statistically correlated up to distances of thousands of kilometers. To drive the spatial synchrony observed in masting, such environmental factors must be synchronized at least as closely as the trees' reproduction. That is, plenty of confounding influences can and probably do reduce reproductive synchrony below that of the critical environmental factor (whatever it may be). But, in order for the Moran effect to be the driving force, spatial synchrony in the environmental factor must be at least as great as that observed in the character under consideration.

Preliminary evidence suggests that this is indeed true in the case of masting by California oaks. In California, for example, mean temperature in April is spatially synchronized more strongly than acorn production by blue oaks. (It has a higher correlation coefficient among sites over similar distances, as shown in Figure 11.) This is consistent with the hypothesis that trees use fluctuations in temperature as the cue for whether to invest their resources in growth or reproduction that year, and that such fluctuations result in geographic synchrony of masting in this species—a Moran effect.

What is the biological basis for focusing on mean April temperatures as a synchronizing cue? This is when blue oaks in California flower and when prevailing conditions appear to influence the number of flowers that get fertilized and produce acorns. There are no experiments to demonstrate how the effect



Figure 9. The California Acorn Survey, begun by the authors in 1994, is an annual assessment of acorn production. More than 1,000 oaks at 19 sites (red dots) from across the range of oaks in the state (shaded area) are sampled. During the survey, one of the authors (Koenig) counts acorns through a pair of binoculars at the Santa Rosa Plateau Ecological Reserve, an undisturbed tract of Engelmann oaks (*Quercus engelmannii*), in Riverside County.



Figure 10. Blue oak, pictured here in Lake County, is widely distributed in California. Spatial synchrony of acorn production in this species appears to encompass its entire range of 20,000 square kilometers.

might work, but warm, dry conditions during flowering do correlate with a larger acorn crop in several oak species, including valley oak (*Quercus lobata*) and blue oak in California and white oak (*Q. alba*) in eastern North America.

Ironically, the possibility that weather conditions enhance pollination, leading to greater seed production, suggests the third mechanism for how masting trees synchronize their reproduction: pollen coupling. As mentioned, enhanced pollination efficiency is an alternative hypothesis to predator satiation as a selective advantage of mast fruiting. However, Satake and Iwasa's work has

further demonstrated that pollen coupling, in the complete absence of environmental fluctuations, can potentially synchronize reproduction among trees throughout an entire forest. The key is the degree to which individual trees depend on pollen produced by conspecifics a long distance away as opposed to nearby trees. This question has been addressed in terms of pollen flow—or how far pollen moves—in wind-pollinated species.

Until recently, pollen dispersal distances were something of a mystery—how can a microscopic pollen grain be tracked across a wide geographic area? Scientists have worked on the problem through a combination of field studies on blue oaks by Eric E. Knapp, now at the U.S. Forest Service Pacific Southwest Research Station, and molecular work on valley oaks by Peter E. Smouse at Rutgers and Victoria L. Sork. Their results suggest that the mean distance of effective pollination (over which pollen actually fertilizes flowers that produce acorns) may be on the order of 60 meters—surprisingly short. If these findings prove generally applicable to wind-pollinated trees, they imply that pollen coupling could play a role in synchronizing trees over modest distances, perhaps as much as a few kilometers. However, they would rule out pollen coupling as a mechanism for synchronizing reproductive timing over thousands of square kilometers.

Unfortunately, environmental fluctuations cannot be physically excluded

over a large enough area to isolate the synchronizing effects of pollen coupling. However, it is possible to gauge the environmental component, and in effect eliminate pollen coupling, by looking at synchrony *between* species. Assuming that the species do not usually hybridize, then pollen coupling cannot lead to interspecific synchrony between the two species, since pollen being produced by one of the species cannot be having any influence on fertilization efficiency or seed production of the other. This approach won't work in cases where inter-species hybridization is common, because the two species could be jointly "pollen coupled," since pollen being produced by one of the species could be fertilizing the flowers of the other. If hybridization is absent, and if no interspecific synchrony is found, it could be because the biology underlying the population dynamics of the two species is not the same, violating the primary assumption of the Moran effect. However, significant interspecific synchrony pretty much eliminates all potential mechanisms for synchronization except for the Moran effect.

As it happens, synchrony of masting between different species is relatively common. For example, Eric M. Schaub, now at Southern Illinois University, and Kelly studied masting in 17 New Zealand tree and grass species. Schaub and Kelly found that seed production is synchronized over an area of some 150,000 square kilometers. Moreover, the masting is associated with unusu-

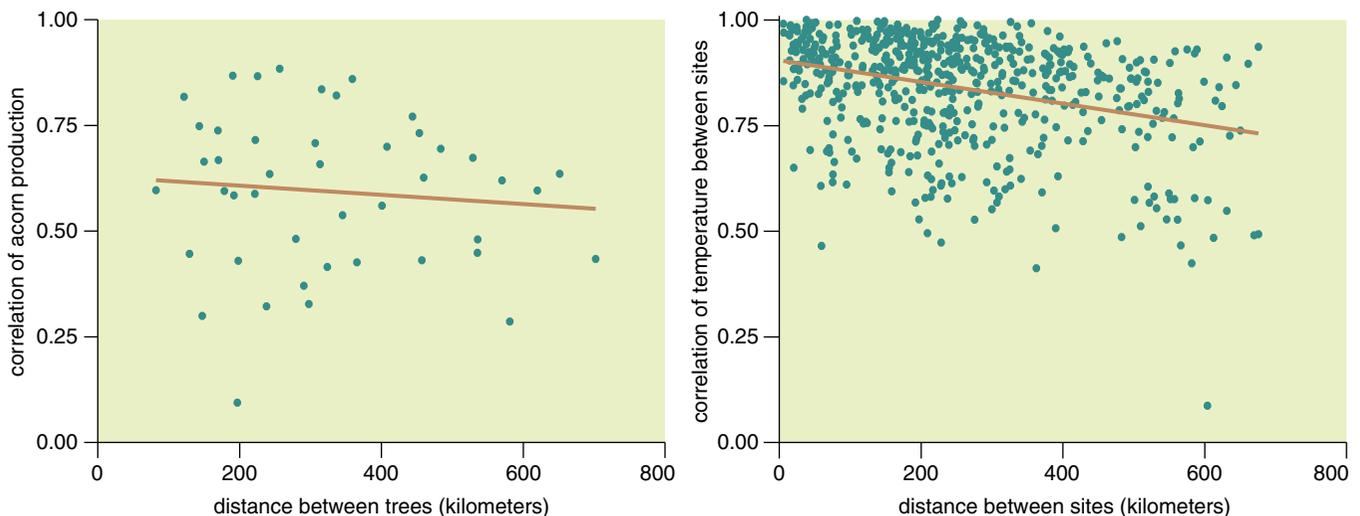


Figure 11. Constancy of the correlation coefficient of acorn production across distances up to 800 kilometers (*left*), as indicated by the shallow slope of the trend line, provides evidence for spatial synchrony of blue oak acorn production in California. (Data are based on the mean acorn crop of 10 sites surveyed annually since 1995.) How the trees coordinate their reproduction so closely is unknown, but the spatial synchrony of mean temperature in April (*right*) across sites is consistent with the possibility that synchrony in environmental fluctuations (known as the Moran effect) drives synchrony in seed production.

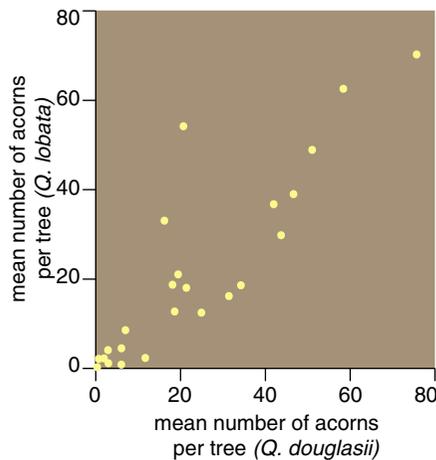


Figure 12. High correlation ($r = 0.88$) of the mean number of acorns per tree for valley oaks versus blue oaks at Hastings Reservation over 25 years (1980 to 2004) indicates that the two species strongly synchronize their production of acorns. Data points toward the upper right corner of the plot represent mast years when both species were highly productive.

ally high temperatures during the summer, a phenomenon linked to the La Niña phase of ENSO events.

The work of Lisa M. Curran, from the University of Michigan, showcases another example of interspecific synchrony. She has investigated masting events involving at least 50 species of Dipterocarpaceae, the dominant family of canopy trees in Borneo. This scale of masting presents a scenario in which an entire forest comprises dozens of species all flowering and fruiting at the same time. Based primarily on records of dipterocarp seed export by timber concessions, she concluded that these trees produce seed crops only every three to four years, again during ENSO events.

These examples prove that an environmentally driven Moran effect alone can be a strong synchronizing agent in masting species, although they do not entirely eliminate the possibility that pollen coupling plays a role in synchronizing reproduction. For our California oaks, the presence of high interspecific synchrony in acorn production between valley and blue oaks, which are closely related but rarely hybridize, suggests that, in these species as well, the Moran effect is a dominant force behind masting.

Masting and Climate Change

The prevalent role of weather as a cue for mast fruiting raises the question of how global climate change might affect masting events and subsequent ecosystem functioning. For example,

unusually high summer temperatures prompt heavy flower and fruit production by several species of ecologically dominant New Zealand *Chionochloa* grasses, an event that governs populations of several insect seed-predator species. Mark J. McKone at the University of Canterbury and other New Zealand scientists have suggested that ongoing global temperature increases will cause considerable decreases in the year-to-year variation in flowering of these species. The effects of smoothing out such variation on seed survival are unknown but potentially disastrous because fluctuations in seed-predator populations will be less pronounced in the absence of masting. Similar detrimental effects could become widespread among ecosystems in which masting trees play an important role. These biomes include the majority of boreal and temperate woodlands and probably a substantial proportion of tropical forests.

Rise and Fall ...

Masting among trees and other plants probably confers significant adaptive benefits. The boom and bust cycle of seeds available to seed predators imposes starvation-satiation regimes that help control predator populations and ensure that when seeds are produced plenty of them go uneaten. Additionally, masting may enhance pollination efficiency. Plants that synchronously produce masses of flowers and pollen once every few years are likely to experience higher pollination rates than plants that produce average amounts of flowers and pollen each year. The benefits so outweigh the costs that masting species more or less forgo reproduction entirely in non-masting years. Teasing apart the relative importance of these ideas will be the focus of future research into masting. However, scientists must also understand how masting will be affected by the worrying decline in California oak populations and also by climate change, problems that portend dramatic changes in the food and nutrient resources made available by masting. Predicting the ecosystem-wide effects of these risk factors is a major challenge to ecologists.

So next fall, don't take those acorns for granted. The fact that they are everywhere, or nowhere, as the case may be, illustrates one of the more spectacular ecological mysteries that you'll encounter as you walk through the woods. Enjoy them while you have the chance.

Bibliography

- Curran, L. M., I. Caniago, G. D. Paoli, D. Astianti, M. Kusneti, M. Leighton, C. E. Nirarita and H. Haeruman. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* 286:2184–2188.
- Elkinton, J. S., W. M. Healy, J. P. Buonaccorsi, G. H. Boettner, A. M. Hazzard, H. R. Smith and A. M. Liebhold. 1996. Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* 77:2332–2342.
- Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schaubert and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science* 279: 1023–1026.
- Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: Why, how, where? *Annual Review of Ecology and Systematics* 33:427–447.
- Knapp, E. E., M. A. Goedde and K. J. Rice. 2001. Pollen-limited reproduction in blue oak: Implications for wind pollination in fragmented populations. *Oecologia* 128:48–55.
- Koenig, W. D., and J. M. H. Knops. 1998. Scale of mast-seeding and tree-ring growth. *Nature* 396:225–226.
- Koenig, W. D., and J. M. H. Knops. 2000. Patterns of annual seed production by Northern Hemisphere trees: a global perspective. *American Naturalist* 155:59–69.
- Liebhold, A., W. D. Koenig and O. N. Bjørnstad. 2004. Spatial synchrony in population dynamics. *Annual Review of Ecology, Evolution, and Systematics* 35:467–490.
- McKone, M. J., D. Kelly and W. G. Lee. 1998. Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators. *Global Change Biology* 4: 591–596.
- Satake, A., and Y. Iwasa. 2002. The synchronized and intermittent reproduction of forest trees is mediated by the Moran effect, only in association with pollen coupling. *Journal of Ecology* 90:830–838.
- Schauber, E. M., D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson, P. E. Cowan and R. E. Brockie. 2002. Masting by 18 New Zealand plant species: The role of temperature of a synchronizing cue. *Ecology* 83:1214–1225.
- Sork, V. L., J. Bramble and O. Sexton. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology* 74:528–541.
- Sork, V. L., F. W. Davis, P. E. Smouse, V. J. Apsit, R. J. Dyer, J. F. Fernandez-M. and B. Kuhn. 2002. Pollen movement in declining populations of California valley oak, *Quercus lobata*: Where have all the fathers gone? *Molecular Ecology* 11:1657–1668.

For relevant Web links, consult this issue of *American Scientist Online*:

<http://www.americanscientist.org/IssueTOC/issue/741>