# *Mast fruiting and ENSO cycles – does the cue betray a cause?*

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**Evidence is mounting that flowering by the mast-fruiting Dipterocarpaceae in Southeast Asia is triggered by ENSO events such that seeds are dispersed at the end of ENSO droughts. These droughts induce substantial defoliation and mortality of canopy trees, producing a favorable environment for seedling recruitment in the forest understory. Therefore, seedling release following droughts may have selected for synchronized, supra-annual fruiting in these rain forests. Currently, mast fruiting in Southeast Asia is generally regarded as an evolutionary response to seed predation by nomadic vertebrates. Separating the two causes for mast fruiting, seedling release and predator satiation, may be difficult if they are coupled in nature by ENSO droughts. Nevertheless, if the cue for masting is environmental, then the post-ENSO seedling environment should be considered a potential cause for masting, and if it operates in conjunction with predator satiation, then it may have provided the initial stimulus for supra-annual synchrony in fruiting.**

Many trees in the aseasonal, lowland rain forests of Southeast Asia exhibit community-wide, synchronized supra-annual production of large seed crops, followed by several years of little or no seed production. Evidence is mounting that this mast fruiting is linked to the El Niño-Southern Oscillation (ENSO) (Ashton et al. 1988, Curran et al. 1999, Yasuda et al. 1999). While ENSO events are being regarded as the supra-annual cue for community-wide fruiting, satiation of seed predators is the presumed selective pressure driving it (Janzen 1974, Ashton et al. 1988, Kelly 1994, Curran and Webb 2000). Here, we suggest that ENSO cycles provide, not just cues, but also a selective pressure for supra-annual fruiting, and further that ENSO cycles could have provided the environmental fluctuations which initiated fruiting synchrony prior to predator satiation.

Droughts in Southeast Asia are associated with supra-annual El Niño events (Leighton and Wirawan 1986, Walsh 1996, Walsh and Newbery 1999). During ENSO droughts, mortality of large trees from drought alone, excluding additional mortality from fires, reaches 3–5% in normal events and 5–25% in severe events (Table 1). For emerging seedlings, the consequence of adult tree mortality is seedling release, as mortality in the canopy translates into increased light levels in the understory (Walsh and Newbery 1999) and decreased root competition from canopy trees (Lewis and Tanner 2000). Such seedling release should provide selection for dispersal of fruits at the end of supra-annual ENSO droughts when precipitation returns.

Are fruiting events associated with the end of ENSO droughts? Detailed monthly data are essential to test this hypothesis because timing and intensity of ENSO droughts and mast fruiting vary throughout Southeast Asia (Ropelewski and Halpert 1987). In western Borneo and much of peninsular Malaysia, fruiting is now known to occur at the time that heavy rains begin following ENSO droughts (Whitmore 1998, Curran et al. 1999). Elsewhere in the region, fruiting following past droughts is evident in over-represented cohorts in age-size distributions (Leighton and Wirawan 1986, Goldammer and Seibert 1990). Recent evidence substantiated the Ashton et al. (1988) hypothesis that flowering in dipterocarps is cued by atmospheric changes associated with pre-drought ENSO events such that sequential flowering of different species is spread over many months of a drought, but fruiting is synchronized precisely at its end (Yasuda et al. 1999)

Fruiting at the end of ENSO events entails risk due to exceptionally severe droughts where some trees abort fruits and germinating seedlings die. For example, the 1982–83 drought in Borneo ended normally with the onset of the rainy season, only to have the latter halted abruptly, extending the drought into a second dry season (Leighton and Wirawan 1986). The consequences in East Kalimantan were extreme mortality of canopy trees (Table 1) but also a complete failure of seedling establishment. Given this risk, the fact that mast fruiting occurs only following ENSO droughts implies a more favorable regeneration environment following ENSO droughts than in non-ENSO years. In fact, if predator satiation were the sole explanation for masting, selection might favor fruiting at the start of the rainy season in a non-ENSO year to avoid calamities of the severe ENSO droughts. Parsimony might argue for year ENSO + 1.

The ENSO-based seedling release hypothesis, proposed here, could be classified as masting based on "environmental prediction" – namely, "large reproductive episodes timed to anticipate favorable conditions for establishment" (Kelly 1994). All such prior cases involve fire as the trigger for mast fruiting where the post-fire environment favors seedling establishment (Kelly 1994, Keeley and Bond 1999). Although fires have been associated recently with ENSO droughts, their historical role is questionable (Goldammer and Seibert 1990). However, defoliation and mortality of large trees from drought alone, not fires (Table 1), should have been sufficient to provide favorable conditions for seedling establishment.

Post-ENSO seedling release probably operates in tandem with predator satiation to reinforce community mast fruiting because both processes satisfy criteria of scale (Keeley and Bond 1999): (1) ENSO droughts recur roughly every 3–7 years, about the length of time needed to substantially reduce vertebrate seed predator populations, (2) within Southeast Asia, droughts occur over large sub-regions, as do migrations of vertebrate seed predators, and (3) ENSO droughts normally end abruptly concurrent with fruitfall and onset of the rains. A third concurrent hypothesis is that increased solar radiation, due to cloudlessness, facilitates greater fruit production during ENSO droughts (Wright et al. 1999).

Table 1. Annualized mortality rates (%) of large trees ($DBH \geq 10$ cm) from drought alone, during years of severe ENSO events and during baseline years for sites in Southeast Asia and the Neotropics. Data are modified slightly for comparison from Woods (1989) for Sabah, Leighton and Wirawan (1986) for East Kalimantan, Kinnaird and O'Brien (1998) for Sumatra, Nakagawa et al. (2000) for Sarawak, Condit et al. (1995) for BCI in Panama, and Williamson et al. (2000) for the Central Amazon. Mortality in baseline years for Sabah, East Kalimantan and Sumatra was taken from the closest comparable sites given by Phillips et al. (1994), and may include some ENSO years with many non-ENSO years.

| | | Annual percent mortality | |
|---|---|---|---|
| | ENSO year | Severe ENSO | Baseline years |
| Southeast Asian Tropics | | | |
| Sabah | 1982–83 | 22.1 | 1.5 |
| East Kalimantan | 1982–83 | 25.2 | 1.5 |
| Sumatra | 1997–98 | 9.8 | 1.8 |
| Sarawak | 1997–98 | 4.7 | 0.9 |
| Neotropics | | | |
| BCI, Panama | 1982–83 | 3.4 | 2.0 |
| Central Amazon | 1997–98 | 1.9 | 1.1 |

Perhaps seed predation alone can explain supra-annual, synchronized fruiting, but parsimony assumes that a masting cue derived from the environment may also imply an environmental cause (Ims 1990). Furthermore, theoretical arguments for the evolution of predator satiation require partial fruiting synchrony based on supra-annual environmental variation, which, in this case, would have been provided by ENSO cycles (Silvertown 1980, Ashton et al. 1988, Lalonde and Roitberg 1992).

ENSO events are global, so if they have contributed to supra-annual fruiting in Southeast Asia, why have they not produced masting elsewhere? First, seasonal environments have annual variation that often outweighs ENSO cycles, so ENSO droughts have stronger relative effects on trees in aseasonal forests (Walsh and Newbery 1999). Seasonal forests, even dipterocarp forests in Southeast Asia, show little or no supra-annual fruiting synchrony (Ashton et al. 1988). Second, ENSO events are strongest in the Southeast Asian tropics at the origin of the Southern Oscillation (Ropelewski and Halpert 1987). ENSO droughts in Neotropical rain forests cause only modest increases in mortality and fruiting (Table 1, Wright et al. 1999, Williamson et al. 2000). Likewise, western Malesia experiences only weak ENSO effects and exhibits no correlation between masting and ENSO events (Wich and Van Schaik 2000). Third, supra-annual fruiting carries risks for fruits dispersed by non-hoarding animals (Silvertown 1980) – namely, populations of dispersers may decline in non-mast years, leaving excess seed undispersed in subsequent mast years. In aseasonal Southeast Asia, outside the dominance of the wind (gyration) and gravity dispersed Dipterocarpaceae (e.g. east of Wallace's line), the dominant canopy species have seeds dispersed by animals and exhibit little interspecific synchrony in fruiting (Whitmore 1998, Connell and Green 2000).

Overall, the unique features of Southeast Asia – severe ENSO droughts that cause substantial mortality of canopy trees, dominance by the Dipterocarpaceae whose seeds are gyration and gravity dispersed, and extreme seed predation by mobile vertebrates – appear to have combined to produce the extraordinary mast fruiting that occurs there and in no other rain forests in the world.

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