

Ecology and the Durian Theory

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The Durian Theory (Corner 1949-1964) is on a base of comparative morphology, yet provides insight on the ecology and evolution of tropical forest. The hypothetical angiosperm archetype that is deduced from it no longer exists; from ecological theory though we may speculate why this is so, and may deduce the conditions in which these plants evolved. What ecological bonuses and limitations does each of the primitive characteristics impose?

Large spiny loculicidally dehiscent capsule or follicles, with large black seeds more or less enveloped in a colourful fleshy aril and dangling on persistent funicles. A large seed provides a large food store, essential in the perennial shade of evergreen forest. In a windless climate fruit dispersal of forest plants is most effectively accomplished by animals, yet the large slowly developing seed must be protected from them until ripe. The significance of colour and movement to attract animal vectors has been discussed at length by Corner. It is astonishing how disinterested even monkeys are with green fruits; we have observed that the embryo and flesh of wild rambutan (*Xerospermum intermedium* Radlk.) fruits matures before the pericarp changes from green to yellow, yet the voracious monkeys always failed to distinguish maturity before the colour change. Experience of modern trees may have led them to fear all green fruits as unpalatable or poisonous; primitive armour, once pierced, provides protection against no predator, but the evolution of specific poisons reduces attacks to a few specialists. When in Sarawak I had the opportunity to identify the food of orangutans set free in Bako National Park, I was struck by the dexterity with which they dismembered the horrid defenses of rotan and nibong cabbages, and wondered whether these primates might be recent immigrants, possibly to the extending Holocene forests; otherwise such plants as the hapaxanthic *Plectocomia*, a particular favourite, would have disappeared as, we can assume, already have many other spiny but palatable organisms of former days.

Moreover, these great spiny primitive fruits are expensive and can only be produced in small numbers at a time; they confine those plants that bear them to stable habitats where their populations are least likely to suffer large fluctuations, and in places where opportunities for establishment are greatest. Such is the case in the shade of the forest canopy, but where is the pioneer with such a fruit? The mature phase of the forest is hence the home of our large seeded tropical fruits, and many more live there still awaiting cultivation; destroy the forest and this bounty will be lost.

Stout, pithy-stemmed, unbranching and monocarpic trees, with a terminal inflorescence. Such a habit and reproductive strategy still occurs in some palms and other monocotyledons, but is rare among dicotyledons. The polygamodioecious tree-ivy *Harmsioplanax* of New Guinea is one example. It is a semigregarious treelet with huge pinnatisect leaves, of mid-mountain glades. As a nomad, however, it produces an abundance of flowers and small fruit as do such monocarpic palms. A large fruited monocarpic progenitor could only maintain cross-pollination, and hence the genetic variability for further continued evolution, by growing in

gregarious stands; each unbranching treelet would thus be analogous to the monocarpic stems of the rhizomatous branching sago-palm *Metroxylon*. A stout pithy stem is the perfect adaptation to the unbranched monocarpic habit; The tube as a supporting structure is cheap and provides adequate tensile strength for a vertical member in a windless environment; while, as every Melanau sago farmer knows, the pithy core, which in dicotyledons expands as the apex enlarges (eg. Mabberley, 1974b), is the bank where insoluble polysaccharides gradually accrete until, in a flamboyant vegetable sneeze, they are converted to soluble sugars and surge up the giant terminal inflorescence into the developing flowers and fruits. The biochemistry of durianology demands further attention!

Large pinnate leaves borne spirally with short internodes. Givnish has elegantly defined the adaptive significance of leaf size and shape: large entire leaves are structurally and photosynthetically efficient individually, but carry a high heat load and are therefore expensive on water resources. They more completely exclude light beneath than small leaves do and thus reduce the leaf area index. Pinnate leaves comprise small leafy organs borne on deciduous twigs; when arranged in dense spirals they will still cast the deep shade of large entire leaves yet bear a lesser heat load. Evergreen trees with large thin leaves, whether entire or variously divided and in dense spirals, are confined to well-watered habitats even in the humid tropics. Some, such as the pinnate-leaved *Chisocheton* and pinnatisect *Heliciopsis* are in the forest understorey and bear large, usually dehiscent fruits; here, as Givnish points out, the large thin leaf is advantageous on the 'gamblers ruin' principle, by spreading a given number of chloroplasts horizontally the chance of encountering sunflecks is increased. Others, such as the small fruited tree-ivies *Harmsioplanax* and *Arthrophyllum* skirt the forest fringe on river banks and in gaps. Here large rapidly transpiring leaves, which prevail among nomad trees of well-watered places, provide the most economic means of building a photosynthesizing mantle for rapid growth and at the same time cast deep shade, deterring competition. In a densely spirally pinnate-leaved slow-growing tree the latter advantage is still conferred, as anyone who has rested in the uncluttered shade of *Dracontomelum mangiferum* Bl. on a Bornean river bank will remember with gratitude.

If now we add a massive inflorescence of large actinomorphic magnoliaceous flowers, with weakly differentiated perianth and many centrifugal stamens, we further define our plant's ecology. Such flowers are a crude means of ensuring cross-pollination, unless self-incompatible. They are expensive to produce, and the greater part of the costly pollen will be wasted, unless the trees are gregarious which, as we have already suggested, they probably were, or the flowers conspicuous and the vectors specific and far-roaming. The simple thin-walled short-lived pollen grain so common among still existing primitive families has, like the fruit, confined them to habitats where the atmosphere is warm and humid at least during the flowering season.

The stage may now be set for the reenactment of angiosperm evolution: we can visualise hills clothed in tall *Araucaria* forest; ferns grow in the deep shade beneath, while Cycadophytes and Caytoniales occupy the open fringes, along rocky ridges and in swampy plains. The gap phase of the *Araucaria* forest would have lacked the fast growing opportunists of modern rain forests. Here, on moist stable fertile slopes, hence especially on basic volcanic soils, the protoangiosperm would have found its niche; from a massive seed a tall shoot rapidly overtopped its gymnosperm seedling competitors in the shafts of light penetrating the crowns of ageing giants, allowing the building of the light-excluding *schopf* of densely spiral large pinnate leaves. Only its own kind could survive beneath its shade, and thus small, temporarily isolated but eventually expanding and coalescing, gregarious stands would accumulate on these slopes. These short unbranched trees hence excluded gymnosperms from the most favourable sites by depriving them of suitable conditions for establishment. This remains the secret of angiosperm

success, and even now it is the gymnosperms which, if allowed to, can finally achieve the greater growth and stature, as the dwarfing of New Guinean angiosperm forest by the scattered araucarias still witnesses.

Here then are the perfect conditions for further evolution and diversification: small gregarious colonies with few flowers and free cross-pollination, temporarily isolated along the slopes and thus allowing rapid local diversification; yet each valley, and each mountain chain, more permanently isolated. The significance of animal dispersal now becomes apparent.

The evolution of the enclosed seed in an eventually dehiscent fruit is seen, then, not to be a response to increasing aridity, for which there is little evidence in the upper Jurassic-lower Cretaceous period of continental drift, but for the need to develop a protective covering for the enlarged endosperm until the seed is ready to germinate.

Why should not cycads have accomplished the same? On the upper slopes of Susungdalaga in Camarines Sur, Luzon, I have seen *Cycas circinalis* L. growing in forest shade on volcanic soils. Their leaflets were sparse and their crowns diffuse; perhaps their less evolved vascular system and physiology prevents them from rapidly building and subsequently maintaining the dense excluding crown of the primitive angiosperm?

Thus the first flowering plants, not gymnosperms, would have provided the environment in which their further evolution could occur. Only angiosperms could survive beneath their own shade and hence only angiosperms could eventually overtop them. The Durian Theory provides a morphological means by which this could be accomplished. This increase in diversity of tree habit would initially have been the main source of increased species diversity in the forest, which in itself necessitated greater subsequent fruit production to overcome declining opportunities for establishment as interspecific competition increased, and led to the extinction of the large-fruited monocarpic ancestors. The evolution within the rain forest of more flexibly arranged, smaller, leaves would also allow a further spread of angiosperm hegemony into the domain of gymnosperms. Yet the sparsely branching protoangiospermous habit and spiral divided leaves still retain their advantage in the forest shade and many modern leptocauls, including a Philippine *Knema* (Myristicaceae) and a New Guinea *Sloanea* (Elaeocarpaceae) with durian-like fruit, retain this habit as saplings, as Corner has noted in other forest trees.

The evolutionary sequence of early angiospermous forest is partly reenacted in modern seral succession on moist hillsides. The seeds of modern forest nomads are small, with little food-store, and germinate in response to light but, once germinated the saplings rapidly build a tortoise-shell of large overlapping leaves, expanded by the early formation of ascending pithy shoots; among them are microperm pachycauls such as *Senecio mannii* Hook. f. (illustrated by Mabblerley (1974a)). This at first, if complete, can effectively deter competition but after a few years the stems and branches begin to open under their own weight, providing the setting for the next stage, which will involve the first true leptocauls. Among them though, and particularly on these well watered sites, the pagoda tree (Corner, 1940) comes to predominate, an ingenious compromise between pachycaul and leptocaul and probably ancient. This, by intermittent rapid extension of a stout pithy leader grows first into a tall unbranched sapling with spiral or whorled leaves; but then, after a period of dormancy, it sprouts a whorl or pseudowhorl of more or less horizontal branches around the apex, bearing dense ascending rosettes, typically of obovate leaves by *Terminalia* branching (Corner, 1940). Thus an aerial blanket of leaves, often large and presumably rapidly metabolizing is early formed which overtops and suppresses its many-stemmed predecessors and, by successive bold extensions, apical dominance is maintained until the final forest canopy is reached. Only then does apical dominance give way to allow the expansion of a dome-shaped sympodial crown, often associated with a decline in the size

and density of the leaves and twigs. The ascending spires of *Alstonia*, *Terminalia*, *Bombax*, *Endospermum*, *Tetrameles* and *Octomeles* proclaim such a stage in the forest cycle. Meanwhile other truly leptocaul species are establishing beneath to fill in the forest frame.

It can be seen then that, first, the complexity of mature phase forest structure must have been formed; this also by its nature provided obstacles to cross-pollination, and thus initiated the evolutionary sequence of floral specialization and diversification by which our modern families are distinguished.

Meanwhile also, microsperm pachycauls evolved into the gap phase of the forest and the alpine forest fringe, and the differing conditions for reproduction there led to the origin of such other taxa as *Senecio* and *Lobelia* (Mabberley, 1973, 1974c) and eventually herbaceous forms.

It is now apparent why the Myristicaceae, primitive in so many respects and with primitive arillate fruit, have nevertheless developed the leptocaul habit with small leaves and plagiotropic branching, and flowers which are small, much reduced and borne on dioecious trees. Here is a family that has evolved with the forest from earliest times: first the fruit, then further evolution of the habit, and subsequently the flower while the earlier evolved fruit and habit continue to retain their adaptive advantage in the shade of the storied modern forest. But the Myristicaceae, as Corner points out, are tied to the rainforest by their fruit; fell the forest and they do not return.

As the origin of the primitive angiospermous fruit must be interdependent with the early evolution of vertebrate vectors, birds and mammals, so the evolution of the structure of the angiospermous rain forest-not by coevolution this time but in response to previous vegetational change-provided the means for their rapid diversification. Animal diversity, once thus initiated, in turn enhanced the coevolution of flowers and their pollen vectors, of plant hosts and their predators, which still continues and defines the modern complexity, long after the possibilities of structure, habit and leaf design had been exhausted and retained or repeated by many families.

In geological time the disposition of land masses has changed, and the area occupied by different climates, but the *range* of climates and soils can rarely have changed. Life itself provides the changing scene. Evolution of species and phyla proceeds from what has already evolved before; similarly it is in those habitats where biotic change has been greatest that we should expect major paths of further evolution to originate, not in the deserts or the mountains but in the lowland forests especially those of the humid tropics.

Why, then, do we find monocarpic pachycauls prevailing in the paramo, and the massive primitive flower more often in the mountains than the lowlands? Evolution has proceeded outwards from the lowland forests where only the ancient fruit and pinnate leaves have sometimes survived the palimpsest of subsequent biotic change in the understory. But the paramo retains the moist open conditions of the primitive angiosperm forest while the pachycaul stem is preadapted to year-round frost (Mabberley 1973, 1974a) and the structural simplicity of the montane forest, though derived and leptocaul, allows the survival of clumsy pollination systems.

It is therefore naive to conjecture the centre of angiosperm origin from modern distributions. Besides, great changes in the distribution of climates have occurred since the Jurassic, necessitating massive migration if not always extinction; even in South-East Asia Muller has shown that temperate species prevailed, presumably on long-vanished mountains, during the Miocene.

Similarly, plants only fossilize under restricted conditions. The most primitive pollen types appear not to fossilize well and it is likely anyway that plant, and possibly also fruit, form diversified both within the rainforest and into other

environments largely *before* flower and pollen diversification. Recent fossil evidence is therefore likely to be misleading. Using the Durian Theory as a basis for prediction we should pursue a different approach and should consciously search out volcanic ash deposits rather than riverine, swamp or aquatic, from the western tropical margins of the great late Jurassic oceans. If they do not exist, or bear no fossils, the origin of the angiosperms will remain enigmatic.

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