THE REPRODUCTION AND ESTABLISHMENT STRATEGIES OF TIDAL PIONEERS

- A Review

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INTRODUCTION

The type of thinking which led Hutchinson (1959) to ask "Why are there so many kinds of animals?" is indicative of the approach to thinking and questioning characteristic of present day ecologists, in their search for the necessary philosophical and theoretical basis, on which all new ecological generalizations must stand. Similarly, the questions of Harper (1967) in "A Darwinian Approach to Plant Ecology" have provided new incentive and direction to the study of plant populations.

This review is an attempt to discuss the questions of Harper (1967) and others - "How can we characterize reproductive strategies and the effects of various parameters on them?" - to seek possible answers from a small section of literature; and to define areas for further consideration. The specific literature chosen for discussion centres around mangroves; occasional direct comparisons will be made with other proven types.

It is worth noting that not all mangroves can be classed as real pioneer species, as the term "mangrove" is a very general name (Macrae 1968). However, most interest has centred around those species which are considered pioneers, and this is reflected in the literature.

Harper (1967) has pointed out the difference between tactics and strategies - where a tactic may be expressed as a specific adaptive mechanism, and a strategy is a certain combination of tactics to produce an overall result and throughout this review, this distinction will be maintained.

It is difficult to avoid falling into the teleological trap of assuming that every feature of anatomy and morphology is of adaptive significance and that one can, by inspection, determine this. Indeed some features to be discussed show no apparent adaptive value. However, if at the outset the problems of teleology are recognised, it is hoped the reader may substitute his own more cautious wording which conciseness may have forsaken.

II Reproductive Strategies

Recent studies of energy allocation have allowed some quantifying for comparison of various strategies and optimisation studies (e.g. Cody 1966, '74). Within plant communities, reproductive strategies have been compared through Reproductive Effort where -

$$\text{Reproductive effort} = \frac{\text{total energy expended in reproduction}}{\text{total energy assimilated (+starting capital)}}$$

(Harper and Ogden, 1970), and this has been extended to whole of life considerations, where the term 'life cycle strategy' is used to express the whole complex time and space pattern of energy allocation by the organism (Harper and Ogden, 1970). Indeed this energy allocation is an extremely important and useful approach in the study of comparative strategies and will be discussed further. However, some tactics cannot be considered in these terms and must be considered separately.

Reproductive Behaviour

Various tactics are available for changing energy 'cost' of reproduction and genetic variability, and selection pressure for some particular behaviour may be intense. Bawa (1974) points out the increased probability of successful pollination through self compatibility can lower the 'cost' of reproduction, because for the same number of fruits, the self compatible species can afford to produce fewer flowers than the self incompatible one. Cliff dwelling plants have evolved woody perennial habit from an annual habit because of erratic dispersal and slow growth (Davis 1951) and this represents different allocation through change of reproductive behaviour. Recent studies of reproductive strategies have been made on plants with diverse reproductive behaviour - annuals, perennials with sexual reproduction only, and perennials with vegetative reproduction. (Harper & Ogden 1970; Abrahamson & Gadgil 1973; Sarukhan 1974 and Ogden 1974 respectively).

Timing of Reproductive Effort

Though really a part of whole life cycle strategy, the timing of reproductive effort has been studied as an approach to reproductive strategies with some success - particularly in attempting to explain the adaptive nature of differences in life histories of organisms of the same taxonomic group (e.g. Cole 1954, Lewontin 1965, Tinkle 1969, Gadgil & Bossert 1970). These studies, dealing mainly with age - specific fecundity - time relationships of life cycles, show how a high intrinsic rate of natural increase can be obtained by producing a few offspring early in life - precocious reproduction is all important.

Little work appears to have been done on correlations of the timing of reproductive effort with some environmental features. It is this timing of activity which is the major implication of Cody's (1974) ecological optimizations. Two possibilities exist in correlation of timing of reproduction of plants. The timing of flowering and propagule production on parent may be during a period of optimal conditions for the parent. This may be typical of plants with a high reproductive effort allocation (r strategists) and often dormancy and germination requirements provide optimal timing for the propagules. Otherwise the propagules may be liberated at the time which is optimal for dispersal and establishment, and so correlated with a large variety of physical environment features.

Reproductive Output

Propagule numbers, sizes and shapes represent complex adaptive compromises in any reproductive strategy - size is generally a compromise with number, and shapes represent compromises between forms for best packing, dispersal, landing and establishment. (Harper et al 1970). Dormancy is an important tactic which enables members of a population to remain insulated from recurrent or sporadic pertubations, and ensures continuation of a population through unfavourable seasons or environmental catastrophies to which the growing plant is not adapted.

Obviously it is important then, in the consideration of reproductive strategies, to consider the relationships between propagule members, size and shape; and dormancy, longevity and vivipary. Some questions posed by Harper (1967) are worth repeating.-

> "1. If seed number is sacrificed in favour of seed size, what increase in survival value of seed is required to maintain the same potential for population increase?
>
> 2. In the face of recurrently hazardous conditions, of specified frequency and magnitude, what is the optimal fraction of seeds remaining dormant or undergoing dispersal?
>
> 3. In what ways is the optimal strategy altered if overcrowding is a more common experience than unhindered population growth?"

These questions are not readily answered, though results of recent work on weedy species (e.g. Gadgil & Solbrig 1972, Abrahamson & Gadgil 1973, Harper & Ogden 1970, Ogden 1974) provide some clues. Consideration will be given to these features in relation to mangroves which may provide some understanding of the reproductive tactics involved.

a) propagule numbers
b) propagule size
c) propagule shape
d) dormancy
e) longevity
f) vivipary

Studies involving numbers of progeny produced, - an approach particularly rewarding in relation to insect taxa (e.g. Price 1973, 1974) and bird clutch size (e.g. Lack 1954, Cody 1966) is also worth considering in relation to plants. As will be discussed later, energy allocation to reproduction is an important criteria for comparing strategies, so that the numbers of propagules produced must be governed by -

1. Size of annual assimilated income;
2. proportion devoted to reproduction;
3. size of units in which it is invested;

so that propagule size, and number represent alternative strategies in the disposition of reproductive resources. Generally, large propagule numbers, small size and high dispersibility, which tend to go hand in hand, are associated with colonizing species. (Harper et al, 1970). As Levins (1968) points out, propagule numbers will have greater weight in environments which are unstable from generation to generation.

A few estimates are available for numbers of propagules produced per plant, though many are cereals which are bred for high yield; and do not provide fair comparison. Sarukhan (1974) reports an average seed crop for Ranunculus sp from 40-140, with a maximum of 287 per plant. Panetta (unpubl. data) gives estimates of seed production for the exotic Baccharais halemefolia in Australia of from 1,185 to 1,463,445 per plant with shading significantly restricting production. Recalculation of data from Cremer (1971) gives estimates of annual production numbers from 5,000 to 270,000 for one area of Eucalyptus regnans and from 320 to 11,760 for another site. Figures for production in rain forests are difficult to obtain, but Ashton (1969) suggests very low rates and infrequent production (e.g. once every 5 to 12 years). Rain forest propagules tend to be large and animal dispersed.

With seed size, (usually measured by weight) Angiosperms show considerable variation, but it is a very stable feature within the species (Harper et al 1970). From the table produced by Harper et al (1970), seeds of woodland tree species tend to fall into the 10^{-4} to 10 gram range with herbaceous perennials and annuals having much lighter seeds. There is a strong correlation between seed size and mode of dispersal.

Some data is also presented by Salisbury (1974), where the average mass of seeds of open habitat (pioneer species) is .00298 gms. The light conditions for the establishing seedling will largely determine the seed size. Salisbury (1974) also noted the largest propagules recorded were pioneers of shingle beach, and later shingle beach succession members were much smaller seeded.

Many of the shapes of propagules are related to dispersal mechanisms, and are classically interpreted as wholly so. However many features of shape may be imposed (Harper et al 1970). Clear evidence of this is in mangroves, where similar modes of dispersal are accompanied by diverse shapes. (See later)

The interrelated features of dormancy, vivipary and propagule longevity have tactical importance in many ways. As described, dormancy may provide a mechanism for avoidance of environmental pertubations, particularly in an unpredictable environment. Timing of establishment, and the wastage of propagules in the case of non-immediate dispersal to suitable sites may be influenced by dormancy and longevity. Vivipary provides enormously increased propagule size as a result of the continued growth of the young embryo while still attached to the parent plant. This will have some bearing on the overall energy allocation as well as the way in which the investment is proportioned between size and number. Pioneer species in particular tend to have dormant seeds though longevity is often restricted by low energy reserves of the light seeds.

Reproductive Effort

The use of Reproductive Effort, developed recently by Harper and co-workers (see earlier text and Harper & Ogden 1970) is suggested as the most satisfactory method of comparison of reproductive strategies (Harper 1967) and life cycle strategies. The formula presented earlier is the basic one, being modified by various workers. Abrahamson and Gadgil (1973) use weight measures to represent energy values, while Harper and Ogden (1970) use calorific conversions for better approximation. The formula is very similar to the Harvest Index of Donald (1962).

Some studies have been made with plants using the formula given earlier, and techniques as described by Harper and Ogden (1970). Harper and Ogden (1970) found that Sencero vulgaris had a Reproductive Effort of 21% regardless of other allocation variations (root-leaf-shoot). Ogden (1974) with the Rhizomatous perennial Tussilago farfara found sexual Reproductive Effort was highly variable from 4 to 23%. Sarukhán (1974) found that Ranunculus species appear to show few denisty dependent reactions with respect to energy allocation, but figures for Reproductive Effort are not given. This provides an exception to the conclusions of Harper (1964) that plants under different levels of density stress modify allocation of energy; sacrificing numbers of propagules but tending to maintain size. Abrahamson and Gadgil (1973) with Golden rods (Solidago spp) showed that Reproductive Effort declines with increasing successional maturity in the community. A conclusion by Harper et al (1970) is similar, in suggesting that annual herbs, perennial herbs and trees allocate respectively progressively smaller fractions of resources to reproductive activities (15-30%, 0 - 15%, 5 - 25%) and early colonizers have high Reproductive Effort. This is in accordance with theories for K and r selection developed by MacArthur and wilson (1967). Plants with 'r' selection imposed will be selectively favoured to allocate a greater proportion of resources to reproductive activities at the cost of the capabilities to propagate under crowded conditions. (Gadgil and Solbrig 1972). 'R' strategists are associated with unpredictable, often catastrophic environments and thus are usually pioneers (Pianka 1970). 'K' strategists, on the other hand, are associated with fairly stable, predictable environments and are characterised by increased allocation of resources to non-reproductive activities (e.g. vegetative growth), and increased utilization of environmental resources, slower development (with greater competitive ability) with delayed reproduction (Gadgil & Solbrig 1972, Pianka 1970).

Dispersal

Dispersal is the active (dynamic) process of transport leading to the passive (static) state of distribution (Ridley 1930). The diaspores (units of dispersal) are transported during a resting phase of their life cycle, and so there is no active adaption during their transport, though obviously there is selection (a more Darwinian definition of dispersal would say the diaspores "selected out" are not dispersed).

The debate between Guppy (1906) and Ridley (1930) as to whether or not the diaspores are adapted for a particular dispersal is reviewed and continued by Van der Pijl (1969). Nevertheless, the dispersal of many diaspores is extremely appropriate in that it will tend to distribute those diaspores in suitable sites, and some diaspores have adaptions which enhance their dispersal, but do little for establishment. The diminished dispersibility of Pacific Compositae reported by Carlguist (1966) provides a good account of adaption in dispersal mechanisms.

Establishment

As with dispersal, adaptions which affect plant establishment are important tactics in consideration of reproductive strategies. Three clearly separable processes are involved in establishment -

a) Fixation
b) Germination
c) Early growth

The question arises as to the limits of consideration of early growth - i.e. when can a plant be considered established. In Darwinian terms, the plant is established as a species when it reproduces, but prior to this time may be considered established in terms of itself alone. (See Van der Pijl, 1969). Dowling et al (1971) and Sheldon (1974) consider seedlings established when the first true leaf appears (growth becomes autohophic). Other criteria could include the ability of the plant to tolerate environmental change, age (especially in crops) or probability of completing a life cycle (see Cremer 1971).

a) Fixation.

The need for stability of a seed prior to germination has not been adequately studied, but it seems a most likely prerequisite for germination of most seeds. The positioning requirements described by Sheldon (1974) suggest that without some stability, the germination requirements (especially water) of Taraxacum officinale and Sonchus oleraceus could not be met. Adaptations which aid fixation prior to germination have been reviewed by Van der Pijl (1969) and include slime secretions, mucilages, hydroscopic boring actions and some seed shapes.

b) Germination

Germination requirements of seeds involve a number of environmental parameters (e.g. light - quality and quantity, temperature, stratification, water availability) and are well documented for many species. In general these can be considered adaptations which provide for germination under conditions for best seedling success. The environmental limits for germination are often narrower than those for further growth (Van der Pijl 1969).

c) Early Growth

The level of hazard involved with an establishing plant decreases with increasing age, and so the earliest stages of growth are most important in establishment (Harper 1967). Thus consideration of Reproduction (and Establishment) strategies leads to consideration of -

1. The ability of the species to withstand the physical and biotic features of the environment, such as frost, drought, soil type, predators, grazing animals (light, EH, PH, salinity, soil fertility and depth, water availability, litter).
2. The ability of the species to withstand interference from other plants (Harper and McNaughton 1962).
3. The duration of 'safe site' features, and the rate of response of the species (Sheldon 1974).

1. The response of the species to the biotic and abiotic conditions prevailing during establishment is particular for that species, resulting from the specific genetic combination, and has been studied widely, largely from three angles: Conditions for optimal seedling growth is an approach useful when dealing with controllable environments. (eg. Agricultural, Johnson 1973). The range of environmental features under which seedling growth will take place is often studied

prior to introduction of new crops to an area in which conditions are known. A further approach is to describe the environmental conditions under which the plants are establishing (e.g. Bjor 1971). Competition can provide the differences which are found between physiological growth optima and ecological growth optima. Individuals of a species are selected for modifications which provide optimal growth under the prevailing ecological conditions.

2. The effects of inter- and intra- specific competition on established seedlings have been widely studied (e.g. Harper and McNaughton 1962). These studies reveal the high mortality rates produced by competition presures on young seedlings (a Density Dependent mortality). Selection at this stage may favour such things as rapid growth and large seed size and adaptations favouring these will be promoted. Plants growing on disturbed sites (i.e. colonizers) tend to have low Density Dependent mortality.

3. With increasing age, the ability of a seedling to withstand environmental fluctuations increases, and the tobranic range widens; thus selection pressures are greatest on the seedling at the earliest stages of growth (Harper 1967). Two things to be considered are:-

(a) duration of 'safe site' features and the degree of environmental fluctuation;

(b) rate of response of the species; in particular the rate of early growth is important in determining how quickly the seedling can move from the stages of greatest sensitivity (and mortality) to stages of greater tolerance (Sheldon 1974).

The degree of fluctuations in the environment is site specific, but certainly some site types are more susceptible to greater fluctuations than others. Sites at the soil-atmosphere interface will fluctuate more in temperature, humidity and water availability, than sites in the soil (Dowling et al, 1971). Similarly intertidal sites may suffer greater fluctuations of waterlogging, salinity and temperature than many terrestrial sites. Sites of colonization may be more exposed to fluctuations than sites with stable vegetation cover.

Plants establishing in sites with great fluctuations may be adapted to avoid the fluctuations, or to tolerate them. Avoidance mechanisms generally facilitate seed burial, through dormancy or some hydroscopic boring mechanism (Roberts 1970, Van der Pijl 1969). Rapid rate of early growth is a common mechanism of increasing tolerance. This seedling aggressiveness is correlated with seed size as an expression of the amount and type of seed reserve material (Harper et al 1970, Ries and Everson 1973). Rapid growth in the first stage of establishment - elongation of the seedling root is considered a prerequisite for successful establishment of pastures species (Mcwilliam etal 1970). Root growth study by Hackett (1973) showed a tenfold increase in root length number and surface area over the 9 - 17 day period after germination for sorghum, though it was suggested that these rates were 5 to 8 times greater than those for barley roots.

The ability for early uptake of nutrients by roots of some species may advantage them in enabling maintenance of a high rate of root (and shoot) growth, though plants establishing under low nutrient conditions may be advantaged by independence of the seed from any external nutrient sources. (Mcwilliam et al 1970).

The seed reserves also affect the emergence of the photosynthetic tissue and hazards of seedling emergence have been discussed (Arndt 1965 a,b). The early emergence of some photosynthetic tissue is essential in maintaining early growth (Mcwilliam et al 1970) and the photosynthetic area is then of overriding importance in the growth of the emerged seedling. In epigeal germination, the cotyledon area is influenced by seed size (Harper et al 1970). Beyond this stage, (autotrophic growth) the influences of the reproductive strategies are felt less and less.

Resource Allocation in Establishment

No studies have been done specifically on resource allocation in young seedlings, though Harper (1967) Ogden (1974) and Harper and Ogden (1970) pictorially show, through weight ratios, the initial development of the root, with subsequent development of the stem and photosynthetic tissue. First shoot growth is dependent on adequate initial rooting (Dowling et al 1971) and subsequent root growth is dependent on successful shoot production. From then on, the root and shoot are inextricably interdependant - each relying on the success of the other.

III Choice of Strategy

Having discussed the features important for making comparisons of reproductive strategies, and some of the tactics involved, it would seem appropriate to consider some of those very closely related factors which would affect the selection pressures bearing on any reproductive strategy. The important factors are:

1. Stability of the environment
2. No. of available colonization sites at any one time
3. Dispersal medium
4. Life expectancy of the individual
5. Competition pressures on the adult plant
6. Predation on propagules
7. Position in sex - successional status
8. Conditions affecting seedling establishment.

3.1 Stability of environment is a feature of speculation, as evidenced by its incorporation into various hypotheses to explain latitudinal species diversity gradients; most of which have remained untested. (Pianka 1966). It can be argued however, that since propagation is so often a means of escaping or avoiding environmental pertubations (Harper et al 1970) that species growing in environmentally stable areas will be subject to less selection for frequent propagation (Pianka 1970). Environmental stability would mean, generally that without instabilities, the species survival would require only insitu replacement (plus of course the initial colonizing propagules, and sufficient propagules to account for seedling mortality); adult plants would need only to produce sufficient propagules to replace the standing population at an even rate (once per lifetime) rather than to colonize new areas, or replace individuals affected by any pertubation. This is the situation alluded to by Ashton (1969) when discussing the infrequent propagule production of rain-forest trees. Harper et al (1970) have commented on the way in which species with low Reproductive Effort tend to have stable environments.

3.2 The number of available colonization sites at any time is also affected by the stability of the environment, as any unstable conditions could create extra sites. (e.g. the creation of sites in estuaries through delta formation and general sediment accumulation (Russell 1964).

Pioneers tend to have more sites to colonize at once than climax vegetation plants, which regenerate slowly through gap-phase replacement (Watt 1947). Thus, within the rain forest, at any one time there tends to be a few small gaps - the forest floor is not a suitable site because of shading - whereas within the more dynamic estuaries areas, large areas may be colonized at one time. (Davis 1940).

3.3 The genetic effects of inefficient seed dispersal can not easily be compensated for by efficient pollen dispersal (Ashton 1969). The way in which selection takes place to minimise seed wastage has been described (Carlquist 1966; Harper et al 1970). A diminished dispersibility in endemic floras of oceanic islands, relative to related species of mainland floras results partially from many of the wind dispersed seeds of the island floras being blown out to sea and wasted. Thus the more efficient and reliable the dispersal medium, the greater the chance of establishment success, and the less the chance of wastage of reproductive energy. Generally this concept seems difficult to quantify, and there is little reference to it in the literature.

3.4 As Harper (1967) points out, if there is a significant risk concentrated in the seed and seedling stages, the annual will experience the risk every year, and the biennial only in its first year of growth. A point which is made by many authors, is the way in which annual herbs, perennial herbs and trees, allocate a progressively smaller fraction of their resources to reproductive activities (Harper et al 1970). 'K'strategists then, select for increasing life span with delayed reproduction, usually interoparity (repeated reproduction) under more constant and predictable physical conditions (Pianka 1970). Increase in structure provides more rigid stability to pertubations - as opposed to the pertubation avoidance of 'r' strategists. Any large scale catastrophy, however, may decimate the entire population of 'K' strategists, whereas 'r' strategists are likely to have seed reserves in the soil.

Shortening of life cycle may be a tactic for the diversion of more resources to reproductive activity in 'r' strategists, as there is a correlation between age of sexual maturity and length of life span (Gadgil & Solbrig 1972). However, as suggested by Goodman (1974) it may be that the high Reproductive Effort allocation causes a shortening of life cycle, rather than vice versa.

3.5 Many types of competition have been described - e.g. competitive exclusion of Gause (1934) (from Lotka 1925) and competitive coexistence of Miller (1967). Empirical evidence has been gathered by a great variety of workers using plant species. Most of the studies, however, deal with competition amongst seedlings (e.g. Harper & McNaughton 1962). The effects of competition on eventual energy allocation to reproduction are worth consideration.

Plants under high competition pressure ('k'strategists) tend to devote fewer resources to reproduction, than those under low competition. (Levins 1968, Gadgil and Solbrig 1972). The lowering of Reproductive Effort means that more available energy is used for vegetative growth to provide advantages in long term competition (Harper et al 1970). Ogden (1974) however, found a different response in Tusselago farfara, where with increased sowing density, seed production was favoured relative to vegetative production, possibly as a means of competition escape.

3.6 As pointed out by Harper et al (1970), predation exerts selection on seed size, succulence and timing of production by affecting chance of establishment success. Ashton (1969) reports the way in which predation may be exploited by some rain forest trees, through related species providing continuing food resource for predatory dispersers. However, when the propagules are not animal dispersed, predation may detract from the reproductive and colonizing ability of the species by reducing the number and viability of the propagules.

3.7 Many important tactics of the reproductive strategy of any species would tend to reflect the successional status of the species - i.e. whether it is a colonizer, an invader or a late stage climax species. Indeed, colonizing species could be expected to have a high Reproductive Effort allocation and in fact do (Abrahamson

& Gadgil 1973, Harper et al 1970), and this is generally disposed in production of large numbers of highly dispersible propagules. Production of propagules would tend to coincide with period of optimal parent growth so some dormancy would provide germination at the best time for establishment. Vegetative reproduction would be minimal (relative to sexual reproductive allocation) to permit dispersal to, and colonizing of new habitats rather than competing for a colonized one. (Gadgil & Solbrig 1972).

3.8 It is convenient to regard the abundance of a species in an area as determined by

a)availability of seed;

b)numbers of micro sites available for seed germination;

c)the ability of the species to withstand the physical and biotic features of the environment;

d)the ability of the species to withstand 'interference' from other plants.

(Harper & McNaughton 1962, Sheldon 1974). Obviously, the most intense selection exists at the stages of seed germination and seedlings establishment, and this is reflected in the reproductive strategy of the plant. Certain adaptations which advantage the establishment of the species (e.g. vivipary) may affect the disposition of the energy allocated to reproduction.

IV. Tidal Pioneers

Having reviewed some of the most important and relevant theories of reproductive strategies, it isnow useful to consider the way in which tidal pioneer vegetation types fit into this comparative picture. An overall view of mangroves will be presented, and some relevant comparisons made. However, little is known of the reproductive strategies of mangroves (Gill, in press). This then is an attempt to synthesise as much as possible of the available published information to produce an integrated picture of the reproductive strategies of mangroves.

4.1 Mangrove areas - estuaries - are generally accepted as being very dynamic (e.g. Russell 1964, Steers 1964, Redfield 1964, Savage 1972) with considerable geomorphological modification and extinction caused by wind wave and tidal action, sand shift, flooding, frost and severe storm wave action. The climatic fluctuations however, will tend to be ameliorated by the proximity of the sea. The dynamic nature of the substrate would mean that at any one time, some intertidal areas would be retrogressing, while other areas would be forming through sediment accumulation. Thus there would be some degree of turnover of colonization sites.

The retrogression and the catastrophies associated with estuarine environments will have some effect on limiting the life expectancy of any plants of the environment. Pioneer species of mangroves are perennials, but life span estimates are not available. Davies (1940) describes propagule production optimum of Rhizophora mangle in Florida during age 10 - 30 years. Gill (in press) has commented on the short juvenile period of Rhizophora, and suggests that this, and other factors, reflect the general lack of competition in the mangrove environment. A limited number of species pioneer at any one site - thus inter-specific competition would be low. It is likely that intraspecific competition is high, because, in general, mangroves tend to form very dense stands, with strong competition for light (MacNae 1968, Hutchings & Recher 1974) and, presumably for root space.

Water is a convenient dispersal medium for plants in intertidal situations. Mangrove propagules are buoyant and are dispersed by wind, wave and tidal action, and the seedlings can only become established in a limited portion of the intertidal area (limited by tidal range, energy of environment etc.) (Gill in press). It is difficult to estimate, but with the ratio of seed space in the medium to land space for colonization, it is possible that large numbers of propagules would have to be dispersed into the sea for some to be cast up in suitable sites. In this respect then, the sea could be considered effective as a disperser of genetic material over long distances, but inefficient in terms of the chances that dispersing propagules have of reaching suitable sites. Davis (1940) comments on the effectiveness of the dispersal medium, but when marked propagules were cast overboard from boats into the currents around Florida, very few were ever recovered from the shorelines.

The mangrove propagules are predated on by flying foxes (ACF Publ), crabs (Davis 1940), fish (Van der Rijl 1969), rabbits (Savage 1972), snails and birds (pers.observation) and probably some insects. The propagules would be particularly attractive to predators, through their large size and succulence. Interestingly enough, the mangroves of Brisbane (Avicennia marina particularly), which are inhabited by flying foxes in summer (Ratcliffe 1947) produce their propagules during the flying foxes' northern migration.

As an environment for seedling establishment, intertidal areas display some features to which any propagules and establishing seedlings would have to show a high degree of adaptation. Two features in particular - the regular submergence, accompanied by effects of waterlogging, substrate instability and tidal scour, and the high salinities associated with the sea water environment, necessitate some adaptations which will be discussed later. In addition, large scale and rapid fluctuations occur in many other environmental parameters (e.g. temperature) demanding extreme tolerance in establishing species.

The mangrove species being considered are essentially colonizers of new habitats, and as such could be expected to be 'r' strategists. As pioneers, however, they are unusual in the development of a perennial woody (tree) habit, characteristic of 'k' strategists. The long life span of the mangrove plants, together with the slow rate of succession to a subsequent vegetation type (see Pidgeon 1940, Walsh 1974) mean that the reproductive strategies must be a compromise in providing propagulesfor constant regeneration, and for colonization.

4.2 Mangrove - Tactics

Typically, mangroves are perennial polycarpic phanerophytes, with sexual reproduction only, and a long life cycle with maximum fecundity during age 10 - 30 years (Rhizophara mangle - Davis 1940). Guppy (1906) has mentioned a type of vegetative reproduction in what was thought to be an infertile hybrid called "Selela", but this appears to be a means of maintaining growth after partial destruction of stem or root systems, rather than a means of colonizing new areas. Other general reproductive features are well described in standard taxonomic form by such workers as Jones (1971), Hou Ding (1957), Graham (1964) and Gill and Tomlinson (1969). Little is known of the pollination biology (Gill & Tomlinson 1969) though Savage (1972) has made some general observations on Florida mangroves, Rhizophora mangle, Laguncularia racemosa and Avicennia germinans. The latter two are considered insect pollinated, but flowers of R. mangle, though possessing nectaries, are inconspicuous and inaccessible to flying animals. Autogamy has been suggested, but Savage (1972) suggests the low fertilization rates found by Gill & Tomlinson (1971) suggest some less efficient process. Van Steenis (1968) has reported the nocturnal flowers of Sonneratia spp pollinated by honeysuckers and probably bats, and also noted the nocturnal flowering of Dolichandrone spp. The border mangrove Excoecaria agalloeha is the only dioecious mangrove

Little work appears to have been done on the correlations of timing of reproductive effort with important environmental factors. McMillan (1971) has suggested that propagule production in Avicennia germinans in Texas, from December to May, is during a period of non-lethal water temperature. Clarke and Hannon (1969, 1970) have correlated establishment success of Sydney mangroves with tidal flow cycle. Low success rates of Aegiceras seedlings is attributed to their fall during a time of regular flooding.

A recompilation of data from Gill & Tomlinson (1969, 1970), Davis (1940), Savage (1972) and Golby et al (1962) shows the following correlations.

a) Flowering of Rhizophora mangle in Florida coincides with the period of most intense rain; the posture of the flowers has been suggested as a rain damage avoidance mechanism.

b) Propagule drop (R.mangle) coincides with a period of decreasing temperatures and radiation levels, which may not favour propagule growth. R. mangle propagules have been shown to initiate rooting more readily at low light levels but at higher temperatures (33°C). (A.M. Gill unpubl. data).

c) The period of propagule production of R. mangle coincides with the periods of best growth (re mid to late summer). Early growth of propagules (on parent trees) is strongly affected by climatic conditions (Gill & Tomlinson 1971)

A.M. Gill (pers.comm) suggests there exists a latitudinal gradient of flowering period for Avicennia marina, where the trees will flower all year round in equatorial regions, and most seasonally in late summer at the southern limits of the range. This would mean propagules drop during winter.

The information suggests that the propagules are produced during times of optimal parent growth, and dropped during periods of poor growth. This is fairly typical of 'r' strategists. Propagule drop may coincide with some environmental optima (e.g. temperature, salinity, flooding) - a correlation of particular importance for non-dormant propagules.

The reproductive ability of mangroves has received passing comment from various workers(e.g. Davis 1940). A few estimates of numbers of propagules and sizes have been made. The data presented in the following table (Table 1) summarizes the recorded information.

Mangrove Species	Annual Production per plant	Shape	Size	Place
<u>Rhizophora mangle</u>	300	elongate - cigar shaped	24-27 gm Fresh wt.	Florida
<u>R. stylosa</u>	-	" " "	15-20 gm dry wt	Qld.
<u>Avicennia marina</u>	300 - 350	disc	range 1-16 g.f.wt.) mean 4 gm.fresh wt.)	Qld.
<u>Laguncularia sp.</u>	few	disc	-	Florida
<u>Sonneratia sp.</u>	-	spherical	10-15 gm. dry wt.	North Australia

Table 1: Reproductive output details of some mangrove species. Data from Davis (1940), Savage (1972), Van Steenis (1968), La Rue & Muzik (1951) and Hopkins (unpubl.)

Colonizing species of mangroves might be expected to produce abundant, highly dispersible (usually small for wind dispersed) propagules, with high viability. In fact it seems that relatively few propagules are produced. I have recorded 95 - 100% 'germination' successes with Avicennia marina, though Hannon (pers comm) has reported difficulty in obtaining germination, possibly because Sydney is so close to the southern range limit of Avicennia in Australia. Mangrove propagules are comparatively large. This size is associated with adaptations which enhance establishment and dispersal. As Harper et al (1970) point out, there seems to be a correlation between large seeds and maritime habitats, as the density of the medium permits dispersal of a large unit. It has been suggested (V.J.Chapman pers. comm) that there may be some correlation between propagule size and energy at the site of establishment (and consequent soil particle size). Rhizophora sp. would be expected to establish on sandy soils, and Avicennia sp. on moresilty soils. However, since all mangrove propagulesare buoyant, they are all equally easily moved by water, so it may be more the ability to resist damage rather than size, which provides the correlation with the energy at the establishment site. Also, Walter (1971) reports Avicennia marina occuring exclusively on sandy soils.

Mangrove propagules exhibit a diversity of shapes. Apart from those mentioned in Table1, there are club-shaped, cannonball-shaped and sickle-shaped propagules; and many others (see Jones 1971). The diversity of shapes is, in part, a reflection of the range of development of vivipary. Vivipary is best developed in mangroves of the family Rhyophoraceae and the growth of the radicle gives rise to the elongate cigar-shap of the propagules. This shape may be an adaptation to provide implanting of the propagules by dropping from the parent (La Rue & Muzik 1951) though many other observers contend this happens only rarely (e.g. Davis 1940, Lawrence 1949, Van der Pijl 1969) and is unlikely to be effective for the lighter propagules (e.g. Ceriops). It is possible that some shapes could aid establishment in turbulent areas, by providing the stability necessary for growth initiation (Sheldon 1974, and earlier text). Thus, round propagules would tend to be rolled around by water movement, more than disc shaped propagules.

While mangrove propagules lack dormancy mechanisms, the need for fixation prior to germination gives rise to the 'seedling dormancy' described by McMillan (1971), where turbulence inhibits early root development in Avicennia germinans. Chapman (1966) suggests that contact with the ground provides some stimulus for rooting, thus floating propagules will not develop roots. The longevity of mangrove propagules, in consonance with the dispersal medium (Vander Pyl 1969) is extreme; propagules of Rhizophora being viable after 12 months, and of Avicennia and Luguncularia, 4 months (Davis 1940). The lack of dormancy, and the longevity make the propagules available for immediate establishment under appropriate conditions, over a long time period.

Many species of mangroves exhibit vivipary. The attention this feature has attracted has given rise to speculation as to the purpose, adaptive value and mechanism of this embryo paracitism. Vivipary seems likely to fulfil a number of roles, a suggestion borne out by the variations or degree and method of development amongst plants growing in the same environment. Some possible roles are providing buoyancy, implanting, salinity avoidance, promoting establishment, and waterlogging avoidance. An important result of vivipary is the enormously increased propagule size and consequent "energy drain" effect on the parent plant, as alluded to in the flow diagram of Gill & Tomlinson (1971). This obviously will affect the disposition of the overall energy allocation.

Carey and Fraser (1932) consider vivipary an adaptation to the growth of seedlings in waterlogged conditions, as the embryos of both Aegiceras and Avicennia are intolerant to waterlogging (Carey, unpubl, through Clarke and Hannon 1970). This may mean vivipary is an avoidance mechanism, providing embryo bouyancy, or a tolerance mechanism, where tolerance of the young plant to waterlogging is increased through the increased size and age resulting from vivipary. Vivipary provides buoyancy in Rhizophora (Gill, in press) as the fruits alone are non-buoyant. The Aerenchyma development in Avicennia propagules (Chapman 1966) is also associated with some viviparous development.

Joshe (1933) suggests that vivipary provides a mechanism for avoidance of germination under saline conditions. This is not well supported by experimental evidence. Genkel (1962) suggests that the viviparous species of mangroves utilize seedlings for exclusion of salt, as he found the chloride ion content of seedlings increased in proportion to size, and the seedlings were adapted to the high salt concentration of the soils before dropping. This was shown true for Rhizophora mangle by Lotschert (1968). Excess chloride ions in the soil delayed seedling drop, and Genkel (1962) concluded that vivipary is an adaptation of the parent to the salt regime of tidal areas.

Conversely, Chapman (1944) reports a salt exclusion mechanism operating in Avicennia nitida, and when seedlings fell from the tree there was an immediate uptake of salt, accompanied by a sudden reduction in respiration rate. Successful colonization by A. nitida was therefore related to the capacity of the seedlings to respond to sudden changes in internal salt content, but this is not necessary in seedlings of Rhizophora.

Walter (1971) discusses the low cell sap concentrations, and low chloride contents of the viviparous mangroves, and the probable glandular transfer mediation by cells located in the cotyledons and surrounding tissue. Walter (1971) also comments on the low chloride levels in seedling tissue of Avicennia, though he considers this species to be non-viviparous. McMillan (1971) considers that since Avicennia displays hypocotyl emergence over a large range of salinities, vivipary does not contribute to salinity avoidance.

Under certain circumstances, the elongate propagules of Rhizophora dropping from the parent tree, may implant in the soft sediment and become established (La Rue & Muzik 1951) though this may happen rarely overall (Lawrence 1949, Davis 1940, Vander Pijl 1969). Although the radicle elongation may enhance this implanting it seems of dubious advantage, as the seedlings would then be competing with the parent, and colonization would not be achieved.

Chances of seedling establishment may be improved through vivipary. The advanced development of the seedling may improve early growth rates (McMillan 1971) but there seems little evidence of this. Root development from the hypocotyl of Rhizophora may take two weeks under optimal conditions (Gill, in press). Ability to establish under pioneering conditions (e.g. on new mud banks) is not necessarily imparted through vivipary , as a foremost pioneer, Sonneratia is non-viviparous. (Joshi, 1933).

Units of dispersal in mangroves vary from fruit to seedlings. Buoyancy is an adaptation of all these units, and dispersal is by water only. However the buoyancy mechanisms differ from species to species. Propagules of Avicennia possess considerable aerenchyma (Chapman 1944) and the capacity for anaerobioses while floating (Chapman 1966). Seeds of Dolichandrone are corky (Van Steen 1968) and those of Nypa have the "coconut like" mesocarp development (Jones 1971). Vivipary may provide buoyancy in mangroves of the family Rhizophoraceae through development of the hypocotyl. (earlier text and Gill, in press). Strand plants and salt marsh plants also have buoyant propagules and various experiments have been carried out to determine floating periods (see Guppy 1906, Chapman 1960). In much the same way as any buoyant object floating in the sea may eventually be cast up or stranded on a shore, the propagules of these tidal pioneers are dispersed to the habitats for which they are well adapted to establish - hence the correlation described by Guppy (1906) between dispersal mechanism and "station".

The "seedling dormancy" described by McMillan (1971) and commented on by many other authors (Chapman 1966, Guppy 1906, Davies 1940) illustrates the requirement of mangrove propagules for some stability prior to early growth for establishment. Other requirements for initation of early growth are not known, though work by Gill (unpublished data) suggests that the appearance of first roots through the hypocotyl sheath of Rhizophora is promoted by darkness, and temperatures of around 33^{o}C. The germination of seeds of salt/marsh species is associated with low salinities at times of rain (Chapman 1960) but no similar correlation is known for mangroves.

The ranges of some environmental features, under which early seedling growth will take place have been described for some mangroves including submergence (0-5 m depth) salinity (0 - 200% sea water) and temperature (0 - 40°C) (Clarke and Hannon 1970, McMillan 1971). In addition, the environmental conditions under which seedlings are naturally establishing have been described (e.g. light EH, pH, nutrients, dissolved O_2, salinity, grazing, inundation - MacNae 1966, McNae & Kalk 1962, Barnes & Green 1972, Walsh 1972) and these have been elegantly reviewed by Walsh (1974). Experiments on mangrove seedlings show that optimal growth may occur under conditions of low salinity, and moderately high temperatures (Clarke & Hannon 1970, Connor 1969, McMillan 1971, Paterson 1966, Stern & Voigt 1959) though results are not entirely consistent. The differences between physiological and ecological optima is described by Paterson (1966) and is suggested as resulting from competition. However, the success of the plants in the field indicates they are well adapted to the prevailing environmental conditions.

Because of the unusual environmental conditions under which mangroves can establish, it seems likely that seedlings possess some adaptations which make establishment possible. Some features of respiration, gas and ion transport, salt exclusion and excretion, and succulence have been described and studied in adult plants, but no work appears to have been done on seedlings. Certainly some mechanisms are different. For example, pneumato phores develop in <u>Avicennia</u> only after several years growth (Savage 1972). The self erecting habit of <u>Rhizophora</u> (Lawrence 1949) and the shunting of oxygen from the leaves down to the roots in seedlings (Gill, in press) may be adaptations to growth under waterlogged conditions. The other important prerequisite of colonizing seedlings is to be able to secure the substrate and this may be accomplished through adaptations in root architecture, as displayed in photographs by Savage (1972). Early root growth is not rapid in <u>Rhizophora</u> (Gill, in press) or <u>Avicennia</u> (pers. observation) although the juvenile period may be short. Thus, although adaptations which enhance establishment of mangroves are not well tabulated, the success of the seedlings indicates that they are well suited to their environment. Davis (1940) reports that in bare areas, seedling survival is almost 100% in the first year, and thinning takes place in subsequent years.

No studies have determined energy allocation in mangroves. Some work has been done on estimating biomass and productivity, (Golby et al 1962, Miller 1972, Heald 1971) but no quantitative estimate of the importance of propagules is made. Heald (1971) observed from litterfall, that flowers were the least important component of annual production after leaves, stipules and twigs. Gill & Tomlinson (1971) have indicated a certain partitioning of resources with respect to the shoots of *Rhizophora mangle* but no quantitative data are presented. However, the development of the woody habit would suggest low allocation of energy to reproduction. This tree habit is associated with slow growth rates (Noakes 1955), a production to respiration ratio (P/R) close to unity (Golby et al 1962) and slow rates of succession (Davis 1949, Chapman 1968). It is postulated that, during succession the value of the ratio P/R will tend to unity, which value, indicating thermodynamic equalibrium, would signify climax.

4.3 Pianka (1970) describes the 'r'-'K' continuum, and the organism characteristics of the two extremes. It is appropriate to consider the relative positions on this continuum of some generalised vegetation types. Colonizing species tend to be 'r'selected - producing large numbers of highly disperible (e.g. wind borne) seeds. The low competition levels at new sites minimises the requirements for seed reserves, so they tend to be small and light. Generation time tends to be short (i.e. plants are annuals) and so growth is rapid. Propagule production would be at a time of good parent growth, and some dormancy mechanism would provide germination at an optimal time. Allocation to reproductive effort would be high, and vegetative growth allocation low. Unpredictable and variable (often catastrophic) environmental conditions promote 'r' selection.

Towards the other extreme, 'k' strategists produce fewer propagules in repeated reproductions. Reproduction is delayed, and life span is long. Propagules are large, to promote seedling aggressiveness. The large propagules tend to be animal dispersed, being too heavy for wind dispersal and dispersary animals would be associated with this vegetation for other reasons. Vegetative competition is intense, and allocation to vegetative growth is high, reproductive allocation low. 'K' strategists are associated with more constant, predictable environments, particularly as frequent pertubations and delayed reproductionare not always compatible. Late succession vegetation types are usually 'K' selected.

Mangroves are perennial woody plants, regularly reproducing after a long juvenile period. Production of propagules coincides with the time of best parent growth, but may favour establishment also. Propagule numbers are low, but each propagule is large. The conditions of establishment of the seedlings are extreme and the dispersal medium (water) is inefficient. The unlikelihood of establishment is overcome by the production of highly viable propagules with large energy reserves, longevity and no dormancy (and hence readily available for establishment over a long period) and high degree of tolerance to environmental extremes. Increased propagule size, enhancing establishment, is not selected against during dispersal. Reproductive allocation is low.

Two features of mangroves - the reproductive strategies and the ecological status - present a paradox. Mangroves are a first seral stage of a primary succession, and yet'K' strategists. There are two possible evolutionary pathways which could explain this dichotomy, and the degree of apparent parallel evolution. Either the woody habit evolved in non-woody halophytes living in estuaries, or woody plants migrated to estuarine areas from inland areas (possibly to escape competition) and evolved salinity tolerance gradually.

It is postulated that selection in estuarine areas was for woody habit, and that the other correlates of 'K' selection were assumed naturally. The development of the woody habit is essential for survival in areas subjected to irregular but frequent, large scale pertubations, in that it provides rigid stability, preventing possible total extinction, and permitting further succession.

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