

# Regeneration of complex notophyll vine forest (humid subtropical rainforest) in eastern Australia – a review

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## Abstract

Summerbell, Gillian (Hornsby Physiotherapy Centre, P.O. Box 1519, Hornsby, NSW, Australia 2077) 1991. *Regeneration of complex notophyll vine forest (humid subtropical rainforest) in eastern Australia. – a review* *Cunninghamia* 2(3): 391–410. Complex notophyll vine forest (CNVF) has been perceived to be fragile and vulnerable to physical site changes and disturbances. High species richness, evenness of distribution and mixing of species provide diverse plant/animal interactions, balanced herbivore activity and a relatively predictable and constant environment. Regeneration of CNVF occurs in small canopy gaps. Environmental heterogeneity and partitioning of resources allows establishment of mature-phase species. Regeneration management aims at community stability, richness and diversity through manipulating successional pathways and re-establishing small canopy gaps. Each area must be assessed before regeneration techniques are implemented. CNVF areas in eastern Australia require active management for immediate and long-term survival. Few are large enough to be self-maintaining with a full complement of species. Each site should be managed in a regional context, to provide resources for mobile species and to conserve rare, ancient and endangered species. Any logging needs to allow for sustained species richness, diversity and highly interwoven plant/animal interactions. Selective logging based on regrowth of the overstorey or recovery of basal areas to levels similar to unlogged forests, completely ignores the composition of the forest and requirements for the community to reach full maturity. Public education, financial incentives, further research, funding aligned with enacted legislation are all necessary for effective management and conservation.

## Introduction

Some 80,000 square kilometres of rainforest were present in Australia before European settlement (Webb & Tracey 1981). Today about one quarter remains.

These rainforests have great biological significance. In Queensland for example thirteen of the nineteen families of primitive angiosperms which evolved on the Gondwana continent some 120 million years ago, are present today (Vandenbeld 1988). The concentration of primitive families in the Australasian region is the greatest in the world (Webb & Tracey 1981). Two-thirds of the plant and animal species found in our rainforests are endemic to Australia (Bell 1981).

Increasing areas of rainforest have been afforded protection under World Heritage status. However, rainforests still face significant natural and man-made threats. Natural ones include fire, disease, landslides and cyclones. Human-induced threats result from tourism, recreational vehicles, introduction of exotic species, clearing for agriculture and commercial resource use (southern Queensland, Victoria and Tasmania). Active management is constrained by lack of financial resources and limited knowledge of rainforest ecology.

## Complex notophyll vine forest in Australia

There are four main types of rainforest: tropical, subtropical, warm temperate and cool temperate (Webb & Tracey 1981).

Complex notophyll vine forest (CNVF), the richest form and most complex type of subtropical rainforest (Webb & Tracey 1981), is classified as subtropical vine forest, raingreen and quasi-evergreen in regions of high and seasonal summer rainfall and eutrophic soil status (Webb 1968b 1978, and Hitchcock 1976). It occurs in patches from Mossman in north Queensland to the Illawarra region in NSW, with the major part in the southern Queensland – northern NSW region. The distribution is determined by climate, topography, microclimate, soil, fire and competition. Rainfall is above 1300 mm, and soils tend to be well drained and basalt enriched (Floyd 1989). CNVF may be species rich. A hectare can contain more than 100 different trees, 60 species of vines, 70 ferns and a host of other plant forms (Churchett 1982). Floristic composition may depend not only on the physical environmental factors, but also on the distribution of relict and narrowly endemic species (Barlow & Hyland 1988).

## Review of regeneration processes

### Disturbance

The forest canopy is a mosaic of gaps, patches of juvenile trees in former gaps and mature forest (Whitmore 1986). The effect of different types of disturbance on rainforest will depend on the disturbance regime within which it has evolved. Disturbance which is unusual to a particular forest type will have a far greater impact than that which falls within the usual disturbance regime (Hopkins 1981).

#### Large-scale disturbance

This may be due to natural or man-made effects; cyclones, landslips, volcanic activity, tectonic plate movement, flooding, wildfires and logging, especially clear-felling regimes. The size of the disturbance can be from several hectares to several hundred hectares or up to many square kilometres (Webb 1977).

#### Medium-scale disturbance

This type of disturbance covers an area from 5 square metres to approximately 10 hectares (Webb 1977). Logging, roadways through rainforest, windthrows, local eddies and downdraughts associated with cyclones, local landslips and small fires may cause this scale of disturbance.

#### Small-scale disturbance or small gaps

This is usually the result of falling branches of a single tree or the death of a single tree.

### Regeneration and succession

Succession is the process through which regeneration is achieved. Succession expresses the differences in colonising ability, growth and survival of organisms adapted to a particular set of conditions on an environmental gradient (Smith 1980). The replacement of one of several species or groups of species by others results from interspecific competition and the interaction of herbivores, predators and disease.

The nature of succession in a given area will depend on seed availability, conditions for germination and liberation of suppressed saplings in relation to fortuitous forma-

tion of canopy gaps, changes in microclimate and predation (Webb & Tracey 1981). Hopkins et al. (1977) divided the species of humid subtropical rainforest into four major groups, describing their survival strategies and their role in the successional process.

#### **Group A, pioneer species**

Short-lived, shade tolerant perennials that grow up to 8 metres high. They begin the regeneration process in areas of medium to large disturbance. Examples are *Rubus rosifolius* and the naturalised *Solanum mauritianum*.

#### **Group B or early secondary species**

With environmental modification these predominate and form a closed canopy. They are fast growing perennial trees (10–25 metres high) living for 15–50 years. Examples are *Euodia micrococca* and *Alphitonia excelsa*.

#### **Group C, late secondary and Group D, mature phase species**

With a canopy present these are more favoured by the altered conditions. Examples of Group C species are *Brachychiton acerifolium* and *Diploglottis*, while examples of D Group species are *Sloanea woollsii* and *Agyrodendron trifoliolatum*. By 40–50 years of regrowth, almost all the vascular species of the adjacent primary forest are represented in the under-storey. It may take another 40–50 years before the mature or Group D species have reached the fruiting stage. Secondary forests are unlikely to become reproductively independent of the adjacent primary forests until they are approximately 100 years old. This four-stage pathway of regeneration is called the 'facilitation' model (see Figure 1).

The 'tolerance' model allows for any species present before disturbance to be able to colonise the area after the disturbance. This model is commonly used to describe succession in small gaps. Opportunistic species often exploit the changed environment first, but not in every case in this model. They do not provide for more advantageous conditions for later species. Later species will only grow if they can tolerate lesser levels of resources. As in the facilitation model, the successional end point is reached when the most shade tolerant species occupy and retain the site (Smith 1980).

Delayed or arrested succession is described by the 'inhibition' model. Here, early colonists prevent the invasion of subsequent colonists or suppress growth of already existing species. This is often the case when trees and shrubs have few seeds or propagules in the soil (Hopkins et al. 1977). Succession may proceed at a later date if the dominant pioneer species is destroyed or damaged by herbivores, fires, pathogens or herbicides.

### **Outcomes of the successional process**

#### **Restoration of the original community**

Following disturbance, secondary succession eventually restores the original community. Webb & Tracey (1981) emphasise that the disturbance must not be too extensive or too frequently repeated, and disturbed areas should be able to maintain patchiness in space and variety of serial stages in time to allow for the total display of all species available. Adequate seed sources of the original community must remain available, either stored in the soil or dispersed from adjacent living plants.

### Deflected community

This occurs where partial intermittent destruction is accompanied by environmental changes persistently unfavourable for the return of the original community (Webb & Tracey 1981). Reasons for the inability of the community to regain its previous composition are discussed in the next section on breakdowns in the successional process.

### Hybrid community

In hybrid communities destruction is more complete and sustained, so that some environmental changes become permanently unfavourable and seed sources become more limited. The disturbed area is colonised by pioneer species. Gradually with slow changes in local climatic and soil conditions, the original community becomes fragmentary and relict (Webb & Tracey 1981).

### New community

Complete destruction of the original community and its seed sources takes place and there are many changes in the physical environment. The site is colonised by a new community depending on the proximity of seed sources of other community types and few of the original species are able to adapt and survive in competition with them.

The process of succession stops (unless delayed or arrested) when the climax stage is reached. This is the point where the community is stable and self-replicating and barring disturbances will persist indefinitely (Smith 1980). Community restoration can take up to 800 years after a widespread disturbance (Hopkins et al. 1977).

## Breakdowns in the successional process

Deflected or arrested succession can result from a variety of factors (Hopkins 1981). Physical site factors such as soil compaction, soil porosity, nutritional status of soils, water table levels, can be changed by a disturbance. The pathway of succession may not proceed along facilitation or tolerance lines due to altered conditions.

Biological site factors can modify the secondary successional process in a number of ways:

- (a) Lack of later phase species in the seed bank can arrest the process. A good example is the 'Big Scrub' in northern NSW, formerly a vast area of lowland subtropical rainforest extensively cleared for agriculture in the early 1900s. The forest regeneration on many of the abandoned areas now appears to be arrested at an early secondary stage (Hopkins 1981). A disturbance can expose the soil seed bank to high surface temperatures. Experiments by Hopkins & Graham (1984) on heated seeds, showed that at 60°C (a temperature reached in the summer months after about one hour's direct exposure to sunlight), half the seeds were destroyed. At 100°C, all were destroyed.
- (b) Succession can be deflected or arrested if an alien species such as *Lantana camara* prevents the establishment of late phase species (see Figure 2).
- (c) Geographical barriers can arrest the successional process. Many CNVF species survive in isolated pockets and largely depend on local seed availability. A major disturbance to one of these isolates is likely to arrest succession if viable seed is not available in the region (Hopkins 1981).

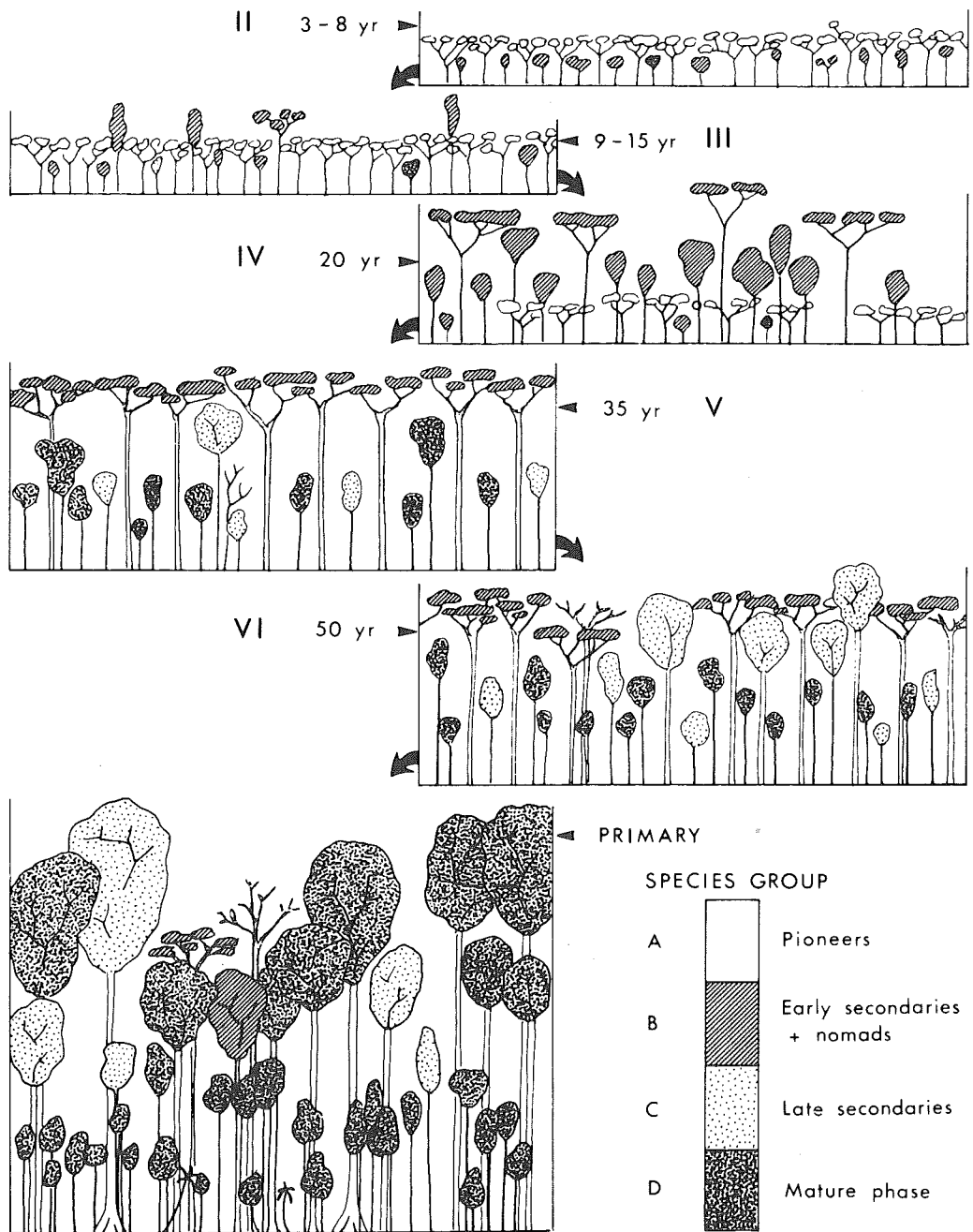


Figure 1. Schematic representation of reconstructive secondary succession in CNVF (from Hopkins 1981) (Equivalent to the Facilitation Model).

(d) Many human activities maintain the continuing occupation of sites by alien or early secondary species. Permanent openings of the forest canopy for roads, tracks and clearings allow these opportunists to occupy higher light areas. Their growth and production of profuse long-lived seeds enable them to quickly spread into other edge areas (Hopkins et al. 1977).

(e) Frequent disturbances in a community can permanently alter the species' composition diversity and hence stability of that system. Cyclone scrubs in the tropical lowland rainforests of northern Queensland are the result of frequent cyclones preventing the re-establishment of mature rainforest (Webb 1958).

### Gap-phase dynamics — the gap environment

Gap creation provides an injection of new life into the rainforest community. The characteristics of the mature (D-type) rainforest species appear to have developed from gap creation. Stocker (1983) has developed a gap regeneration theory which states that in most tropical forests the component species must have evolved in relatively small gaps created by canopy disturbance. Large gaps would have been relatively rare or so infrequent that they would have little or no evolutionary significance.

Gap-phase dynamics affect many different forest processes. These include: forest structure, spatial pattern and life history features of germination, growth, time of flowering, seed dispersers and predators, herbivores, pollinators and pathogens (Bazzaz 1986.) Levels of light in the gap area have a major role in partitioning gap resources. Each species is able to achieve optimal growth in different parts of the gap or gaps of different size (Stocker 1988).

According to the size of the gap, various gap filling mechanisms contribute in gap creation. In *very small* gaps there is sapling growth and increased growth of branches of adjacent trees. In *small* gaps advanced regeneration of suppressed medium seedlings, and resprouting. In *large* gaps there is regeneration from seed bank present in the soil. Most seeds are located in the subsoil layers.

### Reproduction

Four processes interact to generate the seed 'shadow' that finally produces a seedling 'shadow', namely, seed production, predation, dispersal and dormancy (Janzen & Vazquez-Yanes 1986). There is great variation in these mechanisms from pioneer to mature phase species.

#### Seed production

Seed production by A and B-type species occurs regularly. Large numbers of well dispersed seeds have long viability and comprise the majority of seeds in the seed bank just below the soil surface.

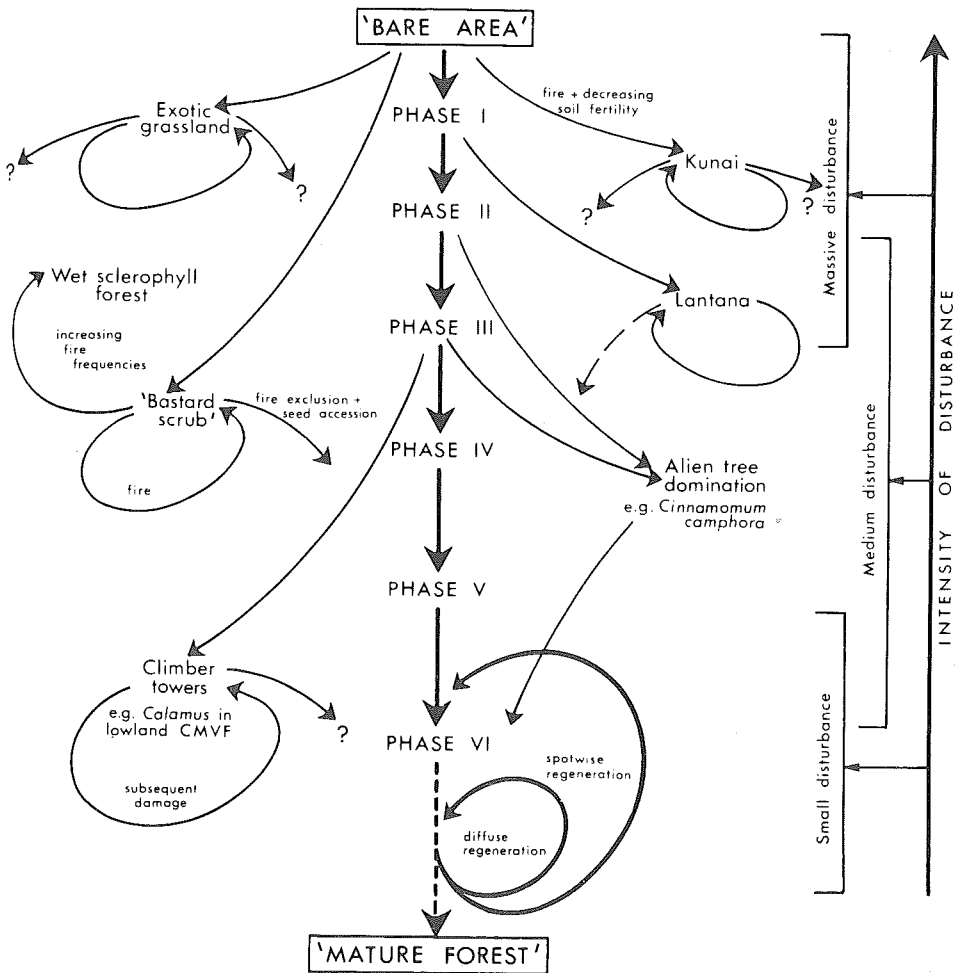
C or late secondary species fruit most years with seed viability mostly limited to several months, although some species can survive up to two years (Hopkins & Graham 1984). Mature phase or D-type species are characterised by infrequent gregarious flowerings which produce massive quantities of fruit (Hopkins 1975). Seeds are of a short life span, surviving from several weeks to several months. The time interval between these large fruitings is usually greater than three years. In the intervening periods, many individuals sporadically produce smaller quantities of fruit. Such gregarious flowering and fruiting appears to be general amongst rainforest tree species (Wood 1956, Ashton 1969, Medway 1972, in Hopkins 1975). During periods of gregarious fruiting, seed predation can be high.

The soil seed bank, according to Janzen & Vazquez-Yanes (1986), contains representatives of only a tiny fraction of the species of trees in tropical and subtropical forests. The seeds are in haphazard proportions having little to do with any forest structure. Hence dispersal agents are essential links in the establishment of seed shadows.

**Seed dispersal**

Various agents act as seed dispersers. These include wind, water, gravity, birds, bats and other small mammals. Seed dispersal is an essential process in maintaining forest diversity and regenerating disturbed areas to the original forest structure. Seed dispersal also provides new inputs of genetic material into isolated remnant areas.

The main dispersal agents in subtropical areas are wind, birds and gravity (sometimes assisted by mammals). Water and bats have lesser roles but in particular areas, can be important contributors (Hopkins 1975).



**Figure 2.** Schematic representation of secondary succession pathway and natural vegetation in rainforest showing some of the variations that can occur in relation to intensity of disturbance (from Hopkins 1981).

Wind-dispersed species are A and B-type species, taller canopy (D-type) species, vines, epiphytes, orchids and ferns. These species have a distinct advantage in medium-large gaps where animal dispersal is diminished.

Birds are attracted to certain colours of fruit. Blue-black and black-red are favoured over red (Floyd 1976). Fruit-eating birds can be divided into opportunists and specialists. Fruits devoured by opportunists are usually small (5–10 mm), many-seeded, often showy and usually juicy. Large fruits attract specialists, and contain few or single seeds. These fruits typify pioneer and climax species respectively (Whitmore 1983). This situation has implications for isolated communities where specialist migratory birds are needed for seed dispersal. Seed dispersal by animals often involves enrichment of the seed by the animal to increase its ability to germinate and also leaching of germination inhibitors.

### Seed predation

Seed predation shows no particular pattern. It can vary markedly from year to year, tree to tree and habitat to habitat. Different species have different susceptibilities to different seed predators (Janzen & Vazquez-Yanes 1986). Mammals and insects are the main seed predators in humid subtropical rainforest. Evidence does show that animal predation directly affects the survival and pattern of distribution of seedlings of particular rainforest species (Janzen 1972, Wilson & Janzen 1972, in Hopkins 1975). Hopkins (1975) feels there is little doubt that damage by plant predators and parasites, whether animal, fungi, bacterial or viral, can be a controlling factor affecting the establishment and survival of plants.

### Seed dormancy and germination

Seeds of subtropical plants have variable dormancy periods. Germination may occur quickly when the seed is moistened or delayed until the hard seed coat is broken down. Bird ingestion and excretion can accelerate the germination process by several months, as in the case of *Cryptocarya glaucescens* (three months if ingested; six months if not). Many of the short-lived fast growing early secondary species have hard seed coats, which remain buried in the soil for many years (Floyd 1976).

In subtropical rainforests with a definite dry season, seeds may remain dormant if the fruits mature in the dry season. Once the rainy season begins, germination commences (Janzen & Vazquez-Yanes 1986). Stocker (1988) examined the role between fruiting, seed predation and germination in shade-tolerant species. He felt that with the favourable establishment environment for shade-tolerant species and the effects of predation on large seeds of this group, immediate rather than delayed germination has evolved.

### Role of pollinators in flowering and fruiting

Plants with a large flower crop tend to be pollinated by large unspecialised pollinators, for example, birds, bats and moths, and tend to flower in synchrony over a short period (Pomeroy & Service 1986). Bawa & Krugman (1986) have suggested that pollinators probably switch from one species to another as the floral resources of one species decline and that of the other increase.

An alternative strategy is to produce a few flowers at a time over a long period, for pollination by specific animal species. These pollinators tend to be birds, butterflies, large moths or large bees (Pomeroy & Service 1986).

Loss of food resources for pollinators or removal of that pollinator from the community may influence pollinator guilds and consequently plant guilds that depend upon



these pollinators (Bawa & Krugman 1986). Management strategies require an understanding of pollination modes and the extent to which various plant species are dependent upon particular pollinators. Unfortunately, very little is known about pollination biology in tropical or subtropical forests.

### **Coppicing**

At a subtropical rainforest site in Queensland, 74 of the 82 regenerating species coppiced after felling and burning (Stocker 1981, in Whitmore 1983). The growth of these coppiced species was slower than for trees regenerating from seed. Webb et al. (1972) observed that plants with coppice growth were taller than plants regenerating from seeds at Mount Glorious in southern Queensland and concluded that coppicing conferred a considerable competitive advantage to a plant.

In Lamington National Park in an area regenerating after storm damage, 35 of the 44 tree species present were suckering or sprouting (Olsen & Lamb 1988). Turner (1976) noticed coppicing in some species on steep slopes at Barrington Tops, NSW. He felt the coppicing pattern suggested an element of genetic control, that would enable the better adaptive traits of tree species in the particular environment to be retained.

## **Rainforest fauna**

### **Birds**

Some 90 bird species regularly breed within the rainforests of NSW but only 38 depend on rainforest for the majority of their food or breeding requirements (Morris 1976). Birds may depend on patches of rainforest scattered over thousands of kilometres. Crome (1975) found seven species of fruit pigeons in northern Queensland were nomadic and migratory, with their movements related to tree species and the quantities of fruit available. Competition between species was minimised by this utilisation of different food plants.

Kikkawa (1968) studied the ecological association of bird species in northern NSW and northern Queensland. In northern NSW, the subtropical rainforest areas supported fewer bird species than the dry habitats and he concluded that the avian fauna was impoverished and did not form a unique association with rainforest. By comparison, the rainforests of northern Queensland included a high proportion of 'regular species', where more than half the species utilised this habitat exclusively. Kikkawa (1968) feels that successful colonisation of subtropical rainforest in northern NSW must have been largely limited to those species that had developed or retained adaptations favourable to wet formations in general. Various authors (Gentilli 1949; Keast 1961 and Brereton & Kikkawa 1963, in Kikkawa 1968) have suggested that the poor faunal diversity in rainforest may be explained in terms of past climate and the patterns of speciation and colonisation on the Australian continent.

### **Mammals**

There are no mammals (excluding bats) which exclusively inhabit the CNVF areas of south-eastern Australia. The 41 species of mammals which have been recorded in tropical and sub-tropical areas are only forest generalists and ecotone species (Winter 1988). Absence of specialists is felt to be due to refugia shrinking some 25,000 to 15,000 years ago below the critical size required to maintain a specialist community. Bats contribute about one quarter of the total number of mammal species using northern NSW rainforests. Thirty-two species have been recorded, some of which exclusively depend on the rainforest environment (Adam 1987).

### **Invertebrates**

Invertebrates act as seed dispersers, seed predators and pollination vectors. Compared with the vertebrates, many of the rainforest invertebrates are highly specialised in their habitat requirements, being restricted to particular host plant species and in many cases having specific hosts for different stages in their life history (Adam 1987).

Invertebrates as herbivores consume between 10 and 20 per cent of plant material. Young leaves and seedlings appear especially vulnerable (Bazzaz 1986). Injured leaves have been shown to lose more nutrients from leaching than uninjured leaves (Turkey 1970, in Golley 1983). These injured leaves decompose earlier, providing nutrients for special plant requirements such as fruit formation (Golley 1983). Insects, by their defecation systems and short life cycles, also provide a quick release of nutrients for plant usage. Insects can have detrimental effects. Overgrazing can upset the successional process by allowing early successional species to persist under high light levels. Insects cause mortality by providing entry for pathogens and changes in tree structure can arise from loss of plant support tissue (Bazzaz 1986).

Herbivory can vary from site to site due to subtle changes in environmental factors or plant composition. Seasonal variation can be marked as a result of seasonal effects on an invertebrates life cycle or seasonal changes in levels of food supplies (Lowman 1982). Some insects require resources from both mature forests and successional habitats. For example, some aroids and orchids are pollinated by specialist species of euglossine bees, but the bees often require early successional plant species for larval resources (Frankel & Soule 1981). Many tropical pollinators have low population densities, which are susceptible to area effects including the stochastic, demographic and genetic events which are characteristic of small populations (Frankel & Soule 1981). Any reduction in area is likely to result in the extinction of some pollinators and loss of essential catalysts for fertilisation of certain plant species.

### **Studies on regeneration of humid subtropical rainforest**

Studies of the recovery of humid sub-tropical rainforest (CNVF) in Australia have largely been based in the Border Ranges and Lamington national parks area. As this is the largest remaining area of CNVF, one would expect recovery ability to be higher than that of small isolated remnants. Observations at O'Reillys in Lamington National Park on an area cleared and burnt have shown CNVF can recover from a severe man-made disturbance, under certain conditions. Hopkins et al. (1977) describe these conditions as the time since the original clearing, the completeness of the clearing, the effectiveness of the burn and the proximity and type of adjacent forest. Succession started with A-type species and followed along the lines of the facilitation pathway. The developing forest in 1977 was becoming increasingly similar to the adjacent primary forest.

Olsen & Lamb (1988) monitored the recovery of an area of forest near O'Reillys after a heavy storm in September 1983 destroyed the forest canopy, creating a large gap. Some isolated trees remained. A year later, early secondary species were growing along with vines, exotic weed species and shrubs. Two years later, primary forest species were regenerating. Thirty-five of 44 species originally present were growing by sprouting. Possible explanations suggested for the quick regrowth of primary forest species after this disturbance were that:

- (a) Propagules of some of the primary forest species were shed from residential trees within the gap, although little seed would have been possible due to substantial crown damage.
- (b) Residual trees may have acted as important focal points for fruit-eating birds, accelerating the arrival of new tree seed.

(c) In microclimatic terms a large gap may really be the equivalent of a 'small gap' in a tropical rainforest because of the lower solar angle. In a gap with residual trees, the overall effect of these factors may discriminate against some secondary species. Regeneration in this situation has proceeded along the tolerance pathway.

Predictions by modelling of recovery times for CNVF with different logging regimes have been made in the Wiangaree State Forest (now part of the Border Ranges National Park), an area of 14,000 hectares (Shugart et al. 1980; Horne & Gwalter 1982). Horne & Gwalter (1982) estimated the time of recovery of the overstorey after full utilisation logging — i.e. 70–80 per cent removal of the basal area of overstorey — to be longer than 200 years. With more selective logging, namely 33 per cent removal of the basal area overstorey and 50 per cent canopy retention method, recovery time would be approximately 30–60 years. Presumably, regeneration would take the pathway of the facilitation model with full utilisation logging and the tolerance pathway with selective practices.

The model of Shugart et al. (1980) was used to assess the consequences of the harvest of commercial species from CNVF both in terms of single harvest or a repeated harvest. The model predicted increases in the basal area of a number of species would peak 30–50 years following logging and indicated that CNVF should have the regenerative capacity to sustain a conservative logging program on a 30-year cutting cycle.

Predictions in both these studies have implications for the reproductive biology of primary forest species. If D-type species do not produce fruit until 40–50 years old and are not reproductively independent of adjacent primary forests until approximately 100 years old (Baur 1964, Hopkins et al. 1977), how could these forests continue to regenerate to the original forest composition if they are logged on a 30-year cycle? Over several cycles there would have to be a shift in species composition to the early and late secondary species, altering the stability of the forest, animal-plant interactions and threatening the survival of some species.

Modelling predictions by Horne & Gwalter (1982) tend to favour increases of group C species in their occupation of the canopy over group D species. *Doryphora sassafras* increases from 0–10 per cent and *Cinnamomum oliveri* from 2–10 per cent of the canopy, while *Endiandra sieberi* decreases from 31–18 per cent. The authors have stated that logging may cause some alteration in the relative frequencies of the major overstorey species due to their different growth rates. Hence, after several cutting cycles, few adult group D species would be present.

## Managements of isolates

### Problems of remnants

Remnants or isolates can be classified into two broad types, artificial and natural, depending on whether the isolation was produced quickly by humans or developed naturally in response to longer term changes in climatic and geomorphological processes that usually involve fire. One would expect the abilities of remnants to adapt and survive the various changes brought about by development would be different. The survival of natural remnants tends to suggest that they have adapted to their isolation (Webb et al. 1985).

Remnants face greater threats to the maintenance of community stability than larger reserves. Remnants have a larger ratio of boundary to core area compared with larger

reserves. Boundary areas serve as entry points for more competitive exotic species which can initiate interference patterns and inhibit successional pathways. A remnant's microclimate is influenced by the surrounding vegetation. It is likely to be different to a larger reserve with lower humidity levels and higher temperatures.

Current knowledge of the boundary dynamics between rainforest and other vegetation types is extremely limited. A large number of remnants are adjacent to eucalypt forests. Many of the early successional gap opportunists have characteristics which can successfully colonise these margins. Fire is one disturbance where these colonisers must have special adaptation as it is an uncommon event in rainforests. Regular fires in these marginal areas cause species impoverishment and gradual contraction of the isolate (Webb et al. 1985).

Remnants generally need an incoming supply of seeds for genetic variety, species maintenance and continuing community viability. The size of the remnant, the distance of the remnant from the nearest seed sources and the boundaries across which seed dispersers must travel will determine seed dispersal processes. Seed dispersal has an important role in gap regeneration processes. Gap regeneration allows a community to maintain its species richness and diversity. Any interference to these processes by exotic species and human activities, namely a decrease in isolate size or increase in gap size and gap turnover rates, will favour the regeneration of early successional species over mature phase species (Webb et al. 1985). A loss of certain mature phase species will set in motion loss of animal species, increased herbivory and susceptibility to disease. Raven (1976, in Frankel & Soule 1981) has emphasised the high level of specialisation and interdependence of tropical species and predicts that the loss of a plant species can trigger the demise of between 10 and 30 animal species. Frankel & Soule (1981) labelled species which have widespread roles with plant/animal interactions as 'key' species. Table 1 shows the cause and effect relationships following the extinction of several types of key species. Gilbert (1980), (in Frankel & Soule 1981) has described 'mobile links' and 'keystone mutualists' in the synthesis of tropical plant-insect relationships. A 'mobile link' is an animal that is a significant factor in the persistence of distant plant-herbivore communities. Keystone plants are usually sources of nectar, fruit or pollen and provide critical support to mobile link species. These plants include tree genera such as *Ficus*, epiphytes, and early successional plants such as *Solanum* and *Passiflora*. Many keystone plants require early successional habitats or gaps.

For survival of animal species, the situation is quite intricate. Soule (1982, in Webb 1987) and other zoologists consider 500 individuals as a safe minimum level for breeding adults, but there are stipulations and complications due to genetic factors and the effects of logging. Thus, species collapse from inappropriate gap dynamics and unwanted edge effects is perhaps the greatest biological threat to the maintenance of community stability in remnant areas.

#### **The management objectives for a CNVF area are:**

1. *A stable community* by manipulation of successional processes (if necessary).
2. *Restoration of the canopy* if it is degraded or disturbed *aligned with the use of canopy gaps*. Where a medium-large disturbance has produced a large canopy opening, reduction to small canopy gaps by the establishment of early secondary species will provide the appropriate environment for the germination and growth of shade tolerant mature phase species. Canopy gaps will need assessment of understorey and soil status and possibly subsequent treatment to provide for environmental heterogeneity.

3. *Restoration of the lower canopy, forest floor and edge areas.*
  4. *Identification of key species* of the particular community and additional plantings (if necessary) within their regeneration and habitat niche.
  5. When a stable community has developed, *different levels of successional change* are required for resources for animal species and continuing community diversity.
- (Webb et al. 1985, Stockard et al. 1985, Hynes 1983, Frankel & Soule 1981)

**The processes by which these management objectives will be obtained are:**

*Thorough assessment of the area*

- natural disturbance
- successional pathway stages
- interference
- exotic species
- rare and endangered species
- key plant and animal species
- human disturbance
- incompatible activities

*Planning and implementation of management plans*

- local objectives
- priorities for action
- techniques of regeneration
- management of incompatible and human activities

*Monitoring and research*

- assess regeneration techniques
- changes in objectives/priorities/techniques?

*Coordination between government agencies and agencies involved in the regeneration process*

(Godfrey et al. 1988, Hopkins et al. 1977, Hopkins & Saunders 1987)

The techniques used will be many and varied as each CNVF area is slightly different in community structure, levels of degradation, physical site characteristics and historical evolution. An explanation of techniques used is given in Table 2.

### **Constraints to management**

Constraints to management are just as much a threat to the future of these rainforests as their small size and geographical isolation. Inscribing these areas in NSW on the World Heritage List does not ensure their continued survival without adequate management. Management needs to be bound to some form of enacted legislation to provide funding for assessment, management practices, research and monitoring. At present there is no effective endangered species and community legislation in NSW.

**Constraints to management are:**

*Funding* — Rainforest management should be intensive and ongoing. The Federal Government has allocated over \$20 million for a National Rainforest Conservation program (Department of Arts, Heritage & Environment 1987), whether funding for regeneration of degraded areas has been included, is unknown to the author. Funding must also come through endangered habitat legislation, as previously mentioned.

*Data on synecological and autecological aspects of humid subtropical rainforest are quite limited* — This must restrict the potential effectiveness of management. The importance of increased research and monitoring cannot be overemphasised.

**Table 1.** Some possible cause and effect relationships following the extinction of four kinds of key species, with particular emphasis on tropical forests (Frankel & Soule 1981).

Ecological category	Cause of local extinction	Effects of extinctions on diversity	Indirect effects
I. Large predators	area effects increases	herbivore density increases	habitat destruction from overbrowsing, compaction, grazing, trampling and predation
	hunting	competitive excusion among prey species	extinction of ground nesters, plants
II. Large herbivores	area effects	extinction of large predators	the <i>Indirect effects</i> in row III
	hunting	loss of early successional habitats	
III. Generalized key species (e.g. bees, butterflies, bats and birds)	area effects	reproductive failure from reduced pollination and seed dispersal in low density plants lacking specialized mutualists	extinction of plants
	loss of early successional habitats		extinction of specialized herbivores extinction of specialized parasitoids and predators destabilization of coevolved food webs
IV. Certain critical plants	commercial collecting or selective cutting	starvation and emigration of generalist pollinators	<i>Indirect effects</i> in row III
	loss of early successional habitats		

*Lack of public awareness of the fragility of rainforest environments* — Human disturbances to small areas can be just as, if not more damaging, than a natural disturbance. Human disturbances can be of an ongoing nature which may not permit the regeneration process to reach beyond the pioneer stage. Management plans must consider all present and future human threats and incorporate appropriate actions to eradicate or minimise these destructive influences.

*Few trained personnel with expertise in rainforest management* — Many of the CNVF areas have only recently come under the protection of World Heritage status, hence management of these areas is in its infancy and few have had time to experience this field of reserve management.

*Lack of communication* — Co-ordination between multiple government agencies could retard the efficacy of management and conservation of rare and endangered species.

## Discussion

The richness and complexity of CNVF is bound in the biotic elements of the community. The vegetation holds the majority of the nutrients within its living tissue, the plant species diversity provides a vast range of resources for animals and a buffer to the overexploitation by herbivores, predators and pathogens. The large variety of animals in turn acts as a catalyst in essential plant reproductive strategies to maintain species diversity.

The type of disturbance and its effects on the physical environment will determine the recovery process. Hopkins (1975) mentions that where the disturbance is artificially maintained by roads and clearings, the ability to regenerate is threatened. The physical effects of machinery may provide inappropriate establishment conditions (Webb et al. 1972). Where a massive disturbance occurs the final composition of the vegetation would also be expected to be determined by the floristic composition of the adjacent forest. This has obvious implications for remnants where the adjacent forest is unlikely to be CNVF.

Considering stability and specialised interrelationships of subtropical species, what reserve sizes will be necessary to preserve all species of CNVF? This question is difficult to answer due to lack of information on rainforest species populations and ecosystems. Ashton (1976, in Webb 1987) considered that 200 mature individuals was the minimum effective population size for rainforest trees. In 1000 hectares of forest (for the complex forests of Borneo), 60 per cent of the species should be left intact and in 2000 hectares, all but the rarest species would be likely to be conserved. Webb (1987) suggests that 'even undisturbed reserves (that is, not too drastically disturbed by people who inhabit all of the surrounding areas) may already be too small to be self-sustaining in the longer term, i.e. on time scales reckoned by centuries. Besides adverse social pressures, biological factors include loss of essential fauna for pollination and seed dispersal, a slow run-down in genetic fitness, and population sizes that are already too small to prevent species extinction.'

Hopkins (1975) feels that substantially larger areas of rainforest are needed to retain 'stability' than are necessary in more simple vegetation types. He predicts that any restriction on this 'habitat species area' could lead to gradual simplification of the community. Many reserves are too small to always contain all the necessary successional stages for the persistence of some herbivore species (Frankel & Soule 1981). The role of key species needs more identification and research. The fact that these species can have a profound role means that management should clearly be preserving and monitoring their activities.

Community education about the fragility of rainforests is needed to assist the preservation of remnants of CNVF. The misuse of Wingham Brush until fairly recently is an example of the little understanding the general public have of rainforest complexity and stability. Community service groups, local media, lectures in schools and interpretative signs on site are useful ways of providing this information.

The general public are not the only ones ignorant of conservation. Mills (1987) expresses much concern at the lack of appreciation of rainforest conservation by government. Pressure on the remnant vegetation of the Illawarra Region increases weekly, not uncommonly emanating from the activities of government departments. The development of service corridors, coal mines and their associated waste disposal dumps and urban expansion have taken their toll in recent years.

**Table 2.** Aims and techniques for the restoration of degraded CNVF sites (Floyd 1984, Stockard et al. 1985 & Kooyman 1988).

Forest	Causes of degradation	Techniques for restoration
Canopy	vine overgrowth	mechanical and chemical means (Glyphosphate, e.g. Roundup) – follow up treatment at periodic intervals; initial canopy vine treatments should be undertaken in the non-growing season.
	large canopy gaps from disturbance	suitable fast growing A & B Group species; or use of clump plantings – a mixture of AB & CD Group species with shrubs and palms and A & B type species in between clumps. Clump plantings provide quicker re-establishment of the rainforest environment, structure and pattern of species distribution. Use of local species where possible.
Rainforest edge	vine overgrowth; exotic species	mechanical and chemical means; treatment here is more successful after the main canopy has been treated, otherwise light conditions will allow edge species especially exotics to enter the rainforest body.
Lower canopy and forest floor	vine overgrowth; exotic species	mechanical and chemical means after the overhead canopy is intact and weed-free for 2-3 years.
Incompatible trees, e.g. <i>Cinnamomum camphora</i>	promote fire, out-compete native species	mechanical/chemical means.
Steep slopes	exotic species	where use of machinery is restricted or it is unsuitable to clear the whole site, contour line clearing is used; clump planting re-establishes a canopy and shades light demanding exotics; ongoing maintenance required.
Exposed sites	high velocity winds	windbreaks to protect seedling trees; examples include <i>Pittosporum undulatum</i> and <i>Acacia melanoxylon</i> .
Frost-prone sites	frost affecting growth of C & D Group species	nurse crop of A & B Group species such as <i>Macaranga tanarius</i> and <i>Commersonia bartramia</i> .
Grassed areas		mechanical and chemical means to remove grass; begin spraying 2 weeks prior to planting and follow up spraying for around 3-4 years; use of newspaper and bagasse mulch will markedly reduce the need to continue spraying.
Cleared lands with remnant trees	agricultural pursuits	fencing to exclude stock; single and multiple clump plantings with a great mix of species and suitable edge species; palms and shrubs can be planted in between clumps

Multiple commercial use of tropical forests may be economically desirable but, in practice, slowly simplifies the community. Logging in humid subtropical rainforests, currently only being practised in Queensland, clearly needs more monitoring and research to justify the 30 to 60-year logging cycles, advocated by Shugart et al. (1980) and Horne & Gwaller (1982). All of the studies undertaken have described a shift in



species from mature phase to late secondary ones with logging in this time-frame. With the current knowledge on CNVF, harvesting every 30–60 years cannot be described as sustainable forest management.

Baur (1964) described rainforest trees as having great variations in diameter growth in individual trees of similar age and species and advocated more emphasis be placed on plantation establishment. He stated that species are known to be capable of producing mature trees in half the time or less from plantations. However monoculture plantations have not been successful to date. Webb (1968a) reported that *Grevillea robusta* (a non-gregarious tree species) 'checked' after about 10 years. Seedlings of *G. robusta* did not persist in these plantations due to intraspecific competition from the adult species. Other species have been susceptible to insect attacks, fungi, pathogens etc. Stocker has described the most useful tropical rainforest species as those possessing a high degree of shade tolerance and suggests growth at high light levels is inversely related to their shade tolerance. Hence, the scope for greatly increasing the productivity of tropical rain-forests by silvicultural modification is limited. Stocker (1983) advocates growing large gap-type species in plantation environments.

Further research is of paramount importance if future management is to intimately understand the dynamics and floristic patterns of the CNVF environment and be able to predict the effects of management practices. Research must largely be based in situ rather than in the laboratory, as Webb (1968a) has illustrated. What happens in an artificial situation is quite different to normal community interactions.

The importance of protecting all areas of humid subtropical rainforest cannot be overstated. Government agencies with control of CNVF areas have to become more aware of their uniqueness, fragility and need for active management. Placing an area under a reserve or national park status without specialised management will not guarantee the stability and viability of this area in the future. Assessments need to be undertaken of each area and plans of management developed.

A system of managed reserves requires conservation agreements with private landholders. These agreements appear most successful where economic incentives are available through tax write-off and rate relief schemes. With only 3 per cent of CNVF in private lands in NSW, it would not be an expensive measure to be able to protect the remaining endangered species.

For management plans to be implemented, they need to be bound to legislation such as the Victorian Flora and Fauna Guarantee Act, 1988 to obtain appropriate funding. This Act provides a strong legislative basis for the conservation of threatened species in Victoria by listing all threatened species and communities, preparing policy statements on each species and community and then preparing management plans for all listed species. At present, there is no similar legislation in NSW, although, the National Parks and Wildlife Service is preparing a discussion paper on projected legislation (Kennedy 1989). One hopes a similar decisive act will be introduced in NSW.

### Acknowledgments

I would like to thank Dr L. Webb for his generous assistance with references, Drs D. Goldney and A. Gillison for their time in critically analysing this paper and Dr J. Stockard for the opportunity to discuss management of degraded areas. Sincere thanks also to Nick Stepkovitch for his support and patience and to Linda Raper for typing this document.

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Manuscript received 15 July 1990

Manuscript accepted 19 April 1991