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Vegetation changes following human disturbance of mid-montane forest in the Wau area, Papua New Guinea

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ABSTRACT. This paper examines the floristic changes that occur following human disturbance in mid-montane forest in the Wau area in Papua New Guinea. The study was restricted to a 1600–2400 m altitudinal range on Mt Kaindi, with disturbed forest, and Mt Missim, with undisturbed forest. Special attention was given to the status of *Nothofagus pullei* which is locally dominant on Mt Kaindi.

A major change in floristic composition was observed between 1800 and 2000 m. The abundance and species composition of ferns and mosses above 2000 m characterizes the floristic differences. *Nothofagus pullei* was found to be a pioneer species with a long life-span, one which does not regenerate under its own cover. There were no other important floristic differences between *Nothofagus*-dominated forest and mixed mid-montane forest. *Nothofagus pullei* locally dominates the canopy and thereby suppresses the growth of other trees.

KEY WORDS: mid-montane forest, *Nothofagus*, Papua New Guinea, vegetation succession, zonation.

INTRODUCTION

Primary forests in South East Asia are disappearing at an alarming rate. In Papua New Guinea the lowland areas and alpine zone are reasonably well explored floristically. The mid-montane zone on the other hand is often neglected by botanists. Floristic knowledge is limited and even less is known of processes of regeneration and succession, important processes in view of the increasing forest changes caused by human activities. Some studies have been carried out on regeneration after logging in lowland forest in Papua New Guinea (Sauli & Lamb 1991, Seddon 1984), but data from montane forest are absent. One of the relatively well studied areas in Papua New Guinea is the Wau area which includes Mt Kaindi (alt. 2362 m) and Mt Missim (alt. 2877 m).

The Wau district (7° 20′ S, 146° 43′ E, Morobe Province; Figure 1) has the advantage that in a relatively small area there are both virgin forests and various

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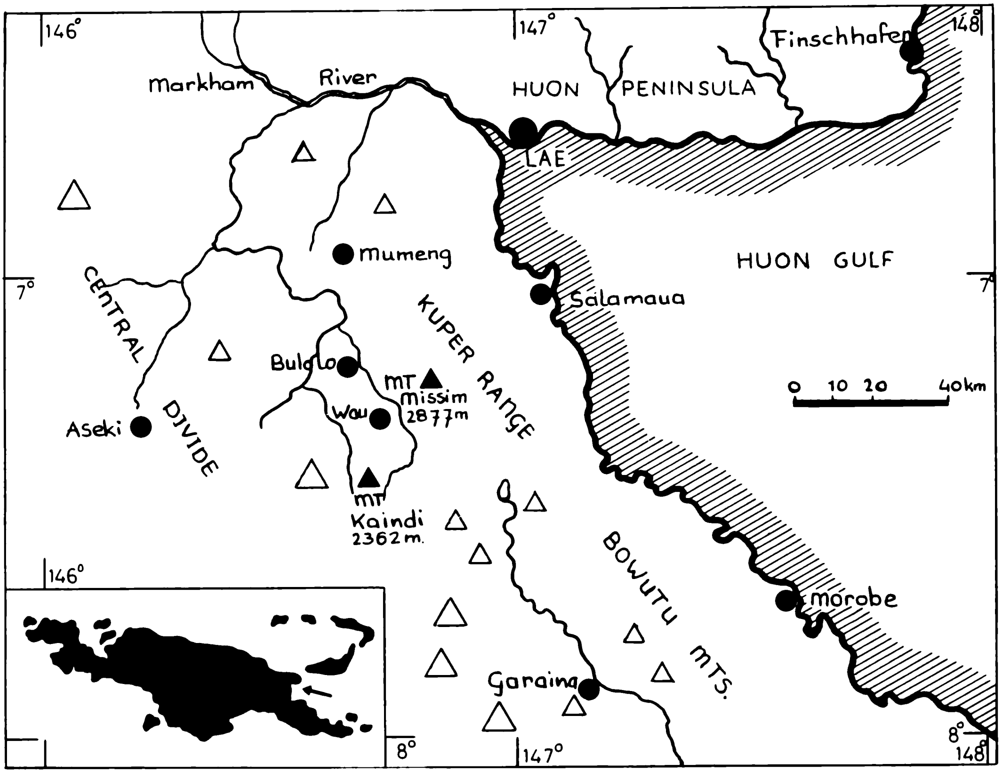


Figure 1. Map of the Wau area, Papua New Guinea, with the research sites Mt Missim and Mt Kaindi. ▲ = research sites, △ = other mountains

stages of secondary vegetation as a result of human disturbance. The disturbance in the research area is directly or indirectly related to mining activities i.e. prospecting for gold, road construction, powerline construction, logging for firewood and construction purposes, and agricultural activities of people occupied in mining. The primary aim of this research was to study the impact of man in mid-montane forest in the Wau area and the trends in natural succession after disturbance.

Research was carried out in the 1600–2400 m altitudinal range of Mt Kaindi, where mainly secondary forest is present, and of Mt Missim which has predominantly undisturbed forest above 1200 m. These mountains were chosen because of their accessibility and the fact that the Wau Research Institute concentrates its research in this region. As these mountains are located relatively close to each other, it is assumed that differences in vegetation are a result of differences in degree and extent of disturbance. The altitudinal range covered by this research can be classified as the lower montane rainforest formation (1880–2745 m) according to Robbins (1960), the lower montane zone (1000–3000 m) according to Paijmans (1976) or the lower montane (lower limit 300–1000 m;

upper limit 1500–2000 m) and mid-montane (lower limit 1500–2000 m; upper limit 2700–3000 m) zone according to Johns (1982).

To evaluate the floristic changes which occur after disturbance the vegetation of these two mountains was compared. Special attention was paid to the status of *Nothofagus pullei* (in terms of presence of seedlings, diameter distribution, height classes, and surrounding possible sources of seed), because of its dominant presence on Mt Kaindi but virtual absence from the research area on Mt Missim. Various other authors have also observed the local dominance of *Nothofagus* species in mountain areas of Papua New Guinea (Kalkman & Vink 1970, Johns 1982).

Nomenclature follows the Flora Malesiana (van Steenis *et al.* 1950–), except for the Euphorbiaceae and the Elaeocarpaceae, for which Airy Shaw (1980) and Coode (1981) respectively were followed.

METHODS

On both mountains, a series of plots, located on ridges and at *c.* 200 m altitudinal intervals, was studied. Where the forest was at least 9 m high, plots of 10 m × 20 m (the longest axis parallel to the slope) were used. Within plots all trees with a diameter at breast height (dbh) over 10 cm were mapped and measured (dbh, branch-free bole height, total tree height). Voucher specimens for identification were taken. Height measurements and sampling were accomplished by climbing trees. Detailed vegetation descriptions in terms of height and cover/abundance were made in two randomly chosen subplots of 2 m × 2 m. All higher plants and ferns were tallied per species. A profile diagram was drawn showing the structural features of the vegetation.

In low secondary vegetation the plot size was reduced to 5 m × 10 m with no subplots; in very low secondary vegetation (height <4 m) all individuals over 1.5 m height were mapped and sampled. When the canopy height ranged from 4 to 9 m, individuals with a dbh >3 cm were mapped and sampled. Specimens of seedlings, herbs, lianas and ferns were collected and subsequently identified.

Succession was studied in more detail in the secondary vegetation in the 2300 m zone on Mt Kaindi using four plots of varying size and age (*viz*: 3–5 years, 10 years, 50 years, >100 years). Further details of the methods used are given in Van Valkenburg (1987, 1989).

GENERAL DESCRIPTION OF THE VEGETATION

Mt Missim

On Mt Missim undisturbed forest is present from 1200 m upwards, surrounded by *Pinus* and *Araucaria* plantations. At 2400 m it is characterized by an abundance of ferns, and a thick cover of mosses and epiphytes on the trees.

The lushness of moss and epiphytic cover on the trees decreases from 2400 m downwards to almost nothing at 1800 m. From 2400 m downwards the groundcover also gradually becomes less mossy and the abundance of ferns decreases; from 1800 m downwards the groundlayer consists solely of dead leaves and tree seedlings. The scrambling bamboo *Nastus* appears from 2100 m upwards; it is present in places with a relatively high light penetration, although these are not necessarily areas of young secondary regrowth. *Castanopsis acuminatissima* occurs from 1600–2000 m; at some places only as very old single individuals with a dbh of *c.* 150 cm. Elsewhere *C. acuminatissima* locally dominates the forest with individuals of intermediate size. No saplings or seedlings were present.

The presence of *Coryphopteris* sp. and *Plagiogyria* sp. in the plots at 2400, 2200 and 2000 m indicates heavily leached soils, characteristic of ridges in the area (P. Hovenkamp, pers. comm.).

Mt Kaindi

The vegetation all over the mountain is disturbed to some extent. West of Mt Kaindi lies the Upper Edie Creek Bassin mining area, and mines on the west slope reach to the summit ridge. On the north and east slope there are extensive areas of anthropogenic grassland. These areas resulted from landslides, abandoned mining leases or forest cleared by settlers. Regrowth is greatly hampered by repeated burning of these grasslands. The plots at 1600 m and 1800 m (Figure 2) provide evidence that these grasslands can be returned to forest if burning is prevented. The 50-year old forest plot (Figure 2) developed after large-scale logging during the first goldrush in the 1930s in the Upper Edie Creek Bassin. Regrowth in the summit area consists of *Homalanthus nervosus*, *Acronychia*, *Euodia*, *Macaranga* and *Nothofagus pullei*. The remaining mature *Nothofagus* and mixed forest high on the mountain is gradually being cleared although large trees are often left untouched. The lower altitudinal limit of remnant forest is gradually increasing, and the average age of the regrowth vegetation decreasing as the human population increases and gold prices rise. Gressit & Nadkarni (1978) give more details on the history and ecology of Mt Kaindi.

The vegetation of the different zones of Mt Missim and Mt Kaindi are compared in Figure 2.

FLORISTIC COMPOSITION IN RELATION TO ALTITUDE

Clear differences in floristic composition in virgin forest on Mt Missim can be discerned at altitudinal intervals of 200 m. A major change in floristic composition was observed between 1800 and 2000 m, where a large group of species have their upper or lower limit of distribution. The abundance of ferns and mosses from 2000 m upwards accentuates the change.

The Elaeocarpaceae constitute an important family of canopy trees dominating the forest locally. Certain species like *Elaeocarpus polydactylus* and *Sloanea* *tieghemii* have a wide range (1800–2400 m), other species are more restricted in their altitudinal distribution, for instance *E. fuscoides*, a canopy tree in the lower montane zone (at 1600 m) and *E. ptilanthus* and *E. trichophyllus* both canopy trees of the mid-montane zone from 2000 m upwards (Table 1).

Table 1. Altitudinal distribution of some representatives of common tree genera on Mt Missim and Mt Kaindi.

Altitude (m)	1600	1800	2000	2200	2400
Elaeocarpus altigenus					*
E. culminicola	*			*	
E. densiflorus			*	*	
E. fuscoides	*				
E. habbemensis					*
E. luteolus					*
E. murukkai			*		
E. polydactylus		*	*	*	*
E. ptilanthus			*	*	
E. pycnanthus				*	
E. trichophyllus				*	
Sloanea tieghemii		*		*	*
Cryptocarya 1					*
Cryptocarya 2		*			*
Cryptocarya 3			*		*
Cryptocarya 4			*	*	*
Planchonella firma				*	
P. monticola			*	*	*
Planchonella 1				*	*
Planchonella 2		*	*		*

The altitudinal zonation is also reflected in the floristic composition of secondary forest on Mt Kaindi. Species dominating the regrowth at 1800 m altitude (*Trema orientalis*, *Pipturus* sp., *Macaranga quadriglandulosa*) are absent from regrowth near the summit at 2350 m. Here early successional stages (of *Nothofagus* forest) are dominated by *Homalanthus nervosus*, which occasionally is also found at 1800 m.

SUCCESSION IN MID-MONTANE FOREST

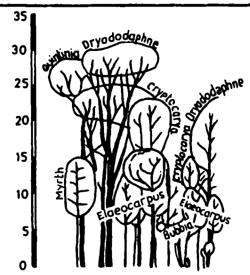
Main changes in species composition

By comparing the secondary vegetation of different ages in the plots of the 2200–2350 m zone on Mt Kaindi with the undisturbed forest of the same zone on Mt Missim an attempt was made to classify species on the basis of time of appearance after disturbance and to give an indication of their life-span. The following species groups can be distinguished (Figure 3):

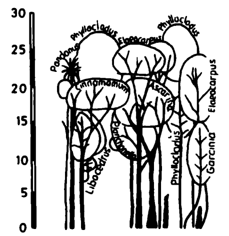
Group A: Herbs, shrubs and vines abundant in the early stages of succession. They disappear soon after canopy closure because they can not tolerate shade conditions e.g. *Polyscias* sp., *Rubus* sp., *Pandorea* sp., and *Scaevola oppositifolia*.

Group B: Herbs, shrubs and vines which are abundant in the early stages of succession, and remain an integral part of the mature forest. Examples are *Cissus* sp., *Embelia* sp., and various Zingiberaceae.

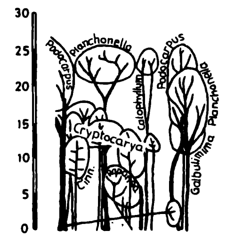
MT MISSIM, VIRGIN FOREST



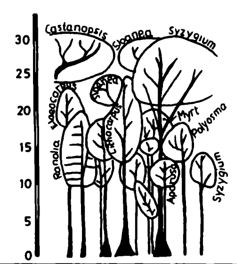
2400M
The canopy consists of large trees (>20 m) of Crypto-carya, Sphenostemon papuana, and locally emergent Quintinia macrophylla and Dryadodaphne crassa. Medium sized (13–20 m) Elaeocarpus altigenus and E. poly-dactylus merge into an understorey (<13 m) of Rapanea leucantha, R. womersleyi, Drimys piperita and Bubbia.



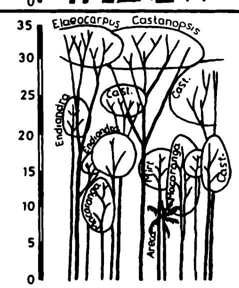
2200 M
The canopy is dominated by conifers and Elaeocarpus accompanied by Pandanus and Planchonella. The sub-canopy consists of Cinnamomum, Ascarina philipinensis, Caldcluvia, Planchonella, Levieria squarrosa and Elaeocarpus.



2000 M
The canopy is dominated by large individuals of Podocarpus, Planchonella monticola, Cinnamomum, Calophyllum and Beilschmiedia. Medium sized trees of Galbulimima and Cryptocarya emerge from an under-storey of Rapanea, Trimera and saplings.



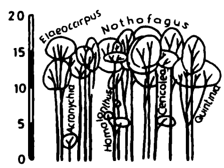
1800 M
Common canopy trees are Castanopsis acuminatissima, Syzygium and Sloanea tieghemii. A subcanopy of Elaeocarpus, Lithocarpus, Polyosma and Randia dominates an understorey of Aporusa, Psychotria, Symplocos and Ardisia.



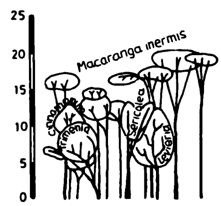
1600 M
The canopy is dominated by large individuals of Castanopsis and Elaeocarpus fuscoides, which overtop Endiandra, Syzygium and Myristicaceae. Smaller trees are mainly Garcinia and Macaranga, Areca palms and Cyathea treeferns in an open understorey.

Figure 2. Vegetation zonation on Mt Missim with predominantly virgin forest compared with Mt Kaindi with various stages of regrowth after disturbance. The main floristic composition is given. The profile diagrams give an impression of the vegetation structure in each zone.

MT KAINDI, SECONDARY FOREST

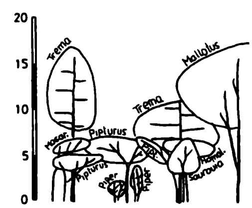


2350 M
About 50 year old forest dominated by Nothofagus pullei, which accounts for 76% of the trees. Other tree species present are Elaeocarpus polydactylus, Sericolea micans, Quintinia macrophylla, Homalanthus nervosus and Acronychia. The undergrowth consists of lianas, scramblers and saplings.



2200 M
Approximately 20 year old forest with a canopy dominated by Macaranga inermis accompanied by Trimenia papuana and Euodia. The understorey is of a mixed composition containing Cinnamomum, Cryptocarya, Galbulimima, Levieria squarrosa, Planchonella monticola and Sericolea micans.

2000 M
No data available



1800 M
Approximately 10 year old forest dominated by emergent Albizia (25 m). The canopy consists of medium sized trees of Trema orientalis and Mallotus paniculatus. The understorey with Homalanthus nervosus, Macaranga, Pipturus and Saurauia is well developed. The herb and shrub layer with Piper, Rubus, and Zingiberaceae is dense.

1600 M
Very poor secondary growth with few small trees (<3 m) of Acalypha hellwigii, Macaranga quadriglandulosa and Pipturus in anthropogenic grassland.

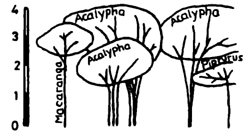


Figure 2. *Continued*

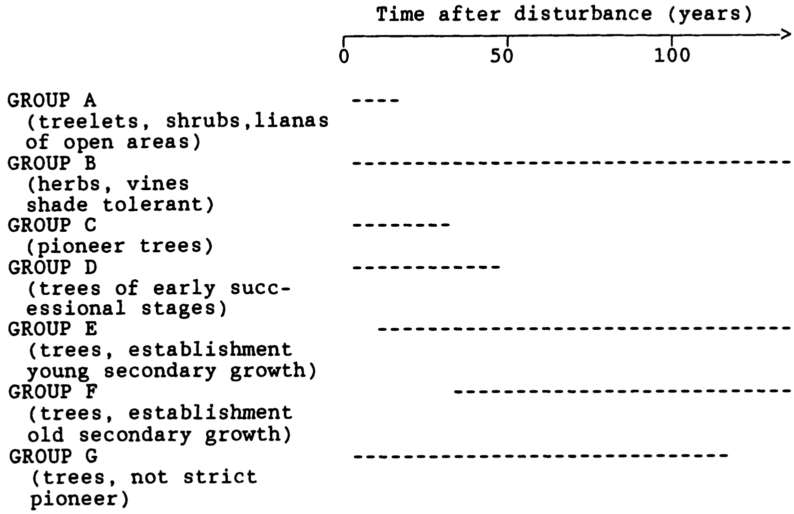


Figure 3. Time of appearance of different species groups in relation to secondary succession on Mt Kaindi (for details see text).

Group C: Pioneer trees with a short life-span, which appear shortly after disturbance. Some of these species dominate the early stages of succession in small gaps (*Macaranga inermis*) or large clearings (*Homalanthus nervosus*).

Group D: Tree species which establish after disturbance, but with a relatively short life-span, but longer compared with species of group C: *Euodia* sp. (7 distinguishable taxa in the summit area of Mt Kaindi), *Acronychia* spp., *Trimenia papuana*.

Group E: Trees which establish in the early stages of succession and remain as trees an integral part of the mature forest both in canopy and understorey. Examples are *Elaeocarpus polydactylus*, *Drimys piperita*, and *Rapanea* sp.

Group F: Trees which are only found in mature forest. These can be regarded as primary species establishing in advanced secondary growth such as *Dryadodaphne crassa*, *Elaeocarpus densiflorus*, *Sphenostemon papuana*.

Group G: Trees which are not strict pioneer species because of a long life-span and are difficult to fit into this system: *Nothofagus pullei*.

Ferns as indicators of successional stages

The occurrences of different species of fern on Mt Kaindi, according to altitude and age of the vegetation, are shown in Table 2. These data clearly show that fern composition on Mt Kaindi forms an indication of the successional stage of the vegetation, independent of altitudinal differences. The species present in the 3–5 year old regrowth at 2350 m, are absent from the older plots, and are probably light-demanding species of open, disturbed areas, disappearing when light conditions deteriorate: *Histiopteris incisa*, *Microlepia* sp., *Nephrolepis* sp., and *Pteris* sp.. *Nephrolepis*, together with *Pteridium aquilinum*, is also a light-demanding

Table 2. Distribution of ferns on Mt Kaindi according to altitude and age of the vegetation

Altitude (m) Age (years)	1600 3–5	2350 3–5	1800 5–10	2250 10–12	2200 15–20	1950 †	2350 >100
Pteridium	*						
Nephrolepis	*	*					
Histiopteris		*					
Pteris		*					
Microlepia		*	*				
Dryoathyrium			*				
Thelypteris			*				
Gleichenia				*		*	
Cyathea				*	*	*	
Calymnodon					*	*	
Coryphopteris				*	*	*	*
Dryopteris				*			*
Hymenophyllum				*	*		*
Asplenium							*
Crypsinus							*
Plagiogyria							*

† high forest showing signs of recent disturbance

species of open areas, present in the 3–5 year old regrowth in anthropogenic grassland at 1600 m. Under the shadier conditions of the 10 year old regrowth at 2250 m, there occur three species which were also collected from the old forest at 2350 m: *Coryphopteris* sp., *Dryopteris* sp., and *Hymenophyllum* sp.

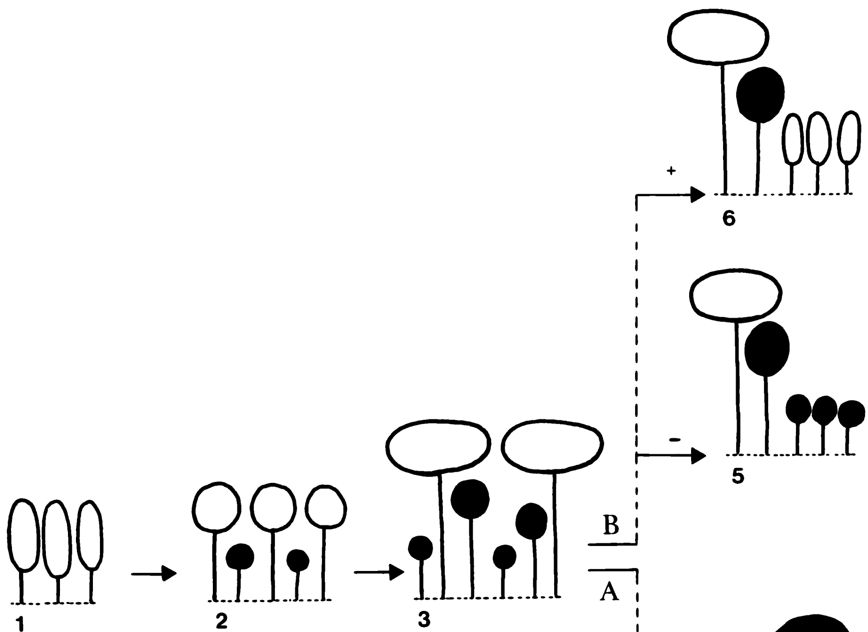
The ferns in the plot at 1950 m confirm that disturbance has taken place, and considering the species composition, this must have occurred some 10–20 years ago.

Position of Nothofagus pullei *in the succession*

The forest in the upper zone of Mt Kaindi is locally dominated by *Nothofagus pullei*, but this species is completely absent from the study area on Mt Missim. The data on presence and absence of seedlings and/or saplings give an impression that the occurrence of *N. pullei* is closely correlated with disturbance and light regime and that the species has a distinct place in the succession. Saplings of the species (trees ≤2.5 m in height) grow vigorously in 3–5 year old regrowth. Seedlings are present in the 50-year old plot under a rather open single layer canopy, which results in a relatively high light intensity on the ground.

Apparently, therefore, seedlings and saplings of *N. pullei* are light demanding, strongly suggesting that the species is a forest pioneer. Seedlings are absent in old forest with a multi-layered canopy and thus dense shade beneath. In the oldest plot *N. pullei* trees are only 25 m high with a maximum dbh of 30 cm. Their architecture shows a vigorous growth suggesting that they have not yet attained their mature form. In the same plot remnants of former trees, evident as decaying trunks 2–3 m high and dbh >50 cm, are found. This supports the impression that the oldest plot does not represent mature forest. The oldest plot on Mt Kaindi has an almost similar floristic composition (except for *N. pullei*) to the plots at 2200–2400 m on Mt Missim, only the position of the genera and species in the forest structure is different. On Mt Kaindi individuals of *Cryptocarya* and *Elaeocarpus* are found in the middle layer only, whereas on Mt Missim these are important canopy trees.

From the above the following possible successional series may be derived (Figure 4). An open area is colonized by *N. pullei*, which temporarily suppresses other tree species. This forest type develops into a vegetation with the main canopy dominated by *N. pullei* and a middle layer of mixed composition (cf. the oldest plot on Mt Kaindi). This forest type then develops into a mature *N. pullei*-dominated forest with tall emergent individuals, such as are present in the summit area. From here two ways of development seem possible. First, if



: *Nothofagus pullei*

: Trees other than *Nothofagus pullei*

A : no disturbance
B : local disturbance
\+ : *N. pullei* seeds available
\- : *N. pullei* seeds not available

1 : young regrowth dominated by *N. pullei*
2 : old regrowth/forest dominated by *N. pullei*
3 : mature *N. pullei* dominated forest
4 : mature mixed forest
5 : mature *N. pullei* dominated forest with local patches of rejuvenation of mixed composition
6 : mature *N. pullei* dominated forest with local patches of rejuvenation of *N. pullei*

Figure 4. Possible forest development phases in forest dominated by *Nothofagus pullei*.

there is no more disturbance, then *N. pullei* will eventually disappear, since unlike the other tree species it does not regenerate under its own cover. A forest of mixed composition, comparable to the forest at the upper zone of Mt Missim will develop (phase 4), if there are no further disturbances during the life time of the remaining *N. pullei* trees. Second, if there follows substantial disturbance, either natural or human, then *N. pullei* will remain an integral part of the forest when disturbance coincides with the availability of seeds (phase 6). Regeneration of the species therefore takes place, leading to a postulated cyclic succession. When no seeds of *N. pullei* are available at the time of disturbance other tree species will dominate the regrowth and mature *N. pullei* forest with local gaps occupied by a mixture of other species will develop (phase 5). This forest type may eventually also change into phase 4, if the mature *N. pullei* trees die.

DISCUSSION

There exist different opinions concerning the altitudinal zonation of the forest in New Guinea. Robbins (1960) recognized a lower montane rainforest formation divided into a broadleaf gymnosperm alliance and a fagaceous forest alliance, the latter subdivided into a *Castanopsis-Quercus* association (below 2290 m) and a *Nothofagus* association (2290–2745 m). Paijmans (1976) recognizes a lower montane zone, with a local predominance of *Castanopsis acuminatissima* (500–2300 m), *Nothofagus* (1500–3000 m), or conifers (2400 m and above).

The distinctly drier aspect of the forest and the scarcity of ferns below 1800 m on Mt Missim agrees with the views of Johns (1982), who recognizes a lower montane zone and a mid-montane zone. With respect to floristic composition, the transition from lower montane forest to mid-montane forest occurs between 1800 and 2000 m on Mt Missim. Representatives of the mid-montane zone (2000–2400 m) are the Podocarpaceae, as well as several *Elaeocarpus* species and the genera *Cinnamomum*, *Cryptocarya*, *Rapanea*, and *Nothofagus*. Representatives of the lower montane zone are Myristicaceae, Sterculiaceae, and the genera *Elaeocarpus*, *Endiandra*, *Castanopsis* and pioneer species such as *Trema orientalis*, *Pipturus*, *Albizia*, and *Macaranga* spp., much different from the pioneer species of the summit area of Mt Kaindi.

Of the *Nothofagus* species, *N. pullei* was predominantly present in the mid-montane zone of Mt Kaindi. Although it was not found in the plots on Mt Missim, it is present in the surrounding forest.

The presence of emergent but dying individuals of *N. pullei* over 35 m in height in the summit area of Mt Kaindi leads to the following ideas. Firstly, they probably form the seed source for the 50-year old plot, suggesting that the time of disturbance coincided with a period of large seed production of these individuals. Secondly, it supports the impression that forest in the oldest plot is still immature.

Apparently, the dominance of *N. pullei* is dependent on the availability of seeds at the moment of disturbance. The annual seed production of *N. pullei* varies quite markedly and the seeds are dispersed by wind (Ash 1982). The distance over which *Nothofagus pullei* seeds disperse as observed in the 3–5 year old regrowth on Mt Kaindi appears to be more than 50 m, in contrast with suggestions by other authors: between 10 m and tree height beyond the edge of crown cover on level ground (Kalkman & Vink 1970, Howard 1973). The greater distance on Mt Kaindi may be attributed to the strong winds in the summit area.

As a result of its rapid growth *Nothofagus* can overtop competitors in the early stages of succession. The competing species remain suppressed in the middle layer of the forest together with the primary species that establish later.

Van Valkenburg (1987) observed the absence of seedlings of *Nothofagus pullei* under dense shade conditions in the old forest plot but presence of *N. grandis* seedlings. Both species were present amongst seedlings in the 50-year old regrowth, with its relatively high light penetration. This indicates a possible difference in light requirements of seedlings of the two species. Although the canopy in *Nothofagus*-dominated forest in New Guinea is generally rather open at 5–8% light penetration, only a few seedlings of *Nothofagus* survive to become saplings (Ash 1982). The positive response of seedlings and saplings of *Nothofagus* to increased light penetration, is also illustrated by Brass (1964). He observed a prolifically regenerating small-leaved *Nothofagus* (presumably *N. pullei*) after disturbance of the forest, high on Mt Kaindi. This is in agreement with observations on plots with regrowth of different ages. There are distinctive ecological differences between the species of *Nothofagus*. *N. cunninghamii* in Australia only regenerates successfully in canopy gaps, as it needs a high light intensity (Howard 1973), but *N. rubra* regenerates successfully under its own cover (Kalkman & Vink 1970). On Mt Kaindi it seems that *N. pullei* does not regenerate well under its own cover (Van Valkenburg 1987).

The only difference in floristic composition between *Nothofagus* forest on Mt Kaindi and mixed forest on Mt Missim is the presence or absence of *Nothofagus*. The undergrowth is not different between the two mountains. Similar observations were made by Kalkman & Vink (1970) with respect to *Nothofagus rubra* forest. They also stated that there is a suppression (in size) of other trees by *Nothofagus*. This latter phenomenon is best demonstrated in the old forest on Mt Kaindi.

Castanopsis acuminatissima, another member of the Fagaceae, has a strategy similar to that of *Nothofagus pullei*. The forest up to 2000 m on both mountains is locally dominated by *Castanopsis acuminatissima*, and sometimes old individuals with abundant suckering at the base of the trunk were encountered. But regeneration from seed under its own cover was never observed. The population can only be maintained by regeneration from seed after disturbance resulting in increased light penetration. This was observed on Mt Missim in 1978 (Johns 1986), where after intensive wind throw in ridges dominated by *C. acuminatissima* a dense mat of seedlings grew when the disturbance coincided with a period of fruit maturation of this species.

It has been proved that the montane forests of Papua New Guinea are far from stable ecosystems, but are, and have been, constantly subjected to disturbances caused by natural events such as landslides, drought, fire and storms (Johns 1982). Small and large gaps are created, in which the forest regenerates via various stages of succession. *Nothofagus pullei* plays an important role in this process. Presently, the situation is changing as human activities are overruling the natural disturbances and taking their toll. At various places, such as on Mt Kaindi, the forest is no longer able to recover to maturity and if intensity and frequency of human activities increase, species such as *Nothofagus pullei* and *Castanopsis* will also disappear because of lack of seed.

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