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Cyclic sequences of vegetation in the plant communities of the Aberdares Mountains, Kenya

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ABSTRACT

Cycles of vegetation change are described for two vegetation types on the Aberdares Mountains, Kenya. The shrubby *Alchemilla argyrophylla* undergoes a cycle of growth and degeneration rather similar to *Calluna vulgaris* in Western Europe; that is the phases are not synchronous unless forced to be so by fire or disturbance. Bamboo *(Arundinaria alpina)* however is monocarpic, patches of stems 0.5 to 5 hectares in extent flower synchronously and thus initiate a series of vegetation changes characterised by *Sambucus africana* which eventually lead back to Bamboo forest. These cycles are of importance in management of montane game reserves in East Africa. The nature of cyclic successions is discussed.

INTRODUCTION

There is no doubt that all vegetation is unstable in the short term. Individual plants die and are replaced; herbivores remove parts of selected species and these species must maintain their numbers by different strategies compared with unpalatable ones; geomorphological and geochemical processes impose slow cycles and trends on the plant cover of the earth. Grubb (1977) draws attention to the overall importance of cyclic change-over of species composition in many plant communities as an explanation of the diversities of species populations. Some plant communities predictably fluctuate around the life-history of the dominant whose death leads to a cycle of events which finally repeats itself. It is possible to refer to these as cyclic sequences and their appreciation gives insight into the dynamics of such communities as well as help in management problems.

In East Africa, plant communities are seldom dominated by one species unless disturbed by man's activities. In the montane zone, however, dominance becomes more and more pronounced and Hedberg (1964) delimits zones of characteristic species up to the alpine zone above the forest level. In general the progression of physiographic vegetation types can be said to pass from montane mixed forest to gymnosperm forest *(Juniperus procera* or *Podocarpus latifolius**) thence into bamboo *(Arundinaria alpina).* Above the tree line there is tussock grassland (of *Festuca pilgeri, Andropogon amethystinus* and *Carex monostachya)* which alternates with what is clearly heath vegetation of various types. It is the purpose of this paper to describe cyclic changes in the bamboo, and the heath vegetation dominated by the Rosaceous *Alchemilla argyrophylla.*

The following account is based on floristic analyses made in 1976, while investigating the boundary zones between plant communities. Two line transects of 30 contiguous 50 cm x 50 cm quadrats were taken at right angles to the boundary between easily discernible plant communities. Analysis of these data by reciprocal averaging allowed identification of the quadrats from the homogeneous ends of the transects These were then taken as representative of the communities, and mean cover could be assigned to each species, as well as to the pH of surface soil from each quadrat. Clearly this resulting figure is akin to a phytosociological releve, and since it is based on non-random sampling the citation of confidence bands would be meaningless.

In the case of the bamboo analyses, 10 1 m x 1 m quadrats were roughly randomised to give a basis for the stem variance figures.

Nomenclature of flowering plants follows Agnew (1975).

* Formerly *P. milanjianus.*

THE ALCHEMILLA ARGYROPHYLLA CYCLE

Description

This shrubby silvery-leaved *Alchemilla* is one of the characteristic plants of the heath vegetation of the moorlands about 3000 m on Mount Kenya and the Aberdares (replaced by *Alchemilla elgonensis* on Mount Elgon). It occurs in burnt bushland edges as well as heathland but in the latter it frequently dominates. The shrub grows from 20 to 70 cm tall in a complex community in which a mosaic of mounds and hollows may be associated with small open patches of grassland and herbs, and in which mole-rats *(Tachyoryctes* spp.*)* disturb large areas.

Alchemilla heath can burn, but these heathlands of the central Aberdares plateau do not seem to have been burnt for some time, and it is possible to find stands of apparently differing ages. I have made the general observation that on the extensively burnt shrubland of Mt. Kenya (Sirimon track head, 3700 m) the regeneration in 1976, two years after burning, included a dense population of *Alchemilla argyrophylla* seedlings. There was no extensive stand of *Alchemilla* heath at that altitude before the fire and it is possible that fire stimulates widespread germination. Figure 1 is a diagram of the supposed course of the *Alchemilla* cycle and incorporates part of a measured transect through a bush, and Table 1 gives the floristic composition of sample areas of the proposed sequence.

Cross-sections of representative stems from three stages in the cycle are shown in Fig. 2. The growth zones are rather tantalizing, for young stems appear to be ageable but the oldest stem seems to have no clear growth zones towards the older wood. The rainfall pattern on the Aberdares is of two principal rainy periods (as in the rest of Kenya to the East of the Rift Valley) but they are hardly separated at higher altitudes. Indeed there were heavy showers during the period of my observations in July 1976 which in the lowlands is invariably dry. The main dry period is January and February and under this regime recognisable annual growth zones could be expected, but note how the new "spring" wide-vessel growth seems to have recently started on these sections. Obviously the phenology of growth on these equatorial mountains would repay investigation.

In the following account of cyclic events the recognisable growth zones are used as indices of annual growth to estimate the duration of various stages of the cycle, but future work should check this against long-term observations.

Pioneer (3-4 years). The establishment phase takes place either as colonisation after disturbances by fire, mole-rats, human interference or as part of the cycle within a mosaic of phases of *Alchemilla* heathlands. Growth rates are unknown but measurements gave a mean of 10 cm of new shoot, leafy to ground level. The flora of this phase depends on its origin. If the result of disturbance, grasses and ruderals are abundant. Creeping plants such as *Carex conferta, Oxalis corniculata* and *Uebelinia crassifolia* are common when the full cycle of growth phases is present.

Building (4-7 years). Here there are erect shoots with naked woody bases, showing 30 cm of new growth of the current year, with abundant flowering. The flora consists typically of abundant bryophytes, and a very diverse assemblage of flowering plants which are frequently creeping or rhizomatous.

Mature (4-8 years). The older shoots lean and finally fall, and the basal bark peels in scales, while new growth averages 25 cm with abundant flowring. Maximum floristic diversity is present but bryophytes are reduced and grasses may be abundant between the spreading bushes of *Alchemilla.*

Degenerate (possibly 10 years). Fallen shoots surround the base of the old plant, while the 10-20 cm of new growth attest the decreased performance here. The ground may be covered with bark scales from the stem bases and the flora is greatly reduced, particularly in bryophytes and grasses.

In general there seems to be no difference between the soils of the study areas exemplified in Table 1 in so far as they were investigated.

Discussion of the heathland cycle

Cyclic sequence in vegetation are characteristic of heaths, where a dominant woody plant has a limited life span; the best known example is that of *Calluna* in Britain (Gimingham, 1972), the study of which was part of research into ecological management for grouse stocking.

The principal heath species of the Aberdares range in Kenya are *Erica arborea* and *Philippia excelsa* which form woodland, and the low shrubby *Alchemilla argyrophylla.* This woodland is dominated by true members of the heath family, and although its soils are sufficiently acid and peaty for it to be regarded as a heathland community its long term dynamics are still unknown. Possibly there is a cycle involved but if so it must be so interrupted by fire, and by invasion by pyrophilic plants such as *Stoebe kilimandscharica* that there can be little evidence remaining as to its characteristics today. Possibly intensive investigation of such sites of pure *Erica arborea* as remain will reveal a cycle. However, the heath shrub *Alchemilla argyrophylla* does give evidence of a cyclic behaviour very analagous to that described for *Calluna vulgaris* in Scotland.

It is difficult to ascribe any evolutionary advantage to the shrub consequent on the development of the cyclic vegetation pattern described. It is possible that this is another feature of the effect of the important mole-rat populations in alpine Africa, as described by Hedberg (1975).

There are numerous afro-alpine plant species capable of rapidly colonising bare ground and these may have evolved as much in response to selection by solifluction as by mole-rat disturbance.

THE BAMBOO CYCLE

Description

Bamboo occurs from 2750-3500 m over extensive areas of all East African mountains (Hedberg 1964). Wimbush (1947) has described the bamboo cycle in general terms. It is a dominant, monocarpic plant which flowers and dies back in patches throughout the forest. Flowering tends to be almost synchronised over large areas. For instance it was easy to find flowering specimens in 1966 over wide areas of the Aberdares bamboo forests but flowering had apparently taken place in the previous decade on Mt. Kenya and flowering specimens were not found there although flowered patches with dead bamboo were common. By 1969 it was difficult to collect herbarium specimens on the Aberdares but a flight over the Mau forest revealed extensive areas of current flowering. Observations in 1968 and 1976 allow the following account to be prepared. Floristic stages are easy to observe and are described below; they are summarised in Tables 2 and 3 and Fig. 3.

Pioneer

Regeneration of bamboo appears to take place from the rare revitalisation of a section of fallen culm or even part of the rhizome system. Very occasional small living shoots can be found even within the dead tangle of stems 2-4 years after flowering but take a long time to become conspicuous clumps. I have not been able to find seedlings in the field, and on the Aberdares at least, I have not found viable seeds, although Dr. P.J. Greenway (pers. comm.) has assured me that they do exist. The tussocks of bushy growth which result from this revitalisation grow slowly for 3-5 years forming thickets of many-stemmed plants 1-3 m tall amongst the *Sambucus* of the previous phase. pH is at its highest and litter cover of the soil is low. The bushes of bamboo enlarge until they join up when the Building Phase begins.

Building

I define this as the stage when the height of the growing stems exceeds the general height of the stand. In fact a rapid increase in general height is obtained and this phase appears to last but a short time, from 5-7 years, and the stems retain the clumped pattern imposed during the pioneer stage. Floristically this period is the poorest, for the light-demanding species of the pioneer stage have been eliminated and the shade-loving species of the mature phase apparently migrate and invade only slowly. I suspect that most of the shade-loving species that are found are survivors from the previous cycle and examination of Table 2 shows this to be true of *Pteris catoptera* and *Cyperus dereilema,* for instance. Even *Sanicula* and *Selaginella kraussiana* can survive in odd pockets in the *Sambucus* stage.

Floristic changes are accelerated by a change in pH of the soil during this period. Since the major event is a fast increasing bamboo biomass, more and more plant nutrients become locked into it and are not available for circulation. We also have to consider the effects of a change in the litter type from predominantly broad-leaved to the strongly sclerenchymatous leaves of the bamboo. Both these events are reflected in a lowering of pH during this period.

Table 2 gives an analysis of sampled stem densities during this and subsequent stages. The dense clumping of this building phase can be seen and needs no further comment.

Mature

As soon as the annual new growth of stems equals the height of the stand (no further overall height increase taking place), the stands can be said to be mature and only slow changes take place for the next 10-15 years. These changes are:

a) the separation of bamboo culms on the forest floor until a more regular, less clumped, pattern is produced;
b) the final change of the forest floor species to those of deep shade, and the elimination of many lianas which were established during the *Sambucus* and Pioneer stages;
c) soil pH continues to decline but not to very low levels. There is often heavy grazing of young bamboo shoots by rhinoceros and elephants, which could be important in hastening or delaying the onset of flowering.

Flowering and Sambucus stage:

Flowering takes place during one season only but 2-3 years pass before the culms fall, and this is most important for the whole system. The culms fall in a haphazard way, making flowered areas extremely difficult to enter. There is a sudden increase in light-demanding broad-leaved species and climbers, dominated by *Sambucus africana*, so that from this to the thicket pioneer stage can be called the *Sambucus* stage. Herb diversity increases slowly, the initial invasion leading to rampant single-species patches of vegetation, particularly climbers, but this is soon broken up by the entry of large mammals. They break the vegetation down into small patches between which trails meander allowing entry of ruderal plants.

Soil pH increases but not immediately because the bamboo culms may take a number of years to rot away. However, as the process continues, more and more of the total nutrient pool is returned to the soil and thence to a much more rapid cycle within the soft-leaved dicotyledonous plants of the *Sambucus* stage, so that by the end of this period the maximum pH is reached.

Ultimately, just before the thicket (pioneer) bamboo stage with which this account began, there is maximum heterogeneity in the vegetation because of the network of large trails which breaks it up, and the persistence of large bamboo culms, some of which may even be upright. The diversity is further increased by uneven invasion by opportunistic ruderal species, and uneven elimination of the old forest floor flora.

Tree species such as *Nuxia*, *Podocarpus* and *Dombeya goetzenii* have their greatest opportunity for establishment and growth during the *Sambucus* phase, for their saplings are suppressed under the high bamboo canopy but are able to grow more quickly after this has flowered. I have not been able to show that the present distribution of these trees is associated with past flowering sites but it is clearly a possibility which could repay investigation.

The possibility of internally operated cycles must be borne in mind when discussing vegetation changes through any cause, and in the National Parks of Kenya today a principal preoccupation is with environmental damage by elephant. This is well documented in Tsavo (Glover 1963), but not so well in the Aberdares where there is considerable evidence of recent elephant damage, which was not there in 1969. It is increasingly difficult to find undisturbed stands of bamboo at low or high altitudes, and some *Cliffortia*, or even *Hagenia* trees on the moorland woodlands are beginning to suffer as well. This is despite the very great area of bamboo/*Sambucus* edge which now exists and which was probably not available before 1965. The *Sambucus* areas of the bamboo cycle hold high potential for grazing and browsing animals and are heavily used so that feeding trails of rhino and elephant form a network within them, and there is nearly always a distinct marginal trail either for passage or for feeding on the marginal bamboo fronds. The stands of bamboo which I visited in July 1976 on the West of the escarpment (Kinangop side) were under great pressure from elephant. Large culms had been pulled down and trampled and I could find very few undamaged emerging bamboo shoots. Conditions on the East (Mweiga and Nyeri) side were much better. There was less damage to mature bamboo and new shoots were plentiful.

In the relatively non-seasonal climate of the tropics, biological events are based on obscure triggers. Tweedie (1965) has documented periodic flowering in upland Kenya Acanthaceae, but we are a long way from an understanding of the phenomenon. The bamboo cycle creates a very high heterogeneity in the area as a whole and is of central importance to its carrying capacity, and so reserve management would gain from knowledge of the physiology and ecology of flowering. Therefore the bamboo cycle itself is a worthwhile subject for conservation, so that if the main flowering area of the bamboo became totally disturbed by big game pressure or by exploitation through agriculture or forestry, a sufficient area for the full development of the natural cycle should be set aside lest an outstanding example of a natural biological process be lost.

Janzen (1976) discussed periodic bamboo flowering and its evolutionary significance which he suggests could be due to a need for overcoming seed predation by spasmodic over-production. In my observation of bamboo regeneration, I have never seen a seedling. All regenerating plants have been traceable to fallen culms, and Wimbush (1947) agrees with this observation. This of course does not argue against Janzen's thesis, but may simply be a feature of a species marginal to the central range (East Asia) of that genus. In any case my observations suggest that the young shoots are the most grazed part of the life cycle. Excessive predation of these could possibly eliminate the bamboo. To follow Janzen and suggest an alternative evolutionary potential for the cycle of bamboo regeneration is not difficult. For surely the diversification of the habitat into mosaics, where the *Sambucus* patches hold prime browse material, would reduce pressure on those very vulnerable 60 cm spikes of high nutrient content on the bamboo woodland floor.

The bamboo is part of a more diverse woody vegetation at the lower part of its range. Groves of *Podocarpus latifolius, Dombeya goetzenii* and *Nuxia congesta* grow amongst the bamboos in favoured sites. Based on my general observation I tend to regard those favoured sites as also the sites of most frequent flowering of bamboo, although I have no quantitative evidence for this. I have also observed seedlings of these tree species most frequently at the edges of bamboo flowered areas, and it it not unlikely that tree species distribution is indeed associated with the flowering pattern of the bamboo.

GENERAL DISCUSSION

Cyclic successions have been recognised for some time, Watt (1947) drew attention to their presence in certain British vegetation, while Kershaw (1973) dealt with them at length and extended the ideas to many situations where a plant species shows a cycle of performance at any one spot without affecting the vegetation as a whole. More recently Grubb (1977) has suggested that this process is responsible for a great deal of the diversity in plant communities in that the "regeneration niche", which is made available on the decline of an individual after its cycle of growth and maturity, is the major potential site for invasion of a closed community.

It is clear that communities which are characterised by cyclical successions are simply those where dominance is such that the major plant species eventually replaces itself but during this process the entry of many different species constitutes an alternating community structure. In the examples presented in this paper the bamboo cycle is more impressive in this respect than the *Alchemilla* because there is a far greater disparity between environments in that cycle than in the *Alchemilla.* But it may be that there is a general principle involved here because long lived dominants must show a certain synchrony in their phases of growth for the cycle to be recognized. If the bamboo culms on the Aberdares flowered and died one or two at a time, replacement by *Sambucus* for a few years would be unremarkable and the whole community would present the aspect of mixed *Arundinaria alpina/Sambucus africana* with abundant lianas. It is the synchrony which gives the major effect and this is lacking in the *Alchemilla,* where the recognition of the various phases in the stands reported on here is probably due to differing ages since their last firing or burning; old stands show a mixture of recognisable phases. This is very similar to the situation in *Calluna vulgaris* in Scotland (Gimingham 1972) where burning is a recognized management tool and even-aged stands are therefore produced which can be said to be predominantly pioneer, building or mature. It is clear therefore that longevity of the dominant and synchrony of life cycle behaviour are both responsible for elevating the diffuse "regeneration niche" into a definite cycle of community events. The ultimate may be the type of cycle imposed on soil nutrient conditions within the ecosystem as suggested by Florence (1965) for Douglas Fir and oak woodland with a time scale of c. 2000 years. Obviously such cycles must be increasingly hard to recognise as more natural vegetation becomes disturbed by man's influence.

REFERENCES

AGNEW, A.D.Q. 1974. Upland Kenya Wild Flowers: a flora of the ferns and herbaceous flowering plants of Upland Kenya. Oxford.

FLORENCE, R.G. 1965. Decline of old growth Redwood forests in relation to some soil microbiological processes. Ecology *46:* 52-64.

GIMINGHAM, C.H. 1972. Ecology of heathlands. London.

GLOVER, J. 1963. The elephant problem at Tsavo. East African Wildlife Journal *1:* 30-39.

GRUBB, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews *52:* 107-145.

HEDBERG, O. 1964. Features of afroalpine plant ecology. Acta Phytogeographica Suecica *49:* 1-144.

— — — 1975. Studies of adaptation and speciation in the afro-alpine flora of Ethiopia. Boissiera *24:* 71-74.

JANZEN, D.H. 1976. Why bamboos wait so long to flower. Annual Review of Ecology and Systematics *7:* 347-392.

KERSHAW, K.A. 1973. Quantitative and dynamic plant ecology. London.

TWEEDIE, M.E. 1965. Periodic flowering of some Acanthaceae on Mt. Elgon. Journal of the East African Natural History Society and National Museum *25:* 92-94.

WATT, A.S. 1947. Pattern and process in the plant community. Journal of Ecology *35:* 1-22.

WIMBUSH, S.H. 1945. The African alpine bamboo. Empire Forestry Journal *24:* 33-39.

— — — 1947. The African alpine bamboo. East African Agriculture and Forestry Journal *13:* 56-60.

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TABLE I

Mean cover percentage of species in three stands of dominant Alchemilla argyrophylla in the Aberdares Moorland.

Only species with 4 or more records are cited. Others (with stand number in parentheses) are: *Anagallis serpens* (2), *Ardisiandra wettsteinii* (1), *Carduus chamaecephalus* (1), *Carex greenwayii* (3), *Haplosciadium abyssinicum* (2), *Helichrysum ellipticifolium* (1), *Helictotrichon milanjianum* (3), *Heracleum abyssinicum* (2), *Hypericum lanceolatum* (3), *Lobelia duriprati (1), Lysimachia ruhmeriana (3), Mariscus kerstenii (2), Ranunculus oreophytus (2), Sambucus africana (3), Senecio schweinfurthii (2).*

Stages of Cycle Present in Stand	1	2	3
	Pioneer and Building	Building and Mature	Mature and Degenerate
No. of Quadrats	23	20	16
Forbs:			
Alchemilla argyrophylla	28.73	35.0	56.24
A. johnstonii	10.22	12.75	
A. rothii	4.13		
Ajuga remota		0.25	0.94
Carduus keniensis	2.83	0.75	
Cerastium afromontanum		1.50	
Conyza subscaposa	0.87		
Dichondra repens	3.70	3.25	
Euphorbia schimperiana	5.22	3.75	
Galium kenyanum	0.43	0.25	
Geranium arabicum		0.50	1.87
Helichrysum cymosum	0.65	2.00	
Hypericum peplidifolium	2.83	1.00	0.62
Luzula johnstonii	4.78	1.00	0.94
Oxalis corniculata	4.78	4.25	7.50
Pimpinella keniensis	5.00	3.75	
Polygonum afromontanum		0.25	0.93
Satureia kilimandschari	0.86	1.00	
Sibthorpia europaea	0.60	0.25	4.07
Sonchus afromontanus	0.22	0.25	
Stachys alpigena		5.25	3.75
Swertia crassiuscula	0.80	1.00	
Tolpis capensis	1.09	0.75	
Trifolium burchellianum	3.69	4.00	
T. cryptopodium	0.43		
Uebelinia crassifolia	1.08	0.75	
Veronica glandulosa	1.74	1.75	
Viola eminii			3.13
V. nannae	5.00	2.00	
Grasses and Sedges:			
Agrostis kilimandscharica	5.87	1.75	1.24
Anthoxanthum nivale			3.12
Carex conferta	5.00	3.00	4.69
Festuca abyssinica		8.25	
F. pilgeri		4.00	
Koeleria capensis	13.91		1.24
Mariscus sp.		2.75	
Pentaschistis borussica	5.21	15.0	0.31
Poa leptoclada	3.05	3.0	2.18
Other species (Number)	2.39(4)	3.00(7)	2.87(5)
Bryophytes:			
Acrocarpous mosses	8.70	2.0	
Pleurocarpous mosses	2.17	1.75	1.25
Leafy liverworts	3.04	1.75	2.19
Mean pH (aq.)	4.62	4.67	4.65
Diversity (H)	3.039	2.732	1.746
Cover Total	138%	137%	99%

TABLE 2

Features of successional stages in the Aberdares Bamboo (Arundinaria alpina)

		Pioneer bamboo	Building bamboo	Mature bamboo young Sambucus	Flowered bamboo-	Mature Sambucus	Old Sambucus
Arundinaria alpina (culms. m^{-2})		3.7	3.4	1.1	trace		
Arundinaria culm variance		4.14	1.76	1.20			
pH mean		5.66	5.24	5.13	5.07	5.06	6.38
Acalypha cf. volkensii	S	0.20			0.73	0.36	
Acritochaete volkensii	W	2.20	8.71	11.80	14.73	9.00	
Australina acuminata	W		1.71				0.67
Cardamine africana	W		1.14	2.80	0.36		0.67
Cynoglossum lancifolium	S	0.40	0.40		2.45		4.50
Cyperus dereilema	W	1.55	5.00	10.40	4.73		
Cyphostemma kilimandscharicum	C	0.40				1.45	3.83
Dichrocephala integrifolia	S					3.45	0.67
Droguetia iners	W	0.20		0.40			
Galium chloroionanthum	C		1.14				0.67
Geranium arabicum	S			5.64		2.0	
Girardinia bullosa	W	0.40				0.36	
Hydrocotyle mannii	W		1.14				0.67
Mikaniopsis clematoides	C	0.60				3.27	
Oxalis corniculata	S				2.91		4.67
Pilea spp.	W	0.60	2.29			0.36	
Poa schimperiana	S					0.72	0.67
Polystichum fuscopaleaceum	I	0.60					0.67
Pseudocarum eminii	C	0.60	0.57	8.10	9.36	3.27	14.50
Pteris catoptera	I	0.20	5.57	1.50	0.73	3.18	2.67
Sambucus africana	S	1.00	1.71		5.27	20.82	42.50
Sanicula elata	W	0.20	2.86	13.00			0.67
Selaginella kraussiana	W		6.71				0.67
Senecio moorei	S				0.36	0.36	2.50
Senecio syringifolius	C	1.80	1.14	2.40	12.55	4.18	2.00
Solanum terminale	I		1.71	0.80		2.18	
Veronica abyssinica	S				2.18	0.73	3.83
Viola abyssinica	I	4.0	0.80	1.1		3.83	
No. of quadrats		20	7	10	11	11	6
Additional species (number)		3	2	2	1	7	9
Additional species (Cover)		1.0	4.57	1.60	0.36	8.89	26.00
Total Ground Flora Cover		11.95	49.97	53.6	63.46	62.58	118.86
Assemblage diversity **($\overline{H}$)**		2.581	2.581	1.923	2.201	2.385	2.465

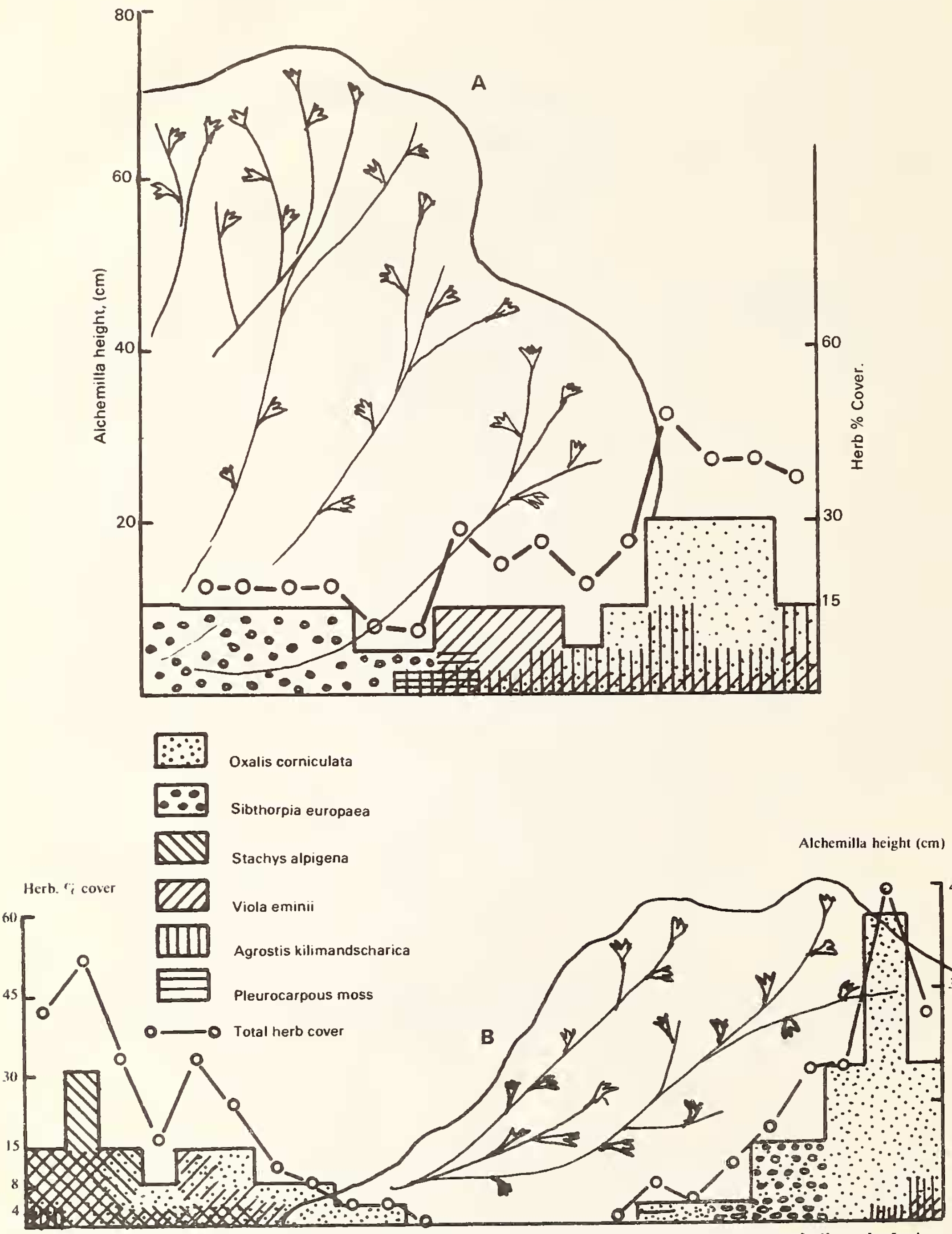
Mean cover is given for species occurring in more than one stand; data are given for six characteristic stands. The major habit of each species is given as: C, climber; I, indeterminate; S, ruderals of disturbed ground, W, woodland floor herbs. These categories have been decided from general observation and herbarium specimens.

TABLE 3.

Cover contributions (as percent of total herbaceous cover) of 4 habitat classes from Table 2.

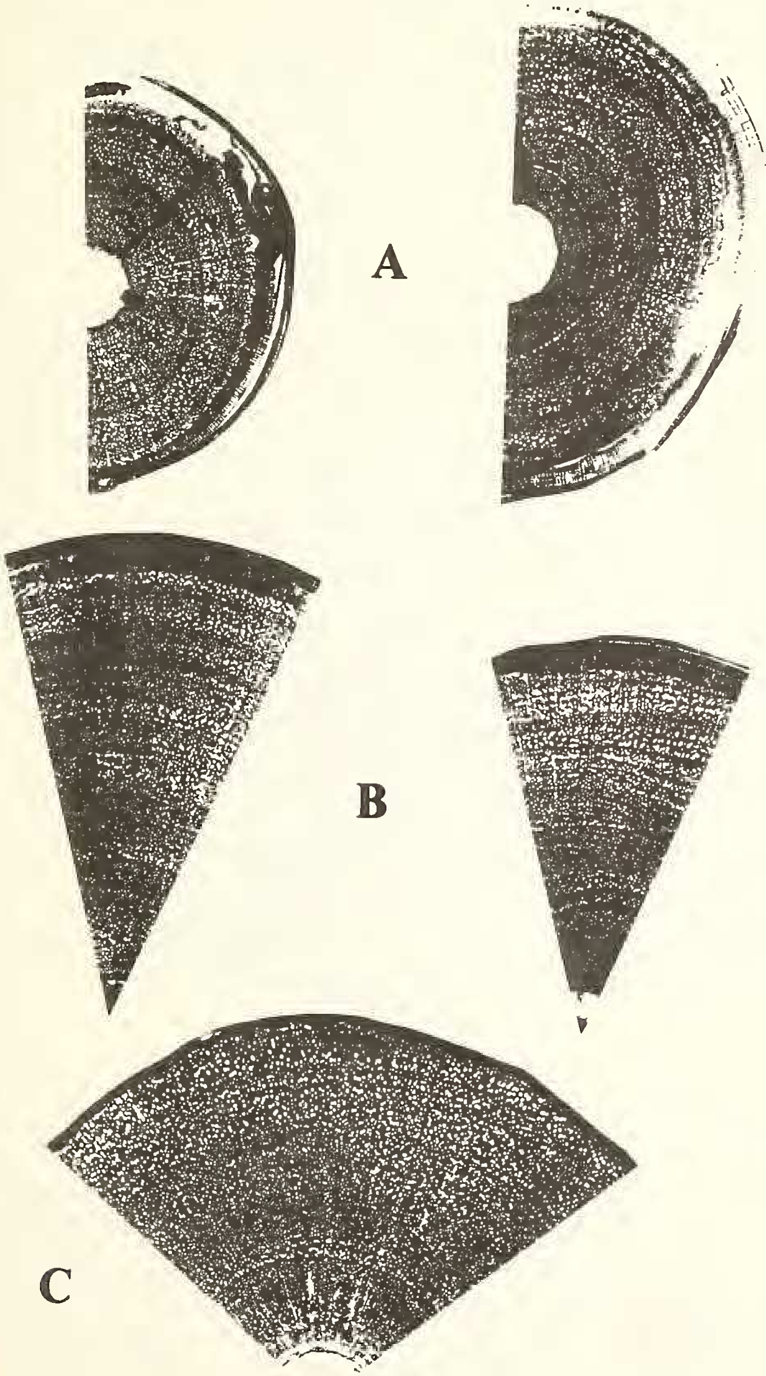
Successional stage

	Pioneer bamboo	Building bamboo	Mature bamboo Young Sambucus	Flowered bamboo	Mature Sambucus	Old Sambucus
Woodland Flora plants (W)	43.1	59.1	71.6	31.2	15.5	2.8
Plants of disturbed ground						
(a) including *Sambucus*	13.4	3.4	0	30.8	53.7	67.2
(b) excluding *Sambucus*	11.7	0	0	22.5	20.6	31.5
Climbing plants (C)	28.4	5.7	19.6	34.5	19.5	17.7
Azonal species (1)	6.7	22.68	5.8	8.6	2.8	6.0



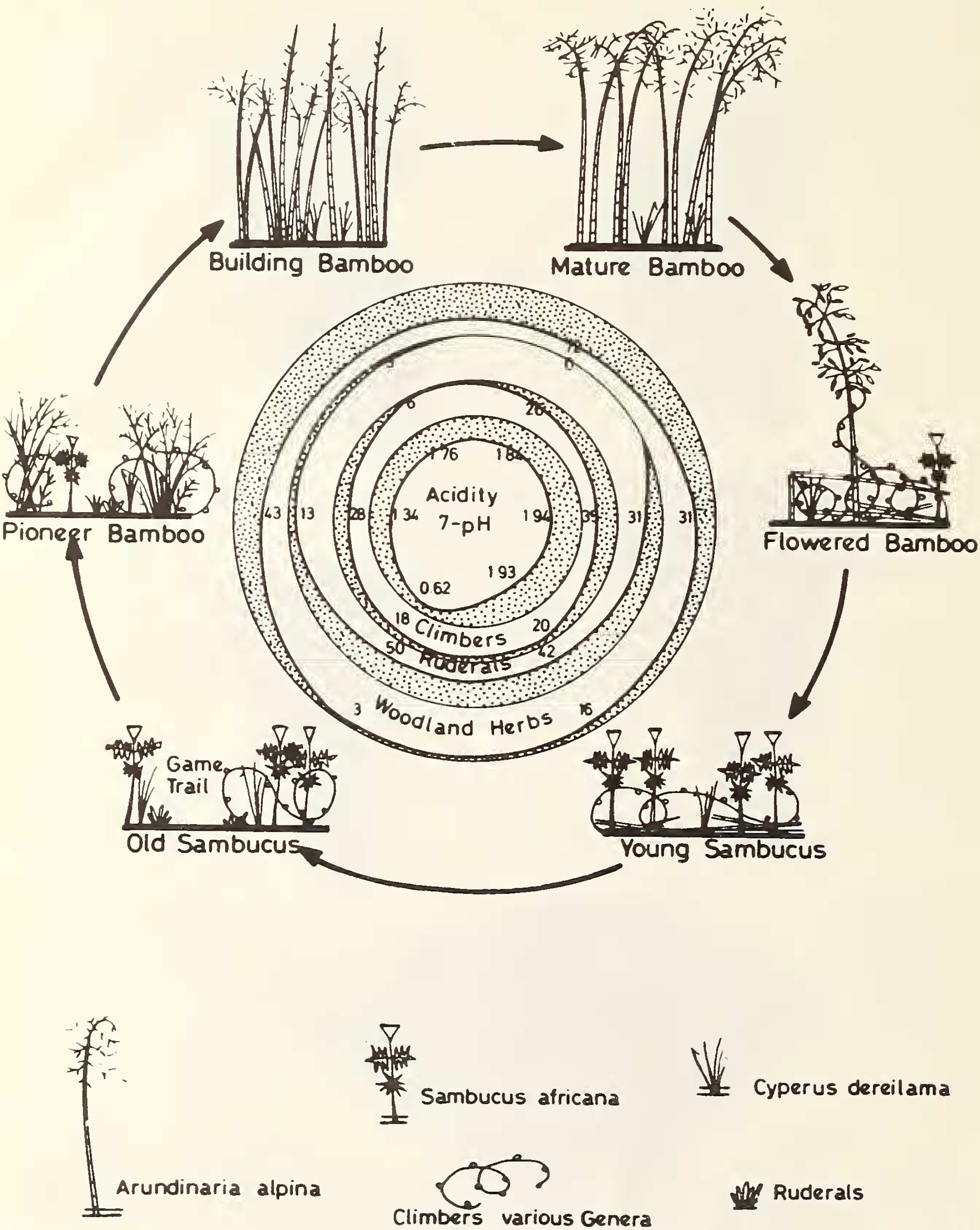
Two diagrammatic representations of transects through changing phases of the *Alchemilla argyrophylla* cycle. In A, a mature bush is suppressing *Agrostis* and *Oxalis* in favour of the shade tolerant *Sibthorpia*. In B, a degenerating bush is allowing entry of *Oxalis* and *Agrostis* both in the centre, where perennial herbs *(Viola, Stachys)* are establishing, and at the margin where *Sibthorpia* is being replaced.

Fig. 1



Sections through stems of *Alchemilla argyrophylla* taken at ground level from (A) pioneer and building, (B) mature and (C) degenerate phases of the successional cycle.

Fig. 2



A diagrammatic illustration of the successional cycle associated with the bamboo *(Arundinaria alpina)* on the Aberdare Mountains. The six phases illustrated do not exist for similar time periods. The course of change of acidity (observed pH substracted from 7) and the percentage cover of three floristic elements are shown as concentric plots. Values from Tables 2 & 3.

Fig. 3