Disturbance ecology and size-class structure of the Mulanje cedar of Malawi, *Widdringtonia whytei*, and associated broadleaved forest

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Abstract

The disturbance ecology and regeneration patterns of the emergent conifer, *Widdringtonia whytei*, and five broadleaved species, *Aphloia theiformis*, *Rapanea melanophloeos*, *Maesa lanceolata*, *Maytenus accuminata* and *Psychotria mahonii,* were inferred from population size structures in the mixed conifer-broadleaved forests of Mt. Mulanje, Malawi. The size-class structures of the emergent cedar populations were characterised by even-sized, disjunct frequency distributions. Seedling recruitment was found in recently burnt sites and not in middle-aged or old-growth forest. This indicates reliance on the catastrophic mode of regeneration for *W. whytei*, which takes advantage of the well-lit, competition free environment after large-scale disturbances provided by fire. The sub-canopy angiosperms primarily had all-sized frequency distributions, with at least some individuals found in each class within their size range, indicating continuous regeneration under a closed forest canopy. These results emphasize the dependence of long-lived conifers such as the Mulanje cedar on large-scale disturbance for regeneration and long-term persistence of the species.

Introduction

The lack of seedlings, saplings, and young trees, and a dominance of larger and older individuals of several forest tree species was initially attributed by plant ecologists to climate change during recent centuries or by the successional status of the forest (see Wardle, 1963, 1978 as an example). Today an extensive amount of literature focused primarily on New Zealand and South America revolves around the ecology and dual nature of southern conifer forests, their long-term periodic behaviour, the significance of large-scale disturbance events, and how these interact to produce phases of regeneration followed by biomass increment and canopy collapse (Enright & Hill, 1995). Based on the scale and severity of natural disturbance, three main categories of regeneration pattern can be observed: 1) catastrophic regeneration refers to the establishment of most of the light demanding population during a short time following infrequent, large-scale disturbances such as fire, mass movement and windthrow, resulting in large discontinuities in the stand structure and large patch sizes; 2) gap-phase regeneration occurs in smaller canopy gaps resulting mostly from the death of one to several trees causing fewer discontinuities in stand structure and smaller patch sizes; 3) continuous regeneration refers to the growth of shade-tolerant species beneath forest canopies, continuously replacing the old and dying trees and resulting in an all-aged structure characterised by large quantities of small stems and successively fewer in larger age-classes as a result of natural thinning, and very small patch size. Note however, these categories are not necessarily temporally and spatially isolated in the landscape as different species apply different strategies depending on their divergent shade tolerances, micro-site requirements and life spans (Enright & Hill, 1995). The stand structure of the emergent conifers *Agathis australis* and *Libocedrus bidwillii* in New Zealand support a cohort regeneration cycle where dense recruitment occurs in successional communities following course-scale disturbance, followed by the absence of regeneration under the self-thinning and ultimately senescing adult trees. Continued mortality creates a higher frequency of canopy gaps which allows for the development of several successive, less synchronous waves of recruitment, thus producing several cohorts in a particular stand (Veblen & Stewart, 1982; Ogden et al., 1987; Ahmed & Ogden, 1987). Similarly, in *Austrocedrus-Nothofagus* forests of northern Patagonia, seedling establishment for both species is abundant following stand-destroying fires and ceases once a closed canopy develops. Blow down by strong winds can then open enough of the old, even-aged canopy for new, sporadic recruitment to occur (Veblen & Lawrence, 1987; Dezzotti, 1996). Furthermore, the regeneration patterns of several conifer species vary according to habitat and competition by associated species (Enright & Hill, 1995). Therefore, an interplay between the catastrophic regeneration pattern and subsequent gap-phase regeneration with senescence of the first cohort or small-scale local disturbances is a common feature of conifer-dominated or mixed conifer-broadleaved forests characterised by long-lived species.

Given the absence of continental land further than 35^0 S in Southern Africa, it is perhaps not surprising that this region is poorly represented by Gondwanan (southern temperate) tree species. Only four genera of conifers are present, *Afrocarpus, Podocarpus, Juniperus, Widdringtonia*, and of these, only *Podocarpus* are considered true forest dwellers (Enright & Hill, 1995). *Widdringtonia* is a monoecious genus endemic to Africa and in which four species are currently recognised (Pauw & Linder, 1997). *W. cedarbergensis* and *W. swarzii* has a limited distribution in the Cape Fold Mountains of South Africa, whereas *W. nodiflora* is found in a narrow belt of habitats with a temperate climate that extend from south-west South Africa to east Africa and Mt. Mulanje in Malawi. *W. whytei* is endemic to Mt. Mulanje. Observations of morphological variation in growth form first led to the hypothesis of the existence of 2 distinct species on Mt. Mulanje. After much confusion regarding the taxonomic status of the 'Mulanje cedars', this idea was finally supported when Pauw & Linder (1997) discovered two sympatric species based on the phenetic, phylogenetic, ecological and biological species concepts. Pauw & Linder (1997) related the observed differences in morphological and life history traits between *W. whytei* and *W. nodiflora* to their divergent fire-survival strategies: The resprouting and highly serotinous species, *W. nodiflora* (multi-stemmed, narrow crowned tree), generally occurs in fire-prone ericaceous scrub and grassland surrounding patches of forest where it is able to coppice after fire and retain its seeds in cones. The accumulation and protection of seeds in cones, fire-synchronised seed release, early switch to adult foliage and seed production are considered to be adaptations to a fire-prone environment. In contrast, the obligate reseeder and weakly serotinous species, *W. whytei* (taller tree, wide crowned), has limited fire survival ability and thus restricted to deep fire-protected valleys and gorges where it is morphologically shaped to compete for light in its forest environment in that juveniles allocate all their resources into vertical growth, forming wide crowns over their competitors at a later stage.

Edwards (1989) reported that the Mulanje cedar is unable to regenerate under the closed canopy of a mature or climax forest (old-growth) due to conditions in the ground layer being unfavourable for germination and seedling establishment. The occasional presence of cedar seedlings and saplings on the edge of the forest in open scrub communities (in association with pioneer species) combined with the absence of new recruitment under middle-aged and mature forest led him to suggest that the Mulanje cedar acts as a forest pioneer. It is the first species to recolonise a burnt site where it persists in the emergent canopy layer while other light-demanding pioneer species are suppressed by shade-tolerant angiosperm species. The cedars are however ultimately and inevitably overtopped by the angiosperm layer when their fitness starts to decrease with increasing age. According to Pauw & Linder (1997), the emergent cedar trees in climax forests of perhaps 500 years old are represented by old and lichen-draped skeletons with no new recruitment to replace the adults, and in the event of a tree-fall gap and subsequent seedling release, the slow-growing gymnosperm seedlings would be outcompeted by the faster growing angiosperms which rapidly fill the gap. It is only at the next course-scale disturbance event when sufficient light reaches the forest floor that significant quantities of cedars will be able to re-establish. Pauw & Linder (1997) found that some of the larger trees were able to survive mild fires by means of their thick bark, subsequently reseeding the burnt area and thus re-entering the successional process. For the above mentioned reasons, fire is considered an essential pre-requisite for large-scale natural regeneration and long-term persistence of the species. However, the timing between fires is critical since too frequent fires don't allow enough time for the trees to reach reproductive status and too infrequent fires result in large scale tree mortality (old age?) before competition-free space is created for their seeds to germinate and seedlings to establish. By considering the age of mature cedars of 120-200+ years, the Edwards (1989) proposed a fire return interval of 100-200+ years for the successful rejuvenation and ultimate survival of cedar stands on Mulanje.

The increasing human population numbers surrounding Mt. Mulanje have caused several threats to the ecosystem, of which most are either directly or indirectly related to varying degrees of deforestation. The most devastating of these is the increase in fire frequency which has been noted by several authors in the literature on the cedars of Mt. Mulanje (Edwards, 1982; Sakai, 1989a; Lawrence et al., 1994; Makungwa, 2004; Bayliss et al., 2007). Some fires are natural but most can be traced to anthropogenic causes such as deliberate fires set by the Forestry Department itself (Sakai, 1989b), hunting fires to flush out game, and crop-burning fires that get out of control and spread onto the mountain (Bayliss et al., 2007). According to French (1986), the problem of fuel-wood collection by rural communities in Malawi is unsolvable since, based on the price of fuel-wood, subsidies would be too great for the establishment of government plantations and private owners almost always convert their land to cash crops with much higher economic returns. Due to the attractive properties of the Mulanje cedars, including its high-valued timber, attractive fragrance, and natural insect resistance the trees has become highly desirable resulting in extensive ongoing illegal logging by the local communities (Bayliss, 2007). The spread of invasive species on the plateau presents another threat to Mt. Mulanje and its native biodiversity. The most serious of these is *Pinus patula*, first planted in Mulanje in 1946 (Edwards, 1982) and has since completely invaded certain areas of the mountain (Bayliss et al., 2007). Extensive damage to cedars has been the result of an invasive species of aphid, *Cinara cupressi*, first reported in Malawi between 1985 and 1986 (Chilima, 1989; Sakai, 1989a), and originally found on the Mexican cypress *Cupressus lusitanica* planted on Mt. Mulanje 80 years ago (Bayliss et al., 2007). The effectiveness of a bio-control program based on the release of a parasitic wasp, *Pausia bicolour*, is not clear and still awaits investigation after all these years (Chilima, 1989; Bayliss et al., 2007). These threats have had huge impact on W. whytei populations across Mt. Mulanje, and today the species is considered as endangered on the IUCN Red List (IUCN, 2010).

Despite the fact that important decisions had to be made in the past regarding the management and conservation of *W. whytei*, little is known with respect to its disturbance ecology, seedling recruitment requirements and developmental or successional patterns over time. The objectives of this study is to examine cedar clusters on Mt. Mulanje, and for each cluster determine the size-class structure of *W. whytei* and the evergreen angiosperm forest by means of diameter and tree height data. Forest dynamics and recruitment strategies of the forest trees on Mt. Mulanje are compared with some of the dominant conifers from the rest of the southern hemisphere, including New Zealand and South

America. It is hypothesized that *W. whytei* is characterised by the 'catastrophic regeneration' pattern proposed by Veblen & Stewart (1980). If large-scale disturbance is central to the simultaneous fire-stimulated recruitment of young *W. whytei* seedlings, then all the cedar trees within a particular patch should have a similar size-class structure, since they all germinated more or less the same time after the last fire. Tree diameters in a particular cluster should thus be normally distributed and characterised by large discontinuities in size classes. It is predicted that where the disturbance history differs between the different cedar clusters, the size-class structures of these stands should similarly be different. The boundaries of previous fires in the landscape should therefore coincide with the boundaries of stands with different size-class structures The angiosperm forest layer is expected to be lower than that of the emergent *W. whytei* canopy since the shade-tolerant evergreen forest only become established once a dense layer of light-demanding pioneer species (including *W. whytei*) provide favourable conditions with respect to shade. The presence of two sites that recently burned, two sites that were disturbed at an unknown time in the past, and two sites with mature forest that has not been disturbed for 200+ years makes this an essential comparative study to investigate the effect of disturbance on stand structures. Although the cedar forests have been repeatedly disturbed in the past resulting in the current stand structure being unnatural and partly a result of anthropogenic activities (e.g. increased fire frequencies and tree logging), this study would still provide a general size-class structure of the remaining trees. Important information could be gained regarding the cedar clusters' responses to natural and anthropogenic disturbance events, the role of disturbance in the dynamics of these mixed angiosperm-conifer forests, and the regeneration strategy of the dominant species present. The current size-class structure is compared with the results from previous studies where possible and recommendations are given for the long-term conservation of the species.

Methods

Study area

Mt. Mulanje is located on the plains of Southeast Malawi near the Mozambique border (see Fig. 1). It is the highest mountain in tropical southern Africa, its sides rising abruptly above the surrounding plains from 600-700m to >3000m at its highest point, Sapitwa peak. Mt. Mchese, a small satellite mountain to the north of Mt. Mulanje separated from the main mountain by the Fort Lister Gap, is included in the Mt. Mulanje massif (Strugnell, 2002). The mountain was first declared a forest reserve in 1927 under the jurisdiction of the Forestry Department of Malawi, comprises a unique mixed mountain ecosystem rich in botanical bio-diversity and now covers an area of 580 km^2 (58 000 ha) of predominantly mountainous terrain (Bouvier, 2006).

Geologically, the Mulanje Massif consists of granite, quartz-syenite and syenite that give rise to steep slopes and shallow dystric-fersialic soils. It has all the attributes of an inselberg, which occur as solitary, usually monolithic, dome-shaped Precambrian rock outcrops in tropical regions (Porembski et al. 1997). The mountain comprises a plateau of basins and deep river gorges at an altitude of 1800m, and steep rocky peaks that often reach 2800m (Warren et al. 2001). Botanically, the dominant vegetation on the Massif includes montane forest (including *W. whytei*) and grassland on the plateau and miombo woodland (mesic-dystrophic savannah dominated by *Julbernardia* and *Brachystegia* species) on the lower slopes. The mean annual rainfall and temperature for the Afromontane forests and grasslands on the plateau is 2500mm and 16 °C, respectively, whereas that for the miombo woodland is 800mm and 21 °C (Orr, 2000). The south-east region of the plateau receives significantly more rainfall than the north-west area due to the prevailing Mozambique coastal trade winds, thereby creating a range of biomes within the mountain ecosystem (Bayliss et al., 2007).

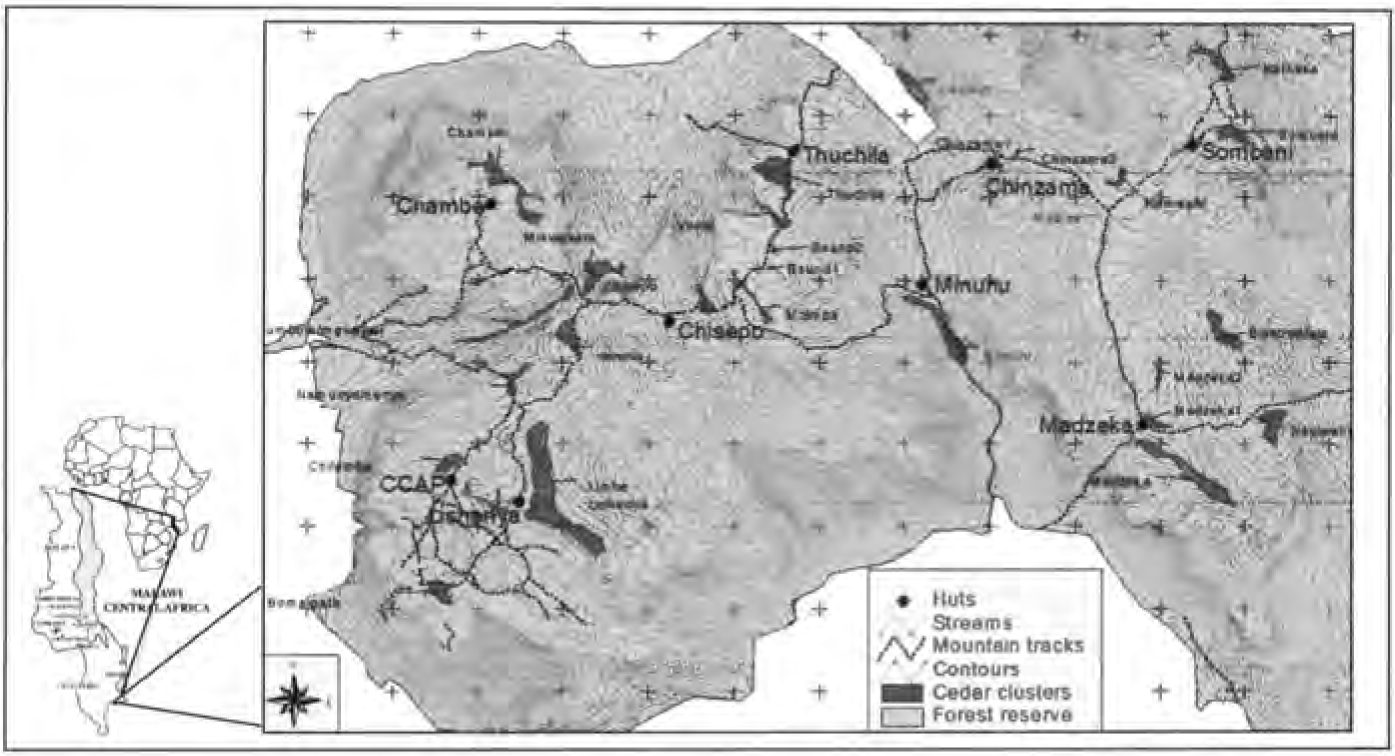

Fig. 1: A composite map illustrating the location of Malawi in Central Africa (left), and the cedar distribution on Mt. Mulanje (modified from Makungwa, 2004).

Mulanje Mountain represents an ecological island of biodiversity. In a comprehensive checklist of the spermatophytes of Mt. Mulanje, over 1300 naturally occurring or naturalised plant taxa, representing 138 families and 622 genera of gymnosperms and angiosperms have thus far been documented for the Massif (Strugnell, 2002). A total of 69 taxa were recorded as endemic to Mt. Mulanje (representing 5.3% of the total floral composition), 25 taxa are characterised by limited distribution ranges (near-endemics), and 13 taxa has wider but disjunct natural distributions. Most of the endemics on the mountain occur primarily in high altitude grasslands, scrublands, rocky terrain, and to a lesser extend in, or at the edge of, lower-altitude forest patches. The cedar populations are found at altitudes between 1525m and 2133m and are primarily confined to hollows, valleys and areas around the base of steep cliffs where protection from frequent grass fires is sufficient (Edwards, 1982). Although several inventories on the available cedar stands on Mt. Mulanje have been undertaken in the past (Edwards, 1982; Sakai, 1989a; Lawrence et al., 1994; Makungwa, 2004), the different methodologies employed by the various authors make direct comparisons difficult. However, these studies all support the observation of low natural regeneration and that the clusters consist of a more or less constant average of 30% dead cedars over time. Sakai (1989a) calculated the total area occupied by cedars on Mt. Mulanje as 1,462 ha, whereas Makungwa (2004) reported a total area of 845.3 ha, representing a reduction of 616.7 ha in 15 years. The stocking levels of live and dead cedar were reduced from 300.75 stems/ha (Edwards, 1982, all stands averaged) to 91 stems/ha (Makungwa, 2004) at Litchenya, and from 568 stems/ha (Edwards, 1982, all stands averaged) to 91 stems/ha (Makungwa, 2004) at Thuchila in a period of 22 years. This reduction in the amount of cedar remaining on Mt. Mulanje illustrates the severity of the problem regarding the conservation of the cedars. The six clusters examined in this study were found widespread across the plateau (see Fig. 1).

Stand structure

This study was commenced on the 7th of June 2010 and lasted for a total of 6 days thereafter, during which one of the six clusters were visited per day. Four transects were laid out through the densest part of each cedar stand examined, except for Nathaka, where five transects were laid out to incorporate the increased environmental variability observed at this site. At each cedar stand, each transect was placed 30m from the next and consisted of a 25m nylon rope marked at 5m intervals. Every 5m down each transect, all tree species found within 5m from the transect in the direct line of sight to left, then at next 5m interval to the right, were recorded. All seedlings and saplings (≤3cm basal diameter, BD) present were counted according to species, and their heights measured. The diameter at breast height (DBH) and height were recorded for all live adult trees present, whereas only the BD of dead, damaged and felled trees, were recorded. In the case of multi-stemmed individuals, only the diameter of the largest stem was measured. Identification of live trees was predominantly done using leaf characteristics, whereas dead trees were identified where possible by their specific bark characteristics. BD was measured to the nearest cm with a measuring tape (circumference converted to diameter) and tree height was measured with the measuring tape for the smaller size classes but with an inclinometer for the larger size classes. The geographic co-ordinates and altitude of the starting point of each transect were recorded with a hand-held global positioning system (GPS MAP 60 CSX).

This information, along with a brief description of each site, is presented in Table 1 in the appendix.

The stand structures were investigated by producing a set of frequency distributions of preselected tree size-classes for both the diameter and height data in Excel. The presented diameter data encompass live, dead, burnt, damaged, and felled trees, as well as seedlings, whereas in the height data felled trees were excluded from the analysis. Attention was focused on W. whytei, and the five most dominant angiosperm species, for each of the six stands.

Results

A total of 398 stems, consisting of the emergent conifer *W. whytei* and the five dominant sub-canopy angiosperm species, *Aphloia theiformis, Rapanea melanophloeos, Maesa lanceolata, Maytenus accuminata* and *Psychotria mahonii* were included in the diameter analysis of this study. A subset of these (360 stems), were used in the analysis of height data for all six stands visited, the difference being primarily due to the absence of height data for felled cedars.

At the Sombani cedar cluster, the size-class structure (both diameter and height data) of *W. whytei* is relatively disjunct and characterised by a bell-shaped distribution with most trees lying in a narrow size range (middle sized classes, Fig. 2 in appendix). Although a few older trees were present, trees in the largest size-class were absent. No seedlings or saplings were present under the emerging cedar and subdominant angiosperm canopy. At Nathaka cedar cluster, which burned 2 years ago, *W. whytei* is dominated by younger tree size classes. Seedlings were most abundant at this site (22 encountered), and some of the larger middle-sized trees survived the most recent fire. The largest size classes are completely absent from this stand. Cedar trees at Chinsama were much less disjunct in terms of size-structures and rather represented by an all-sized distribution. However, tree densities (numbers encountered) were less at this stand compared to the densities recorded at most of the other clusters. Trees in the largest size-class were not present in this cluster and seedlings were rarely recorded. The second highest number of seedlings (nine encountered) was recorded from Bvunje cedar cluster, which burnt four years ago. From both the diameter and height data of W. whytei, it is clear that some of the older and larger individuals survived the last fire at this site, although not many. The height-structure appears to me more disjunct than the diameter-structure due to the absence of middle-sized trees in the height data. In the dense, old-growth forest of Litchenya at site 1 and 2, cedar densities are low, size-class structures are represented by bell-shaped distributions and the majority of trees encountered are narrowly distributed in the middle to large size classes. No seedlings or young trees were recorded at this site. However, an observation was made of two seedlings that were not located within a transect at Litchenya 2, where some large cedars were felled as well. The largest tree in terms of diameter encountered in this study was felled at Litchenya at site 1 and measured 120cm. Similarly, the tallest live tree was recorded from Litchenya 1 and measured 45m.

The broadleaved forest canopy is lower than that of the conifer resulting in smaller size-class structures (Fig. 3-7 in appendix). Note that the scale used in the figures was kept similar for the sake of comparisons between the conifer and the angiosperms. When considering the fact that the angiosperm species recorded were mostly in the first three size-classes with respect to both diameter and height, and that their maximum size is more or less half that of W. whytei, it is clear that the dominant angiosperms present are to some extend represented by all-sized stands in that within their size range, individuals were recorded in most size classes, although with some variability in the relative proportions that make up these size classes. Seedlings were present at all sites for most angiosperm species, including *A. theiformis*, *R. melanophloeos*, and *M. lanceolata* (fig. 3-5 in appendix). Seedling recruitment for *A. theiformis* was lower at Litchenya (1 seedling) compared to the burnt sites (5 and 6 seedlings), although this trend could be due to a sampling error. *R. melanophloeos* showed at most sites the highest numbers of stems in the smallest size class, with successively less stems in the larger classes (Fig. 4). *M. accuminata* and *P. mahonii* (Fig. 6 & 7 in appendix) had more disjunct distributions in that *M. accuminata* was completely absent from the recently burnt sites, Nathaka (2 years ago) and Bvunje (4 years ago), and *P. mahoni* was not present at the most recently burnt site, Nathaka, and at the mature forests of Litchenya. Large numbers of seedlings of P. mahoni was found at Sombani and Chinsama, the two sites that have not been disturbed in the recent past, but are not completely mature or developed yet. Furthermore, in the mature forests of Litchenya, P. mahoni is replaced by a related species not included in the size-class analysis, *P. zombamontana*. The presence or absence of these species at the various stands with different disturbance histories could be an indication of their different habitat requirements or successional status in the development of the forest since the last fire.

DISCUSSION

One of the most important observations of the current study with respect to the Mulanje cedars was the disjunct distributions in the size-class structures of the different clusters, both with regards to the diameter and height data. The narrowly distributed size-classes of the cedar populations in the different clusters could be interpreted as even-aged stands that all originated at varying ages since the last fire. Fires take out relatively large chunks of the landscape at any particular disturbance event and this type of recruitment can therefore be interpreted as the catastrophic regeneration pattern. Large numbers of seedlings establish in a relatively short period in the open and well-lit, competition-free environment after a fire. This results in the formation of even-sized stands of cedars, with the different sizes or stages observed in the different patches being a result of different disturbance histories. In Both *Austrocedrus* and *Fitzroya* stands of South America, course-scale natural disturbances such as the deposition of volcanic ash, lava flows, landslides, wind, and fire are important stand-initiating disturbances, making these conifers comparable to *W. whytei* with respect to the ecological game they play: being light-demanding, stuck in a closed-canopy forest, and thus requiring disturbance to regenerate and replace itself (Enright & Hill, 1995). However, both these species show evidence of an initial cohort following catastrophic disturbance, and as these even-aged stands age, the regeneration mode becomes of fine-scale gap-phase that produces more continuous age structures (Enright & Hill, 1995; Veblen & Lorenz, 1987). Similarly, *Agathis* and *Libocedrus* stands of New Zealand demonstrate periodic recruitment following large-scale disturbances, followed by gap-phase recruitment of a second, more depleted cohort (Enright & Hill, 1995). Data from Ogden et al. (1987) on *Agathis australis* supports a 'cohort regeneration model' in which high rates of recruitment occur after a large-scale disturbance, followed by self-thinning 'ricker' stands in which seedling establishment is rare, thus producing a 'regeneration gap'. Increasing tree senescence over time creates a higher frequency of canopy gaps which allows a second, less synchronous wave of recruitment. It does not appear as if the fine-scaled gap-phase regeneration pattern is a common strategy employed by the cedars of Mt. Mulanje. The cedars at each stand were relatively even-sized with no recruitment in mid-aged and mature forest stands. However, the spread around the dominant size-class observed at Sombani and the presence of a fairly all-sized distribution at Chinsama might indicate that regeneration in canopy gaps caused by the death of one to several trees is not entirely impossible. Note however, this pattern could just be a result of these two sites being more anthropogenically disturbed in the past, relative to the other sites. The few seedlings observed in intact and mature forest at Litchenya 2 (not part of analysis) could either be a result of a previous planting programme or illegal logging resulting in some degree of fine-scale gap-phase regeneration.

Edwards (1982) noted higher densities of cedar trees at Thuchila compared to Litchenya where a more extensive evergreen forest thrived and concluded that this was a result of the different climates experienced by these two sites in that drier conditions at Thuchila were more suitable for cedar regeneration and stand development. Based on the results from this study, the lower densities of cedar at Litchenya is more likely to be due to the natural thinning process being more progressed or advanced at this site. From the six cedar clusters visited, Litchenya has experienced the longest period of time without natural disturbance and the trees present were in large size classes and old. Therefore, senescence of old trees is higher at Litchenya, and in the absence of new seedlings to replace them, it is natural for cedar densities to decrease with an increase in time since the last fire.

The smaller size-class structures found in the broadleaved species relative to the emergent cedars are indicative of their sub-canopy status. From a temporal perspective, it indicates that the angiosperm forest only established once high regeneration of light-demanding pioneers (including W. Whytei) has occurred. The pioneer species act as a nurse stand that creates a favourable micro-environment with respect to shade, and perhaps moisture, for the shade-tolerant broadleaved species. The predominant trend of the angiosperms being represented by all-sized (≈all-aged) frequency distributions supports the hypothesis that they are primarily shade-tolerant and continuously regenerates below the emergent cedar and sub-dominant angiosperm canopy. The higher recruitment of A. theiformis seedlings at the recently burnt sites might indicate a lower shade-tolerance in this species relative to the rest of the broadleaved species.

Due to the sampling technique utilized in this study (as opposed to using quadrants and sampling all species present), the following information regarding the presence or absence and relative abundances of the different species should be interpreted with caution from the figures. The absence of *M. accuminata* in the recently burnt sites is an indication of its nature of occurring primarily in forests and forest edges, often on rock outcrops in mountainous regions and along streams (Van Wyk & Van Wyk, 1997). It either has no adaptations to survive fire and is therefore only present in middle-aged to old-growth forest or its distribution might reflect its high levels of shade-tolerance in that it is only able to establish once a dense layer of pioneers provide enough shade for germination and growth. The absence of P. mahonii from Nathaka and Litchenya, and replacement of it by P. zombamontana at Litchenya, indicates that the former species might be considered mid-successional with respect to the temporal perspective of its establishment after the last fire at any particular site, or that it is characterised by intermediate levels of shade tolerance and thus not able to thrive in too open or too closed environments.

Since *W. whytei* has a much longer lifespan relative to the dominant broadleaved species (Edwards 1982), the turnover rates of the angiosperm forests are higher than that of the long-lived conifer canopy. During the 200+ year's lifetime of the conifer, the angiosperm canopy might experience several natural diebacks followed by new regeneration and canopy closure. This cycle will carry on until the all of the cedars have senesced and the entire canopy consists of broadleaved evergreen forest (various such systems were observed on the mountain). The only way to recruit new cedar seedlings is by 'resetting' the system through means of disturbance such as fire. However, care should be taken regarding the fire management program since firstly, the anthropogenic increase in fire frequency have resulted in several regions burning too regularly for the cedars to reach reproductive maturity, leading to a decline in total cedar stand densities over time, and secondly, the fire-break system applied for the conservation of the cedars often affects the fire frequency of the grasslands and associated bulbs on the plateau, which are meant to burn at an interval of one to a few years, resulting in undesirable changes in community composition and subsequent reductions in biodiversity.

A detailed spatial, size and age analysis of the cedar stands on Mt. Mulanje is required in order to outline the borders of previous disturbances to prevent sampling a patch characterised by different disturbance histories and thus not detecting the true stand structure of each site accurately. In mature, old-growth forest with thick undergrowth it is either difficult or impossible to distinguish natural occurring cedars from those of previous planting programmes from field observations alone. This could result in current stand structure that is not completely congruent with the natural disturbance history of the stand, and only a detailed spatial analysis combined with age- and size-structures, and perhaps a genetic study on the cedars, could potentially clarify their true origins. Due to the difficulty of ageing large numbers of trees, size is often used as a substitute for age but the relationship between these two parameters is highly variable and depends on the species and stage of stand development (Veblen 1986). Another benefit of an age analysis compared with size analysis is that dendrochronology could provide info regarding relative growth rates over long time scales and the dates of past environment-changing events, thus ensuring a better comprehension of the dynamics of the forests over time.

Conclusion

The even-sized and disjunct size-class distributions of cedars in the different clusters on Mt. Mulanje indicate that these trees originated in a narrow time frame following disturbance. This study, along with several other studies, does not support the idea that most long-lived conifers that show no recruitment are climatic relicts that are unable to regenerate under the current conditions. It rather emphasizes the importance of large-scale, stand-devastating disturbances such as fire in this case, to the successful regeneration and long-term survival of these gymnosperms. The cedar trees of Mt. Mulanje acts as a national symbol of heritage to the local communities and an important attraction for tourists. The result from this study could potentially be incorporated into the current management plans of Mt. Mulanje in order to ensure the conservation of the species for future generations.

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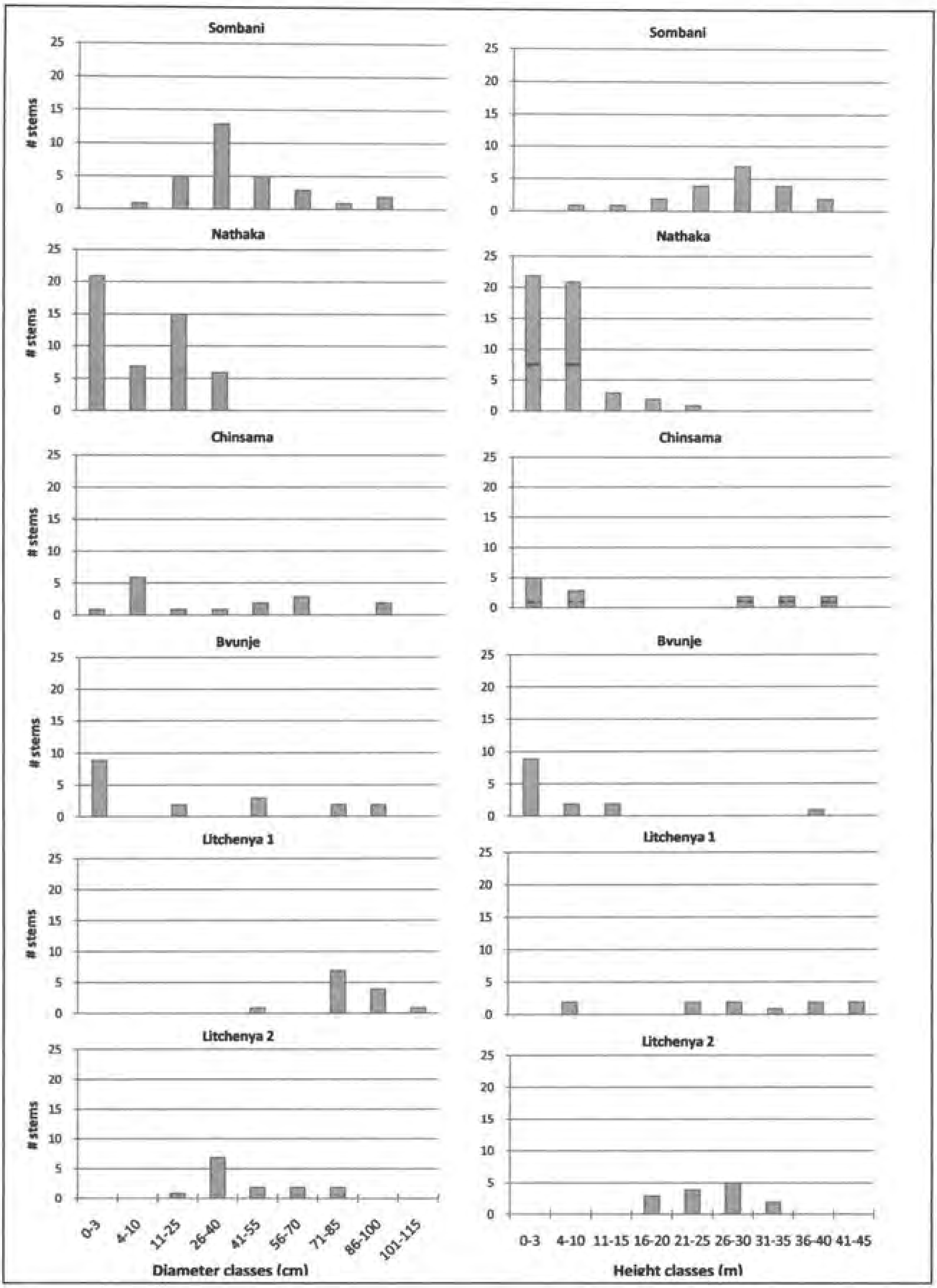
Appendix

Table 1: Geographic co-ordinates and altitude of each transect at each cluster; a brief description of each site is included.

Cedar cluster/transect #	GPS co-ordinates	Altitude (m)	Site description
Sombani - 1	S15°53’29.9” E35°42’36.5”	2105	Access moderate. Slope 15-35°. Disturbed in past. Secondary growth. Average canopy cover 75%.
- 2	S15°53’30.8” E35°42’38.1”	2094	
- 3	S15°53’31.0” E35°42’38.4”	2105	
- 4	S15°53’32.0” E35°42’39.6”	2100	
Nathaka - 1	S15°52’49.7” E35°42’01.8”	2078	Access easy. Slope 10-20°. Burnt 2 years ago. Some large trees survived. New undergrowth. Average canopy cover 5%.
- 2	S15°52’49.5” E35°42’02.5”	2071	
- 3	S15°52’49.6” E35°42’03.0”	2071	
- 4	S15°52’49.5” E35°42’03.5”	2070	
- 5	S15°52’49.2” E35°42’01.1”	2069	
Chinsama - 1	S15°53’52.2” E35°39’15.7”	2132	Access difficult. Slope 30-45°. Moist. Next to Chinsama river. Disturbed in past. Thick, lush undergrowth. Average canopy cover 75%.
- 2	S15°53’52.8” E35°39’15.6”	2145	
- 3	S15°53’53.0” E35°39’15.9”	2145	
- 4	S15°53’51.5” E35°39’16.4”	2157	
Bvunje - 1	S15°55’29.6” E35°35’55.3”	2012	Access moderate. Slope 15-40°. Part of valley burnt 3 years ago. New undergrowth. Average canopy cover 25%.
- 2	S15°55’30.4” E35°35’55.8”	2054	
- 3	S15°55’31.2” E35°35’56.3”	2056	
- 4	S15°55’31.3” E35°35’59.6”	2064	
Litchenya 1 - 1	S15°58’03.9” E35°33’14.3”	1888	Access very difficult. Slope 40-50°. Old-growth forest. Dense undergrowth. Moist. No natural disturbance for 200+ years. Average canopy cover 90%.
- 2	S15°58’03.9” E35°33’13.1”	1896	
- 3	S15°58’03.6” E35°33’12.5”	1892	
- 4	S15°58’03.7” E35°33’11.6”	1885	
Litchenya 2 - 1	S15 °58’26.6” E35°33’05.1”	1835	Access moderate. Slope 20-40°. Old-growth forest. Dense undergrowth. No natural disturbance for 200+ years. Average canopy cover 80%.
- 2	S15°58’23.7” E35°33’02.4”	1850	
- 3	S15°58’22.1” E35°33’02.8”	1866	
- 4	S15°58’21.0” E35°33’02.4”	1848	



Sombani

Nathaka

Chinsama

Bvunje

Litchenya 1

Litchenya 2

Fig. 2: Composite diagram with histograms illustrating the frequency distributions of the size classes of *W. whytei* for all the cedar clusters examined on Mt. Mulanje during June 2010.

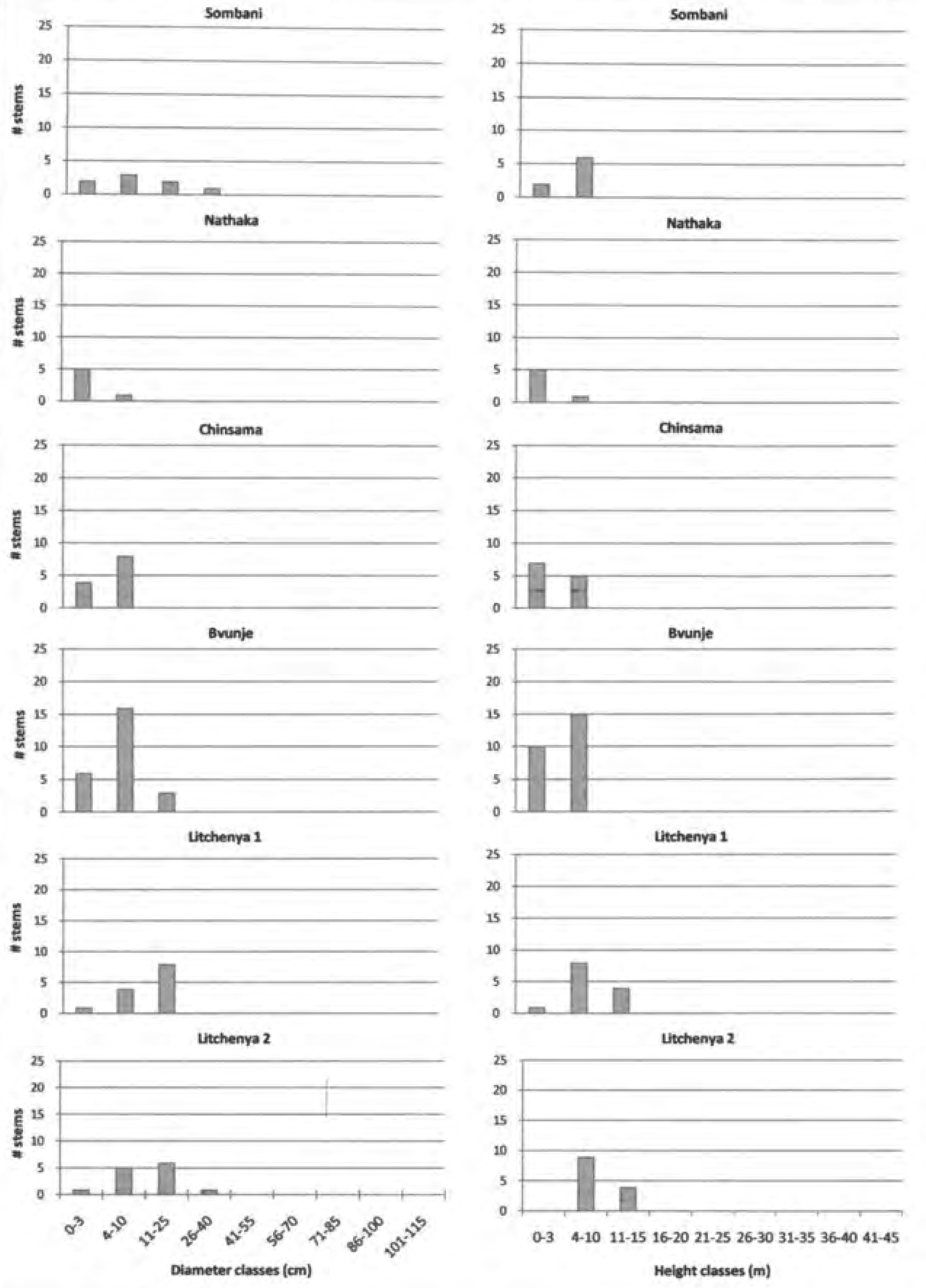


Fig. 3: Composite diagram with histograms illustrating the frequency distributions of the size classes of *Aphloia theiformis* for all the cedar clusters examined on Mt. Mulanje during June 2010.

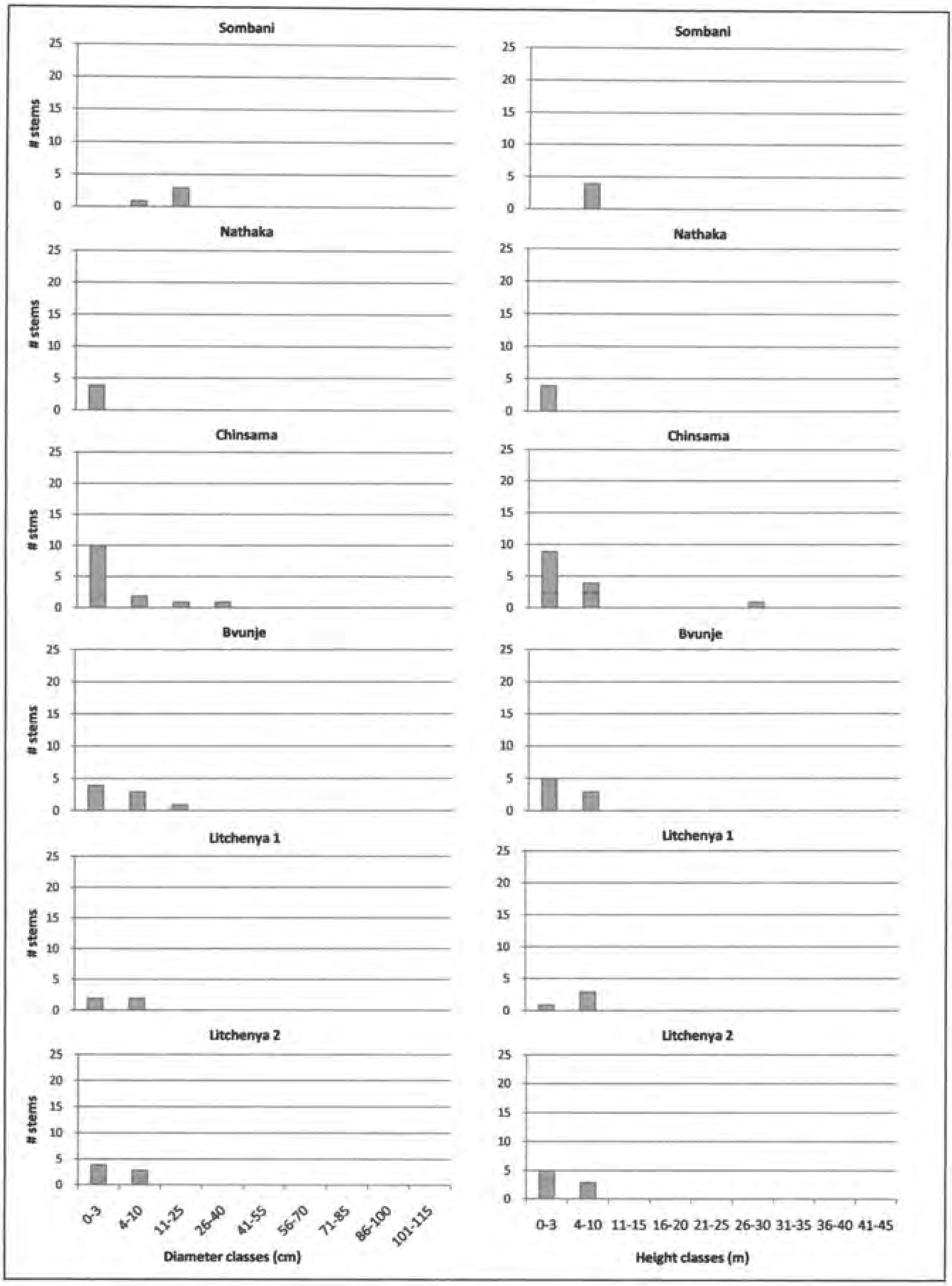


Fig. 4: Composite diagram with histograms illustrating the frequency distributions of the size classes of *Rapanea melanophloeos* for all the cedar clusters examined on Mt. Mulanje during June 2010.

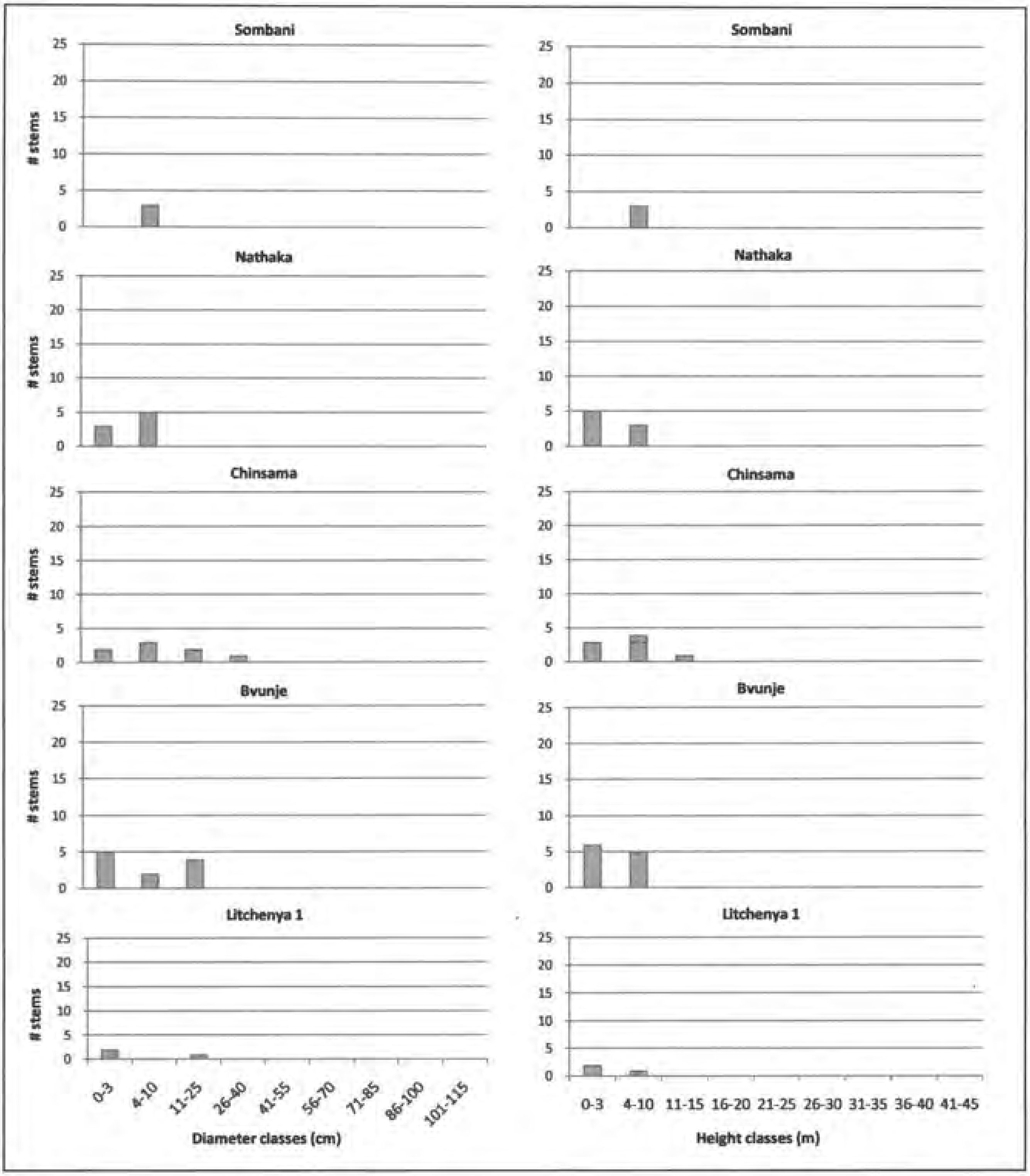


Fig. 5: Composite diagram with histograms illustrating the frequency distributions of the size classes of *Maesa lanceolata* for all the cedar clusters examined on Mt. Mulanje during June 2010. Note: not present at Litchenya 2.

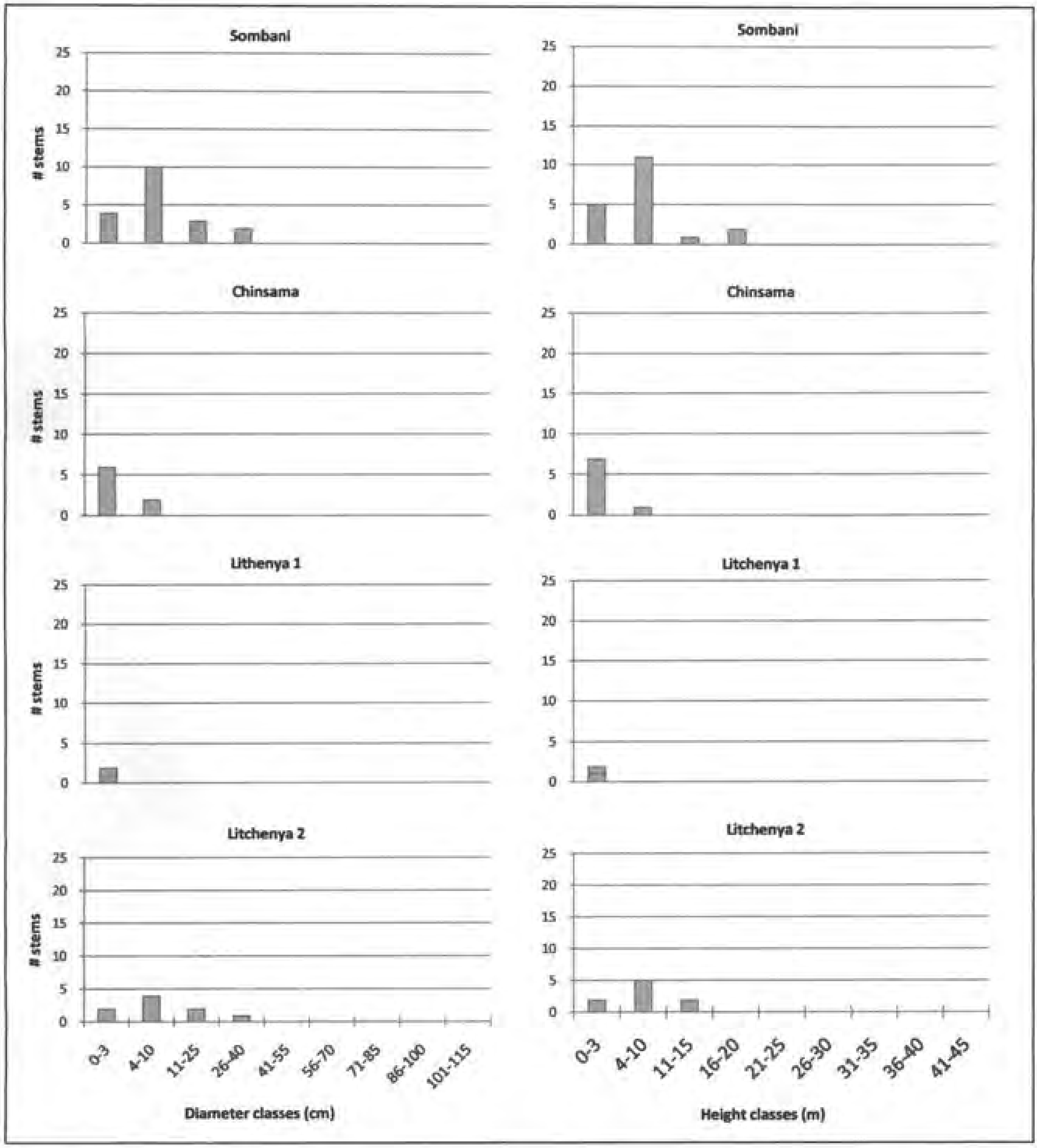


Fig. 6: Composite diagram with histograms illustrating the frequency distributions of the size classes of *Maytenus accuminata* for all the cedar clusters examined on Mt. Mulanje during June 2010. Note: not present at Nathaka and Bvunje.

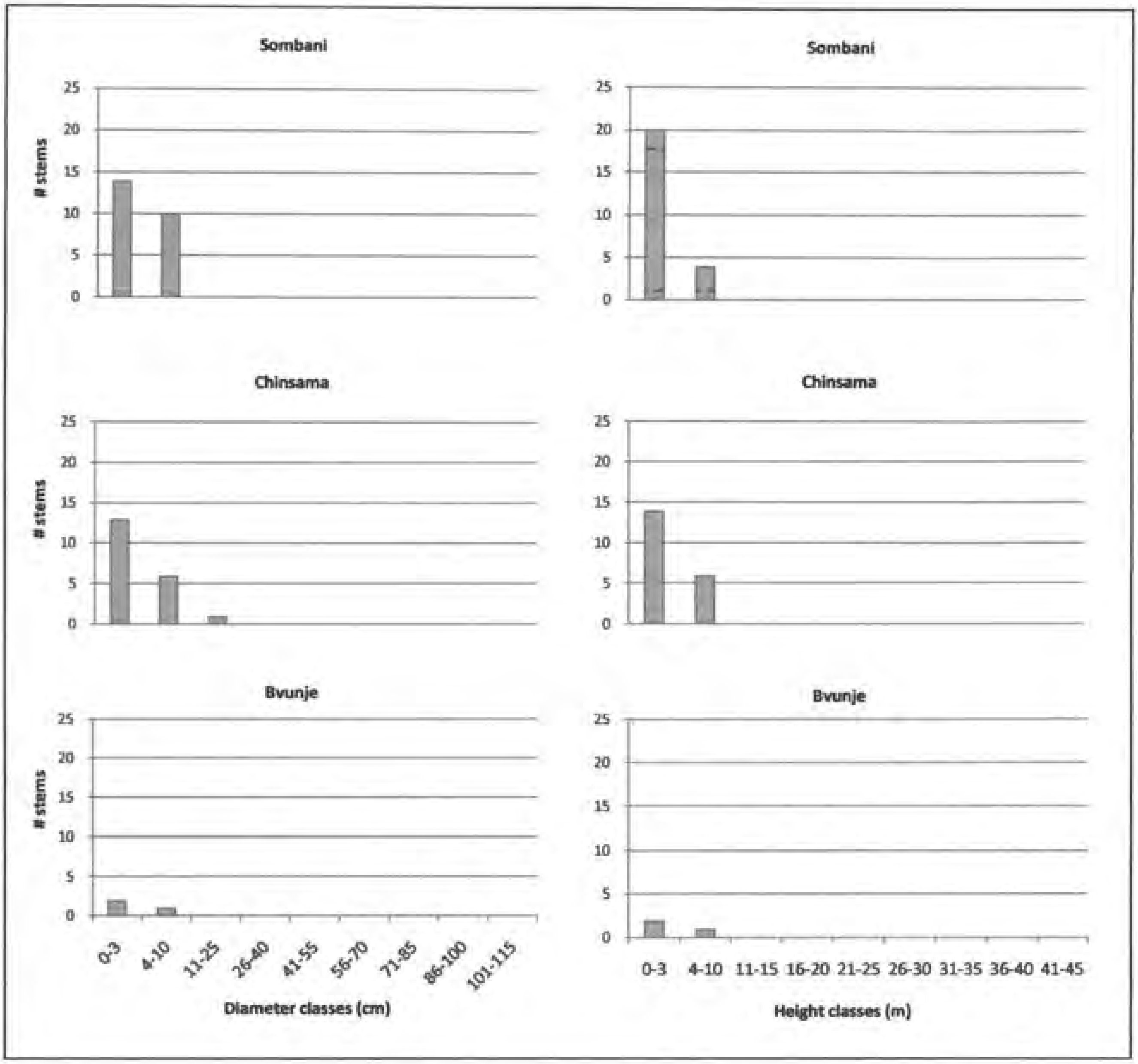


Fig. 7: Composite diagram with histograms illustrating the frequency distributions of the size classes of *Psychotria mahonii* for all the cedar clusters examined on Mt. Mulanje during June 2010. Note: not present at Nathaka or either of the sites at Litchenya.