Chapter Three

Associations of Woody Plant Species Along a Gradient of Forest Use

Abstract

I identify four associations of woody plant species around Chitre Village: mixed broadleaved, oak/laurel, rhododendron, and clearings. Ordination analysis indicates the associations are distinguished by distance, canopy closure, relative moisture, successional status, and % slope. Mixed broadleaved forest has highest diversity and equity of species, yet the lowest total number of species. TWINSPAN preferential species of the mixed broadleaved association are all late-successional species, whereas those of the oak/laurel association are mesic habitat pioneers, and those of clearings are disturbance- and sunlight-tolerant pioneers. The distributions of species are more strongly influenced by anthropogenic factors than environmental heterogeneity. Most late-successional species decrease sharply with proximity to the village because they are heavily harvested. Most species that occur exclusively near the village have been transplanted or protected there for cultural reasons. Analysis of large relict stumps and trees near the village center confirms the entire study area was formerly covered in mixed broadleaved forest.

Introduction

Plant species occur in complex and poorly-understood associations in broadleaved forests of the Temperate Sikkim-East Nepal Himalaya (TSENH, Shrestha et al. 1990a, Carpenter and Zomer 1996). The complexity arises from diverse historic, climatic, and topographic influences (Kanai 1966, Dobremez 1972, 1976, Stainton 1972, Grierson and Long 1983, Schweinfurth 1984, Singh and Singh 1987), as well as more recent anthropogenic influences (Kanai et al. 1975, Schweinfurth 1983, Shakya 1983). A better and more objective understanding of the vegetation ecology of these forests is required for effective conservation and sustainable use. In particular, the increasing impact of human influences, both traditional and recent, requires objective assessment.

Most patches of natural forest that remain in Nepal have been influenced by centuries of subsistence use. Even where forests have been left uncut by virtue of their proximity to religious sites or distance from human settlements, livestock grazing has often skewed their composition. Subsistence activities that most impact biological diversity in the TSENH are those that selectively remove woody plant species from natural forests, because selective removal gradually alters the structure and composition of plant communities. The result is anthropogenic species turnover, whereby disturbance-tolerant species flourish and others are displaced because habitats become unsuitable. In forest ecosystems, anthropogenic disturbance most frequently benefits widespread habitat-generalists that thrive in early-successional habitats. The species most often displaced are rare or endemic habitat-specialists that require large blocks of late-successional forest (Ranney et al. 1981, Harris 1984). Anthropogenic species turnovers differ from those brought about by natural (non-anthropogenic) processes because the spatial and temporal patterns of subsistence extraction are uniquely linked to the needs of human communities.

Maintaining the natural structure and composition of plant communities is a fundamental component of biodiversity conservation. The three-dimensional arrangement of plant communities provides an array of microhabitats to which endemic animal species have adapted to over their evolutionary history (Hilden 1965, James 1971, Cody 1985).

It is difficult to know with certainty what “natural” or pre-exploitation conditions of Himalayan forests were, particularly in the TSENH, where humans have utilized all but the most forbidding terrain. Some of the best remnants of primary temperate Himalayan broadleaved forest are found in Nepal's Arun Valley, which lies between the upper limit of cultivation and the lower limit of coniferous forest (Shrestha 1989, Carpenter and Zomer 1996). Some of these forest patches, including the forest above Chitre Village, were permanently settled only recently, so the initial effects of anthropogenic influences are still apparent. In 1992, many of these forest remnants were assimilated into the Makalu-Barun Buffer Zone (MBBZ; Nepali et al. 1990, Shrestha et al. 1990b). Management goals of the MBBZ are to: 1) optimize sustainable use of forest resources, and 2) conserve biological diversity through forest co-management and village-level development (Shrestha et al. 1990b). Forest co-management, however, cannot conserve biodiversity if the empirical knowledge of that biodiversity, and the biological processes that support it, are inadequate or lacking (Chapter 1).

The objectives of this chapter are to analyze plant species assemblages along a gradient of anthropogenic disturbance extending out from Chitre Village, and to interpret the distributions of woody plant species along this gradient with respect to environmental and anthropogenic influences. I hypothesize the non-random distributions of woody species are more influenced by anthropogenic disturbance than by environmental heterogeneity. This chapter also provides botanical and phytoecological foundations for Chapters 4-6.

Methods

Data Collection

I collected vegetation data at ten 9-ha (300 x 300 m) plots distributed along a distance/disturbance gradient extending from the center of the village to an area too distant (~2 km) and too rugged for normal use by humans or livestock (Fig. 2.5). I used a plot size of 9-ha because vegetation data were collected in conjunction with animal data, and areas of at least 9 ha were required to encompass several breeding territories of songbirds (Engstrom 1981). All plots were established between 2200-2600 m elevation.

Unlike prior floristic studies in the region, I established study plots within a limited area and according to distance and use criteria, rather than at sites manifestly representative of different vegetation types. Previous phytogeographic studies have invariably sought to describe natural plant associations encountered along lengthy altitudinal transects. Stands chosen for study were, *a priori*, floristically distinct from one another, and preferably showed little or no sign of human disturbance (e.g., Yoda 1967, Stainton 1972, Ohsawa et al. 1973, Kanai et al. 1975, Shakya 1975, Ohsawa 1983).

Eight of my ten plots were established along a major footpath (N. *NAmche-jAne bAto*) heading north from Chitre Village, where the aspect was generally southwest (Fig. 2.5). I was unable to locate undisturbed sites on southwest-facing slopes between 2,200 and 2,600 m elevation, so I established two plots several hundred meters off the main trail on predominantly northeast-facing slopes. One of these was located at a forest-interior pasture (Bhelli), the other (Chakedho), was located where the terrain was so rugged and forbidding that it was visited only by the most intrepid bamboo cutters for just a few hours each year. I measured the distance of study plots from the village following the most direct footpath.

Within each 9-ha plot, I established six parallel trails 50 m's apart. Along each of these trails, I established sampling points at 50-m intervals. There were, therefore, 36 sampling points in each 9-ha plot, one at each intersection of a 50 m x 50 m sampling grid (Fig. 3.1). At each sampling point, I measured twelve woody plants >1.5 m height using a 3-level point-centered-quarter (PCQ) technique (Cottam and Curtis 1956, Mueller-Dombois and Ellenberg 1974). Within each of the four PCQ quadrants (Fig. 3.1), I measured the nearest woody plant in each of three diameter size classes: >25 cm diameter at breast height (DBH), 10-25 cm DBH, and 2-10 cm diameter at base (DAB; measured at ground level because most were too small to measure at breast height). For each plant, I recorded species, girth, and distance from the sampling point. I also measured elevation, aspect, and % slope at each sampling point. High-quality elevation data were not available at the time, so I estimated elevations from three sources: a 1964 Survey of India topographic sheet (Government of India 1964), an early handheld global positioning device (Model 45, Garmin International, Olathe, KS), and a barometric altimeter.

No comprehensive field guide was available for identifying Himalayan trees, so I initially identified plants with names given by local informants and later verified scientific names with the assistance of regional experts (D. Long, K.R. Rajbhandari, P.R. Shakya, T.B. Shrestha). Local informants sometimes did not differentiate between similar-looking botanical species, so seven of the local names they gave each constituted two botanical species (Table 3.1). I segregated *Meliosma pinnata* and *Rhus chinensis* (local name *sAno pAte bokimla*) *a posteriori* based on ecological information provided by Grierson and Long (1983) and local informants. Trees >10 m tall were designated *Meliosma pinnata* because *Rhus chinensis* does not exceed 10 m in height (Grierson and Long 1983); those <10 m tall were designated *Rhus chinensis* if they were <650 m from the village center (in secondary vegetation) and *Meliosma pinnata* if they were >650 m from the village center (in mature forest). It was not possible to segregate data for the other species-pairs *a posteriori*, so I analyzed the data according to local taxonomic entities. With three of these pairs (*Berberis aristida* and *B. insignis, Spirea bella* and *Hypericum hookerianum*, *Symplocos ramosissima* and *S. sumuntia*), the species were so similar in their habitat associations (Grierson and Long 1983) that ordination analysis would have placed them very close to one another if they had been analyzed as separate entities. With the remaining three pairs (*Prunus* *venosa* and *Ilex fragilis*, *Prunus napaulensis* and *Prunus* sp., *Lindera pulcherrima* and *Neolitsea foliosa*), the second species was encountered so rarely that data for the predominant species overwhelmed data for the secondary species, making the second species irrelevant to the classification (I was able to judge the relative abundance of species pairs in the field after experts pointed out the name discrepancies).

In order to understand the structure and composition of the pre-settlement forest at Chitre, I assessed large relict trees and tree stumps (>50 cm DAB, Fig. 3.2) in a 25 ha (500 m x 500 m) plot at the periphery of the village (Chitre Kharka study plot and areas immediately south and east, Fig. 2.5). At >50 cm DAB, each was at least twice the age of the village. I determined their density by mapping their locations relative to north-south and east-west baselines laid out on the ground. Local assistants identified stumps to genus by visually inspecting the wood grain.

Data Analysis

I use the computer program TWINSPAN (two-way indicator species analysis; Hill 1979, Jongman, et al. 1995, McCune and Mefford 1995) to identify ecological associations (groupings) of woody plant species. TWINSPAN has been used widely for divisive classification of ecological communities (Ter Braak 1986, Kent and Coker 1992, Metz 1998, Zomer et al. 2001). Basic functions of the program are summarized by Gauch (1982).

I perform several TWINSPAN classifications using different input variables (presences-absence, frequency, basal area) and subsets of data (selected size classes, with or without ubiquitous species) in order to determine which indicator species and species groupings emerge most consistently, then select the most robust and easily interpreted classification for subsequent analysis. I contrast TWINSPAN species associations generated by this classification on the basis of dominant species, TWINSPAN preferential species (those more than twice as likely to occur on one side of an ordination axis, Kent and Coker 1992), and species diversity indexes.

I analyze relative frequencies and species associations along the distance/disturbance gradient by segregating the ten 9-ha plots into six distance categories (<100 m, 100-300 m, 300-500 m, 500-900 m, 900-1200 m, 1200-2100 m). The results are analyzed as percent frequency rather than absolute frequency because the spacing of plots was uneven (Fig. 2.5), the width of distance categories varied, and the number of plots per category ranged from 1-3.

For each TWINSPAN species association, I calculate species diversity (H'; $-\sum p_i \ln p_i$, where p_i = proportion of *i*th species, Shannon and Weaver 1949, Barbour et al. 1987), effective diversity (D; exp(H'), the number of equally-abundant species needed for the average proportional abundance of species to equal that observed in the dataset), and species equitability (J'; H'/H'_{max}, where $H'_{max} = \log_n$ of the number of species, Pielou 1969).

I use the computer program DECORANA (Hill 1979, Jongman, et al. 1995, McCune and Mefford 1995) to perform an environmental ordination of species associations. Because the vegetation and environmental data I use are not multivariate normal or homogeneous with regard to variance, I do not perform formal statistical tests, and I use the analysis only for descriptive purposes.

I designate species as late-successional or pioneer species based on references from the regional botanical literature (Stainton 1972, Ohsawa et al. 1975, 1986, Tsuchida 1983, Schmidt-Vogt 1990, Sundriyal and Sharma 1996, Chettri et al. 2002) or rarely, if a species' ecological attributes are not available in the literature, on information provided by local informants or personal observation (also see Chapter 5).

I conduct nearest-neighbor cluster analysis (McCune and Mefford 1995) to determine how different each of the ten vegetation plots is from a “stump plot” representing pre-settlement conditions at the village center. I compare the plots on the basis of species frequency and basal area of trees and stumps >50 cm diameter DAB. I use relativized Basal Area Ratio (Σ tree basal areas/total ha, Greig-Smith 1983), standardized to the norm, as the input variable because it masks gross differences in total tree basal area between the stump and regular vegetation plots while emphasizing relative proportions of species. I estimate tree densities and effective sampling area with formulas provided by Mueller-Dombois and Ellenberg (1974).

Results

The most robust and easily interpreted TWINSPAN classification results from the input of frequency data for all species (n = 51), all size classes (n = 3), and all sampling points (n = 360). The classification yields four associations, which I designate as mixed broadleaved, oak/laurel, rhododendron, and clearings. Figure 3.3 illustrates an ordered two-way table of the selected classification (whereas the original table is contiguous, each association is displayed separately in Figures 3.3.1-3.3.4 to facilitate binding). Table 3.2 summarizes TWINSPAN abundant, indicator, and preferential species for each association.

TWINSPAN classification allocates 26% of the 360 sampling points to the mixed broadleaved association, 37% to oak/laurel, 14% to rhododendron, and 23% to clearings. The mixed broadleaved association occurs furthest from the village, and oak/laurel, rhododendron, and clearings associations occur progressively closer (Fig. 3.4, average distances are roughly 1540 m, 717 m, 692 m, and 313 m, respectively). The mixed broadleaved association has high canopy closure, averaging 92%, whereas canopy closure for oak/laurel, rhododendron, and clearing associations average 82%, 85%, and 52%, respectively.

Ordination analysis indicates the four TWINSPAN associations are distinguished primarily by distance from village center, canopy closure, and relative moisture, and secondarily by successional status and % slope (Fig. 3.5). The clearings, oak/laurel, and mixed broadleaved associations are distributed in ordination space along a gradient from near-village, open, south-tending environments to distant, closed-canopy, north-tending environments (Fig. 3.5). The rhododendron association occurs in relatively open, south-tending, environments at mid-distances.

The total number of species is highest in forest clearings ($n = 40$), and lowest in rhododendron and mixed broadleaved associations ($n = 35$, respectively, Table 3.3). Species diversity and effective diversity are highest in the mixed broadleaved association, lowest in oak/laurel, and significantly different among all associations ($P < 0.001$). Species equitability is 30-40% higher in the mixed broadleaved association than in other associations.

Many individual species have skewed abundances with respect to distance from village center. Five cultivated or semi-cultivated species occur almost exclusively near the village center (*Ficus auriculata*, *Salix* sp., *Taxus baccata*, *Juniperus recurva*, *Prunus cerasoides*). Three xeric habitat pioneer species are most abundant within ~500 m of village center (*Alnus nepalensis, Berberis aristida, Rhus chinensis*), whereas another three (*Eurya acuminata*, *Lyonia ovalifolia*, *Rhododendron arboreum*) also occur in distant mature forest (Fig. 3.6). Among mesic habitat pioneers, *Hydrangea heteromalla* and *Symplocos theifolia* are most frequent in secondary forest ~500-900 m from village center, whereas *Viburnum erubescens* is relatively abundant along the entire distance gradient (Fig. 3.7). Many late-successional species are frequent only in closed-canopy forest. Others increase noticeably (e.g., *Acer campbelli*, *Ilex sikkimensis*, *Lindera assamica*, *Prunus napaulensis*) or sharply (e.g., *Lindera pulcherrima*, *Litsea elongata*, *Meliosma pinnata*, *Persea clarkeana*, *Quercus oxyodon*) with distance (Fig. 3.8). Some locally rare late-successional species (*Betula alnoides, Michelia kisopa, Schefflera impressa*, *Skimmia arborescens*, *Tetracentron sinense*) occur only at distances >1200 m. *Castanopsis hystrix* is unique among late-successional species insomuch as it is absent (was not detected) beyond ~600 m from village center, and *Ficus neriifolia* has a uniquely bimodal distribution.

Cluster analysis of relict stumps and trees (Fig. 3.9) indicates the pre-settlement forest at Chitre Village was most similar to the present-day forest at nearby Hile and Bagalekhop vegetation plots (600 m and 800 m from village center, respectively) with regard to species composition of trees >50 cm DAB (primarily *Quercus* spp., *Persea* spp., and *Magnolia campbellii*, Appendix 3.1).

Discussion

Species associations

Alternate TWINSPAN classifications based on different input variables and data subsets are largely consistent with the classification I chose to analyze. Preferential species of the four associations strongly reflect the increasing degree of anthropogenic influence at greater distances from the village. Preferential species of the mixed broadleaved association (Table 3.2) are, for example, all characteristic species of late-successional (primary) mixed broadleaved forest. Similarly, preferential species of the oak/laurel association are all understory and subcanopy pioneer species associated with disturbed mesic environments. Late-successional species that occur in the oak/laurel association occur at too low frequency for TWINSPAN to recognize them as indicator species (Fig. 3.3.2). Preferential species of the rhododendron association include both late-successional species (*Quercus lamellosa* and *Myrsine semiserrata*) and early-successional species (*Rhododendron arboreum* and *Lyonia ovalifolia*). Abundant *Rhododendron arboreum* and *Lyonia ovalifolia* suggests the rhododendron association might result from anthropogenic disturbance, but these species also occur naturally in primary forest (Ohsawa et al. 1986). Preferential species of the clearings association are all disturbance- and sunlight-tolerant pioneers.

The species associations I identified at Chitre differ somewhat from vegetation types previously described for the region because of differences in location, spatial scale, and the objectives and methods of analysis. Existing regional classifications were created from subjective lists of “characteristic” species (e.g., Kanai 1966, Stainton 1972, Grierson and Long 1983), or species lists from “representative” plots or *relevés* (e.g., Yoda 1967, Shrestha et al. 1990a, Shakya 1975), whereas I sampled within a relatively small geographic area where relatively few forest types were represented, and I did not sample herbaceous species or woody species <2 cm DAB.

Most authors describe temperate broadleaved forests of the TSENH as dominated by oaks, and designate constituent forest types with names such as “evergreen oak” (e.g., Kanai 1966, Yoda 1967) or “*Quercus lamellosa*” forest (Champion 1936). Other authors stress the co-dominance of laurels (Lauraceae) by designating forest types as “laurel” (Champion 1936) or “oak-laurel” (e.g., Shrestha et al. 1990a, Shakya 1995). Stainton (1972) argues against designating forests as “laurel forests” because laurels are abundant in a wide range of forest types across the region, and usually dominate the subcanopy rather than the upper canopy. Stainton (1972) argues that the mixed, species-rich, character of temperate broadleaved forests should be stressed when naming, because dominance or co-dominance seldom extend beyond a limited area.

The list of representative species for my mixed broadleaved association is comprised of relatively few species because I only report species that TWINSPAN designates as abundant (Table 3.4.1). The more comprehensive lists of Kanai (1966) and Stainton (1972) are of characteristic species recorded at multiple locations (Table 3.4.1). Stainton’s (1972) lower temperate mixed broadleaf forest corresponds least well to my mixed broadleaved association because Chitre lies at the upper altitudinal limit of his forest type. Stainton's upper temperate forest type corresponds even less well, but some Chitre species that are absent from his lower temperate forest do occur in his upper temperate forest (Stainton 1972). Chitre's mixed broadleaved association best corresponds to Stainton's "*Quercus lamellosa*-dominated forest," which is a transitional (ecotonal) type that lies between his lower temperate and upper temperate broadleaved forests (1980-2590 m, Stainton 1972).

Among the abundant species of Chitre's mixed broadleaved association, species of *Meliosma*, *Myrsine*, and *Ficus* are more dominant at Chitre than reported elsewhere. *Meliosma* and *Myrsine* are smaller-stature subcanopy species, so they were possibly underreported in other studies. Only Kanai (1966) previously indicated *Ficus* spp. as important components of mixed broadleaved forest (his 1500-2300 m *Castanopsis* zone), so the abundance of *Ficus neriifolia* in Chitre's mixed broadleaved association might be unusual.

Chitre's oak/laurel association appears to be derived from mixed broadleaved forest which has been altered by humans. Some of the same late-successional species that occur in primary mixed broadleaved forest occur at each sample site (Fig. 3.3.2), yet all TWINSPAN abundant, indicator, and preferential species are early-successional, mesic habitat, pioneers (Table 3.2). In particular, *Hydrangea heteromalla* and *Symplocos theifolia* characteristically occur in mesic canopy openings created by tree felling and forest-interior pastures (N. *khArka*, Chapter 1). The intermediate position of the oak/laurel association in ordination space between mixed broadleaved and clearings associations also suggests it is derived from disturbed primary forest (Fig. 3.5).

Metz (1998) also found certain stands of "broadleaf-evergreen forest" in central Nepal to be dominated by "subcanopy" species. He attributed dominance of *Symplocos ramocissima* or *Rhododendron arboreum* to poor regeneration among the expected late-successional canopy species. Chettri et al. (2002) report *Symplocos ramocissima* can dominate mixed broadleaved stands in Sikkim after the canopy has been thinned.

Many researchers have classified stands dominated by *Rhododendron arboreum* as a subtype of mixed broadleaved forest (Table 3.4.2). Shakya (1975) and Shrestha et al. (1990a), for example, classify them as evergreen oak or evergreen broadleaved forests "dominated by *Rhododendron arboreum*." Conversely, Stainton (1972) recognizes an *R. arboreum* forest, but acknowledges other associated canopy species can range from "almost entirely absent" to "typical of upper temperate mixed broadleaved forest."

Stainton (1972) asserts *R. arboreum*-dominated stands can occur naturally where soil properties limit the growth of other canopy species, but that most rhododendron stands have anthropogenic origins (also see Yoda 1967, Schmidt-Vogt 1990). Richard (1980) indicates rhododendron stands are created by catastrophic events (fire, landslide), then perpetuated by human influences (grazing, felling, burning). *R. arboreum* is known to exhibit pioneering traits on steep, exposed, shallow-soiled, south-tending, ridges and slopes (Stainton 1972, Ohsawa et al. 1986), and to proliferate after fire, which thins the forest canopy and removes the litter layer (Schmidt-Vogt 1990). Schmidt-Vogt (1990) suggests *R. arboreum*-dominated stands originate as mixed-species stands, from which other canopy species are gradually eliminated by natural mortality of shorter-lived species or by felling by humans (also see Oliver and Sherpa 1989). I was unable to ascertain whether any *R. arboreum* stands at Chitre are of natural origin. The location of the association in ordination space suggests it could be a stable "late-successional" sere of relatively open, south-tending, environments.

The forest clearings association at Chitre corresponds with "pastures" and "clearings" associations reported by previous researchers (Table 3.4.3). *Viburnum* spp. and *Berberis* spp. are particularly consistent across classifications. Early-successional associations of the region are not well studied, however, in part because disturbed sites are often avoided when employing representative or relevé sampling (e.g., Dobremez 1976).

The clearings association has higher species diversity than other associations because it includes species introduced for cultural or utilitarian purposes (*Ficus auriculata*, *Juniperus recurva*, *Taxus baccata*), species protected for ornamental purposes (*Prunus cerasoides*), and species invading disturbed habitats from lower elevations (*Leucosceptrum canum*, *Rhus chinensis*).

As Stainton (1972) observed, "if the forest was more extensive and less damaged ... the difficulties of classifying [mixed broadleaved] forest in Nepal ... would be easier." Data on additional environmental variables, particularly on soil properties, might have provided greater insight into the history and successional patterns of Chitre's woody plant associations, but it was not feasible to gather these data given the resources and expertise available.

Species distributions

Species that occur almost exclusively near the village center are cultivated for tree fodder (*Ficus auriculata*, Chapter 2), introduced or transplanted for cultural/religious uses (*Salix* sp., *Taxus baccata*, *Juniperus recurva*), or retained for ornamental purposes (*Prunus cerasoides*, which reportedly arrives by natural dispersal).

Xeric habitat pioneers (*Alnus nepalensis*, *Berberis aristida*, *Eurya acuminata*, *Lyonia ovalifolia*, *Rhus chinensis*) tend to be most abundant within ~500 m of village center because they respond positively to the relatively xeric conditions of highly disturbed forest. *Berberis aristida* and *Lyonia ovalifolia* are resilient to browsing and lopping because they are relatively unpalatable and also able to resprout from underground roots (Oliver and Sherpa 1989, Schmidt-Vogt 1990).

Some xeric habitat pioneers (*Eurya acuminata*, *Lyonia ovalifolia*, *Rhododendron arboreum*) also occur in mature forest as "undifferentiated canopy components" (Ohsawa et al. 1986). Xeric habitat pioneers that are heavily harvested for fuelwood (*Lyonia ovalifolia*, *Rhododendron arboreum*; Chapter 2) are disproportionately infrequent within 300 m of the village, and *Berberis aristida* is disproportionately frequent 100-300 m from village center because it is a pasture-associated species.

Mesic habitat pioneers (*Hydrangea heteromalla*, *Symplocos theifolia*, *Viburnum erubescens*) are also relatively unpalatable (Singh 1982, Schmidt-Vogt 1990, local informants). *Hydrangea heteromalla* and *Symplocos theifolia* are canopy-gap pioneers ("biological nomads"; Halle et al. 1978, Pickett 1983). *Hypericum hookerianum, Gaultheria fragrantissima*, *Spiria bella, Smilax rigida,* and *Rhus succedanea* might also be gap-pioneers at Chitre, but most individuals were <2 cm DAB and therefore not recorded. *Viburnum erubescens* is abundant even within 100 m of village center because it is cultivated for living fences (Chapter 2).

Most late-successional species decline with proximity to the village because they are of high value (Chapter 5) and harvested at unsustainable rates. *Ficus neriifolia* has a unique bimodal distribution because in addition to being heavily harvested in disturbed forest it is retained or semi-cultivated near the village for tree fodder (Chapter 2). *Castanopsis hystrix* is absent beyond ~600 m from village center because Chitre lies near the upper limit of what was formerly an extensive *Castanopsis* forest, which is now converted almost entirely to cultivated fields (1500-2000 m; Kanai 1966, Stainton 1972, Shakya 1975), with only "thickets and shrubberies [of *Castanopsis*] surrounding the topmost villages" (Stainton 1972).

Pre-settlement forest

Relict stumps and trees near the village center confirm an important assumption of the study design; that where village croplands and pastures now occur there was once a primary broadleaf forest similar in structure and composition to the current forest further along the distance/disturbance sampling gradient. It is not possible to completely distinguish between covarying effects of proximity and aspect, however, because study plots near the village were located on south-tending slopes and plots far from the village were on north-tending slopes. In mountainous terrain, human settlements tend to be on south-facing slopes because southern exposures offer relatively high insolar radiation, facilitating crop growth and providing comfortable temperatures and humidity in dwellings (Kleinert 1983, Zurick 1989). The lower flanks of mountains are also preferred because soils are deeper and the daily period of direct sunlight tends to be is longer (Schroeder 1985).

Conclusions

The most robust and easily interpreted TWINSPAN classification for tree species associations at Chitre Village is based on frequency data for all species, size classes, and sampling points. The classification yields four associations: mixed broadleaved, oak/laurel, rhododendron, and clearings. The average distance of sampling plots from village center were 1540 m for the mixed broadleaved association, 717 m for oak/laurel, 692 m for rhododendron, and 313 m for clearings. Associations are distinguished primarily by distance from village center, canopy closure, and relative moisture, and secondarily by successional status and % slope.

TWINSPAN preferential species (those more than twice as likely to occur on one side of an ordination axis) for the mixed broadleaved association are all characteristic species of primary mixed broadleaved forest. Those for the oak/laurel association are understory and subcanopy pioneer species associated with mesic environments, whereas for the rhododendron association they are both late- and early-successional species, and for the clearings association they are disturbance- and sunlight-tolerant pioneer species.

Total species is highest in the clearings association, and includes species introduced for cultural or utilitarian purposes, species protected for ornamental purposes, and species that invade disturbed habitats from lower elevations. Species diversity and effective diversity are highest in the mixed broadleaved association and lowest in the oak/laurel association. Species equity is 30-40% higher in the mixed broadleaved association than in other associations.

Xeric habitat pioneers are most frequent within ~500 m of village center, although some also occur in the subcanopy of mature forest. Mesic habitat pioneers are most frequent ~500-900 m from village center, although *Viburnum erubescens* is frequent through the study area. Many late-successional species are frequent only in distant closed-canopy forest, and some occur only beyond 1200 m from the village center.

The species composition and density of large remnant stumps and trees near the village center are similar to those in current stands 600-800 m away, indicating the entire length of the distance/disturbance gradient at Chitre was formerly covered in mixed broadleaved forest.

Ordination analysis confirms my hypothesis that the distributions of woody plant species at Chitre are influenced more by anthropogenic factors than by environmental heterogeneity. Distance from village center has greater influence over species distributions than any other factor considered. North-south aspect also had a significant influence, as is expected in a region where orographic phenomena create cooler, moister, conditions on north-facing slopes (Troll 1967, Stainton 1972, Spurr and Barnes 1987). It is not possible to completely distinguish the effects of distance from the effects of north-south aspect, because study plots near the village were located on south-facing slopes and those far from the village were on north-facing slopes (Fig. 2.5). The effect of slope, which is negatively correlated with soil depth (due to gravity and erosion), and positively correlated with mesic conditions (because steep slopes and gullies receive less direct sunlight), was also moderate. The weak effects of elevation and east-west aspect indicate these effects are relatively homogeneous across the study area.

TABLE 3.1. Plant taxa analyzed as single entities. Constituent species listed in order of descending abundance.

Local name given	Botanical name(s) applied in this study	Constituent species
BAkhreghÃs	*Spirea bella*	*Spirea bella* *Hypericum hookerianum*
BhAle kharani	*Symplocos ramosissima*	*Symplocos ramosissima* *Symplocos sumuntia*
Chutra khÃda	*Berberis aristida*	*Berberis aristida* *Berberis insignis*
Sano pAte arupAte	*Prunus napaulensis*	*Prunus napaulensis* *Prunus* sp.
Shingkawli	*Lindera pulcherrima*	*Lindera pulcherrima* *Neolitsea foliosa*
Thulo pAte arupAte	*Prunus venosa*	*Prunus venosa* *Ilex fragilis*
SAno pAte bhokimla	*Meliosma pinnata* or *Rhus chinensis**	*Meliosma pinnata* *Rhus chinensis*

* Trees identified by local informants as *SAno pAte bhokimla* were designated as *Meliosma pinnata* if >10 m tall (*Rhus chinensis* grows <10 m tall, Grierson and Long 1983); those <10m tall were designated as *Rhus chinensis* if <650 m from the village center (in secondary vegetation) and *Meliosma pinnata* if >650 m from the village center (in mature forest).

TABLE 3.2. Characteristic species of TWINSPAN woody plant associations.

Association	Abundant species	Indicator species[A]	Preferential species[B]
Mixed broadleaved	*Acer campbellii* *Eurya acuminata* *Ficus neriifolia* *Lindera pulcherrima* *Litsea elongata* *Meliosma pinnata* *Myrsine semiserrata* *Persea clarkeana* *Prunus venosa* *Quercus lamellosa* *Quercus oxyodon* *Symplocos theifolia* *Viburnum erubescens*	*Ficus neriifolia* *Litsea elongata* *Persea clarkeana* *Quercus oxyodon*	*Acer campbellii* *Ficus neriifolia* *Ilex sikkimensis* *Lindera assamica* *Lindera pulcherrima* *Litsea elongata* *Meliosma pinnata* *Myrsine semiserrata* *Persea clarkeana* *Quercus oxyodon*
Oak/laurel	*Eurya acuminata* *Hydrangea heteromalla* *Symplocos theifolia* *Viburnum erubescens*	*Symplocos theifolia* *Viburnum erubescens*	*Hydrangea heteromalla* *Symplocos theifolia* *Viburnum erubescens*
Rhododendron	*Eurya acuminata* *Lyonia ovalifolia* *Myrsine semiserrata* *Rhododendron arboreum* *Symplocos theifolia* *Viburnum erubescens*	*Rhododendron arboreum* *Myrsine semiserrata*	*Lyonia ovalifolia* *Myrsine semiserrata* *Quercus lamellosa* *Rhododendron arboreum*
Clearings	*Berberis aristata* *Eurya acuminata* *Lyonia ovalifolia* *Symplocos theifolia* *Viburnum erubescens*	*Berberis aristata*	*Berberis aristata* *Viburnum erubescens*

[A] Species that occur commonly in plots on one or the other side of an ordination axis.

[B] Species that are more than twice as likely to occur on one side of an ordination axis than the other.

TABLE 3.3. Relative diversity of woody plant species[A] in TWINSPAN species associations.

Association	Total species	Species diversity H' [B]	Effective diversity D[C]	Species equitability J' [D]
Mixed broadleaved	35	2.82	16.82	0.10
Oak/laurel	38	1.99	7.34	0.07
Rhododendron	35	2.49	12.02	0.07
Clearings	40 (36[E])	2.25 (2.20[E])	9.53 (9.00[E])	0.06 (0.06[E])

[A] Woody plants >2 cm DAB (not absolute plant species diversity). [B] Species richness weighted by species evenness (Shannon and Weaver 1949, Barbour et al. 1987). [C] Number of equally-common species (MacArthur 1965). [D] Distribution of individuals among species (Pielou 1969). [E] Species introduced for cultural purposes omitted (*Ficus auriculata*, *Juniperus recurva*, *Salix* sp., *Taxus baccata*).

TABLE 3.4.1. Composition of the mixed broadleaved association at Chitre compared to that of similar forest types reported elsewhere in the Temperate Sikkim-East Nepal Himalaya (woody taxa only, listed alphabetically).

Present study, mixed broadleaved association[A], Chitre (2200-2600 m)	Kanai (1966), evergreen oak forest, Taplejung/Darjeeling (2200-2800 m)	Yoda (1967), evergreen oak forest, Maedane Kharka, east Nepal (2270 m)	Stainton (1972), lower temperate mixed broadleaved forest, east Nepal (1500-2100 m)	Shrestha et al. (1990a), oak-laurel zone, Makalu-Barun, east Nepal (2600 m)	Shakya (1995), oak-laurel forest, Makalu-Barun, east Nepal (2000-2700 m)
Acer campbellii	*Acer spp.*	*Acer campbellii*	*Acer spp.*	*Acer sp.*	*Acer campbellii*
Eurya acuminata	*Actinodaphne spp.*	*Acer spp.*	*Actinodaphne reticulata*	*Acer campbellii*	*Acer sikkimensis*
Ficus neriifolia	*Arisaema spp.*	*Betula cylindrostachys*	*Alnus napalensis*	*Acer sterculiaceum*	*Acer sterculiaceum*
Lindera pulcherrima	*Betula alnoides*	*Buddleja sp.*	*Betula spp.*	*Alnus nepalensis*	*Alnus napaulensis*
Litsea elongata	*Brassaiopsis mitis*	*Carpinus viminea*	*Bucklandia populnea*	*Daphne bholua*	*Berberis asiatica*
Meliosma pinnata	*Castanopsis spp.*	*Castanopsis indica*	*Caprinus viminea*	*Eurya sp.*	*Betula alnoides*
Myrsine semiserrata	*Cinnamomum spp.*	*Cinnamomum spp.*	*Castanopsis tribuloides*	*Eurya cerassifolia*	*Cinnamomum tamala*
Persea clarkeana	*Corylus ferox*	*Edgeworthia spicata*	*Camellia kissi*	*Ilex dipyrena*	*Cardiocrinum giganteum*
Prunus venosa	*Edgeworthia gardnerii*	*Eurya acuminata*	*Cinnamomum tamala*	*Ilex sikkimensis*	*Daphne bholua*
Quercus lamellosa	*Elaeocarpus ganitrus*	*Eurya spp.*	*Cornus oblonga*	*Lindera pulcherrima*	*Eurya cerasifolia*
Quercus oxyodon	*Euonymus spp.*	*Lithocarpus elegans*	*Daphniphyllum himalayense*	*Litsea elongata*	*Helwingia himalaica*
Symplocos theifolia	*Eurya spp.*	*Lithocarpus spicata*	*Dodecadenia grandiflora*	*Lyonia ovalifolia*	*Ilex sikkimensis*
Viburnum erubescens	*Ficus spp.*	*Litsea elongata*	*Ehretia macrophylla*	*Magnolia campbellii*	*Lithocarpus spicata*
	Gaultheria griffithiana	*Magnolia campbellii*	*Engelhardtia spicata*	*Mechelia doltsopa*	*Lindera pulcherrima*
	Ilex spp.	*Michelia carthcartii*	*Eriobotrya elliptica*	*Persea clarkeana*	*Lyonia ovalifolia*
	Ligustrum confusum	*Michelia excelsa*	*Eurya acuminata*	*Prunus sp.*	*Magnolia campbellii*
	Lindera spp.	*Persea fructifera*	*Evodia fraxinifolia*	*Quercus glauca*	*Michelia sp.*
	Lithocarpus spp.	*Quercus sp.*	*Homalium nepalense*	*Quercus lamellosa*	*Persea spp.*
	Litsea elongata	*Quercus glauca*	*Juglans regia*	*Quercus oxyodon*	*Prunus sp.*
	Lyonia ovalifolia	*Quercus lamellosa*	*Leucosceptrum canum*	*Rhododendron arboreum*	*Quercus lamellosa*
	Machilus spp.	*Rhododendron arboreum*	*Lindera spp.*	*Rhus sp.*	*Rhododendron arboreum*
	Magnolia campbellii	*Schima wallichii*	*Lithocarpus spicata*	*Schefflera impressa*	*Rhus succedanea*
	Mahonia napaulensis	*Symplocos ramosissima*	*Litsea spp.*	*Symplocos sp.*	*Symplocos sp.*
	Michelia spp.	*Symplocos theifolia*	*Mallotus nepalensis*	*Tetracentron sinense*	*Tetracentron sinense*
	Neillia thyrsiflora	*Trachelospermum sp.*	*Meliosma pungens*	*Viburnum erubescens*	*Tetradium fraxinifolium*
	Osbeckia sikkimensis		*Michelia spp.*		*Viburnum erubescens*
	Osmanthus suavis		*Neolitsea spp.*		
	Pentapanax spp.		*Persea (Machilus) spp.*		

[A] TWINSPAN "abundant" species.

TABLE 3.4.2. Composition of the rhododendron association at Chitre compared to that of similar forest types reported elsewhere in the Temperate Sikkim-East Nepal Himalaya (woody taxa only, listed alphabetically).

Present study, rhododendron association[A], Chitre (2200-2600 m)	Shakya (1975), deciduous maple/evergreen oak transition zone, dominated by *R. arboreum*, Mayam Danda, east Nepal (2500 m)	Shrestha et al. (1990a), temperate evergreen broadleaved forest, dominated by *R. arboreum*, Makalu-Barun, east Nepal (2740 m)	Shakya (1995), *Rhododendron arboreum* forest, Makalu-Barun, east Nepal (2100 m)
Eurya acuminata	*Acer campbellii*	*Betula alnoides*	*Alnus napaulensis*
Lyonia ovalifolia	*Acer sterculiaceum*	*Daphne bholua*	*Carpinus sp.*
Myrsine semiserrata	*Berberis sp.*	*Litsea cubeba*	*Castanopsis hystrix*
Rhododendron arboreum	*Daphne bholua*	*Lyonia ovalifolia*	*Lithocarpus spicata*
Symplocos theifolia	*Dodecania grandiflora*	*Rhododendron arboreum*	*Lyonia ovalifolia*
Viburnum erubescens	*Leucosceptrum canum*	*Rhus sp.*	*Quercus glauca*
	Lindera pulcherrima	*Symplocos sp.*	*Rhododendron arboreum*
	Lyonia ovalifolia	*Viburnum erubescens*	
	Magnolia campbellii		
	Mahonia napaulensis		
	Pieris formosa		
	Rhododendron arboreum		
	Sarcococca sp.		
	Symplocos sp.		
	Viburnum sp.		

[A] TWINSPAN “abundant” species.

TABLE 3.4.3. Composition of the clearings association at Chitre compared to that of similar vegetation types reported elsewhere in the Temperate Sikkim-East Nepal Himalaya (woody taxa only, listed alphabetically).

Present study, clearings association[A], Chitre (2200-2600 m)	Pasture, Taplejung / Darjeeling (2200-2800 m), Kanai (1966)	Pasture/shrub transition, eastern Nepal (1100-2500 m), Tsuchida (1983)	Pasture/shrub transition, *Quercus* zone, Arun Valley, east Nepal (1900-2000 m), Ohsawa et al. (1975)
Berberis aristata	*Alnus napaulensis*	*Arundinaria sp.*	*Berberis sp.*
Eurya acuminata	*Berberis insignis*	*Eurya sp.*	*Lyonia sp.*
Lyonia ovalifolia	*Cotoneaster congestus*	*Maesa sp.*	*Sorbus sp.*
Symplocos theifolia	*Cotoneaster nitidus*	*Osbeckia sp.*	*Symplocos sp.*
Viburnum erubescens	*Rhododendron spp.*	*Rhododendron sp.*	*Viburnum sp.*
	Rosa sericea	*Rosa sp.*	
	Viburnum erubescens	*Viburnum sp.*	

[A] TWINSPAN abundant species.

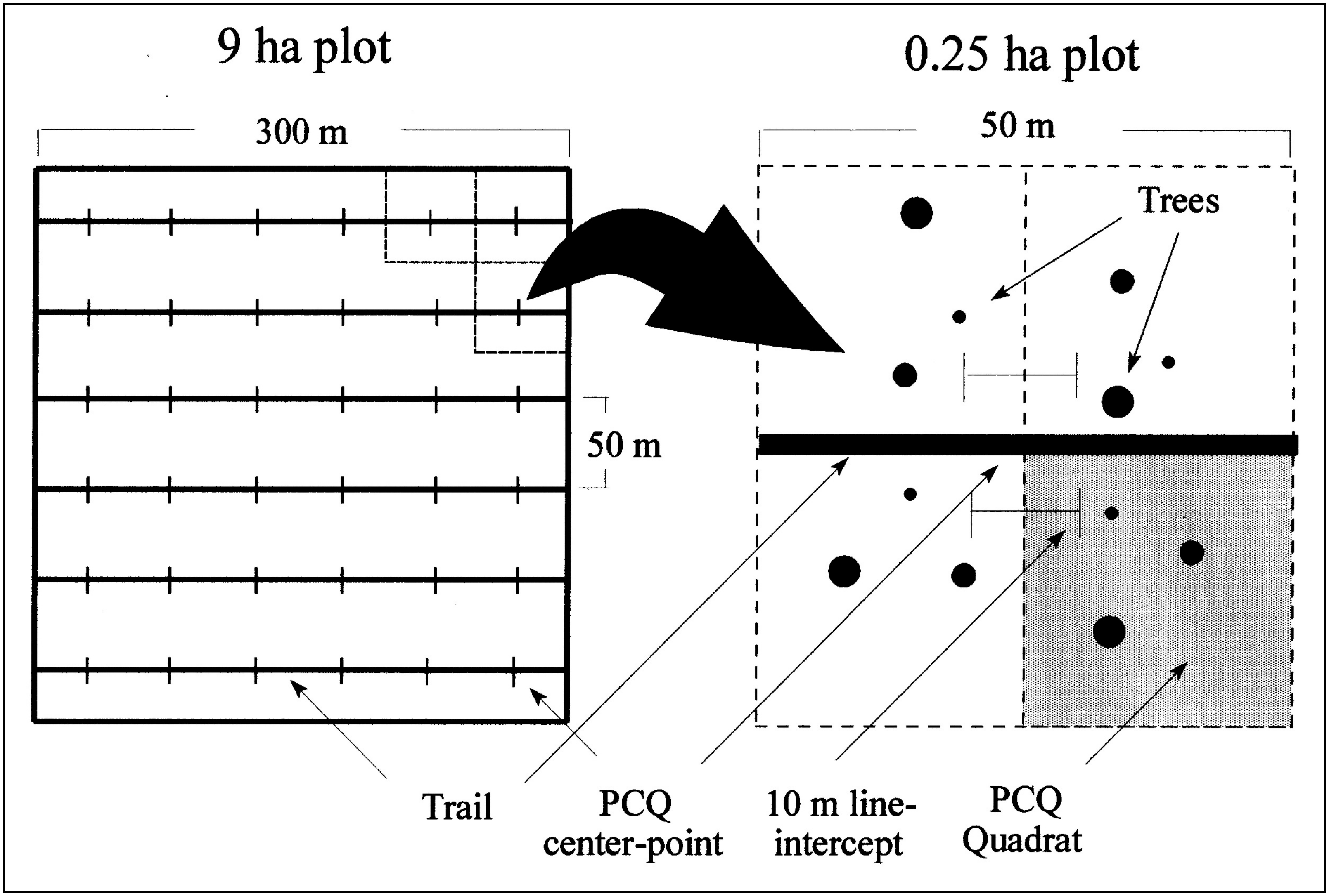


FIGURE 3.1. Configuration of 9 ha and 0.25 ha study plots.

FIGURE 3.2. Large stumps and trees at the periphery of village croplands were studied to assess the structure and composition of the pre-settlement forest.

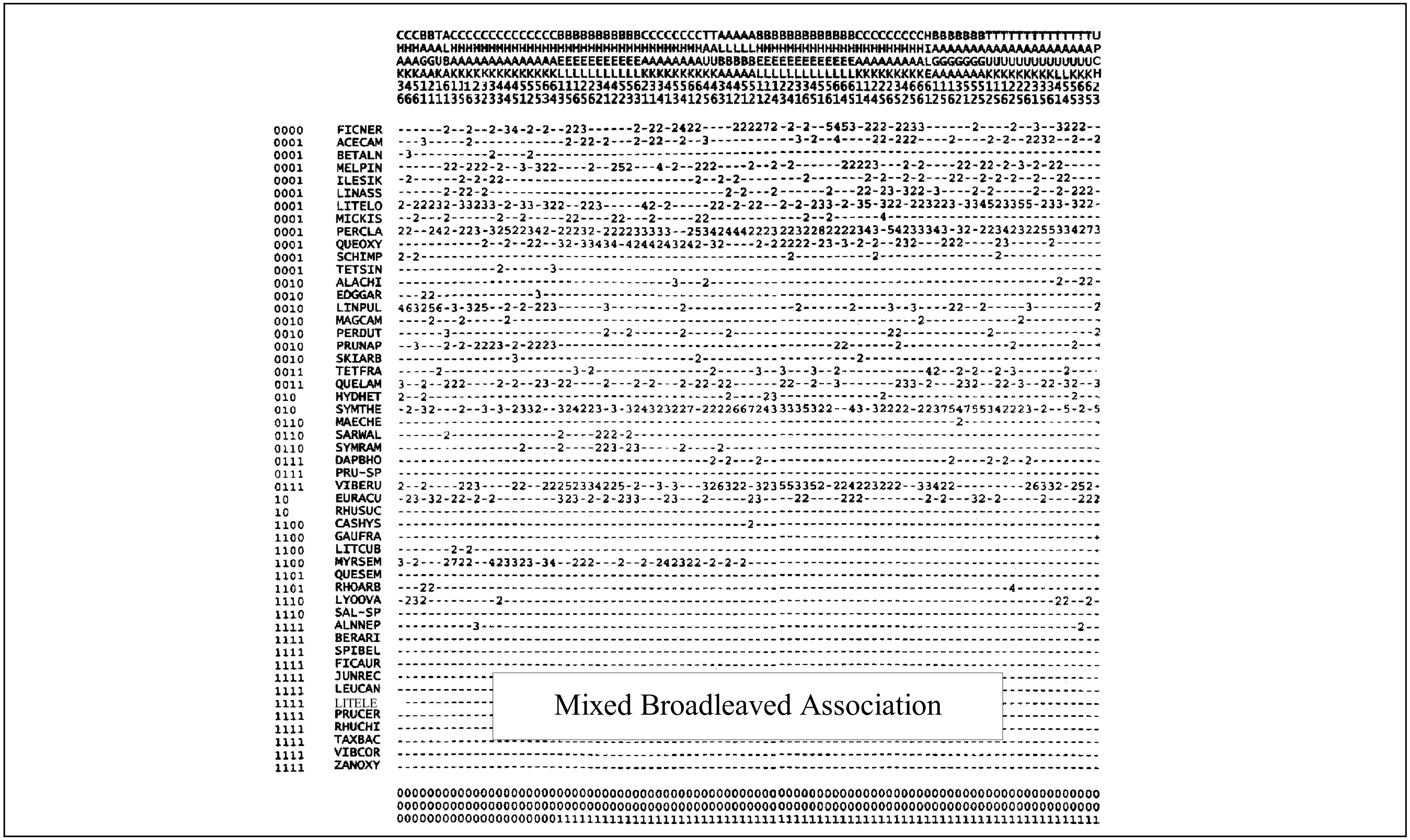


FIGURE 3.3.1. TWINSPAN ordered two-way table of tree species associations, part 1: mixed broadleaved association. Columns are 9-ha plots; rows, tree species (see Appendix 1.2 for code definitions). Based on frequency of all size classes.

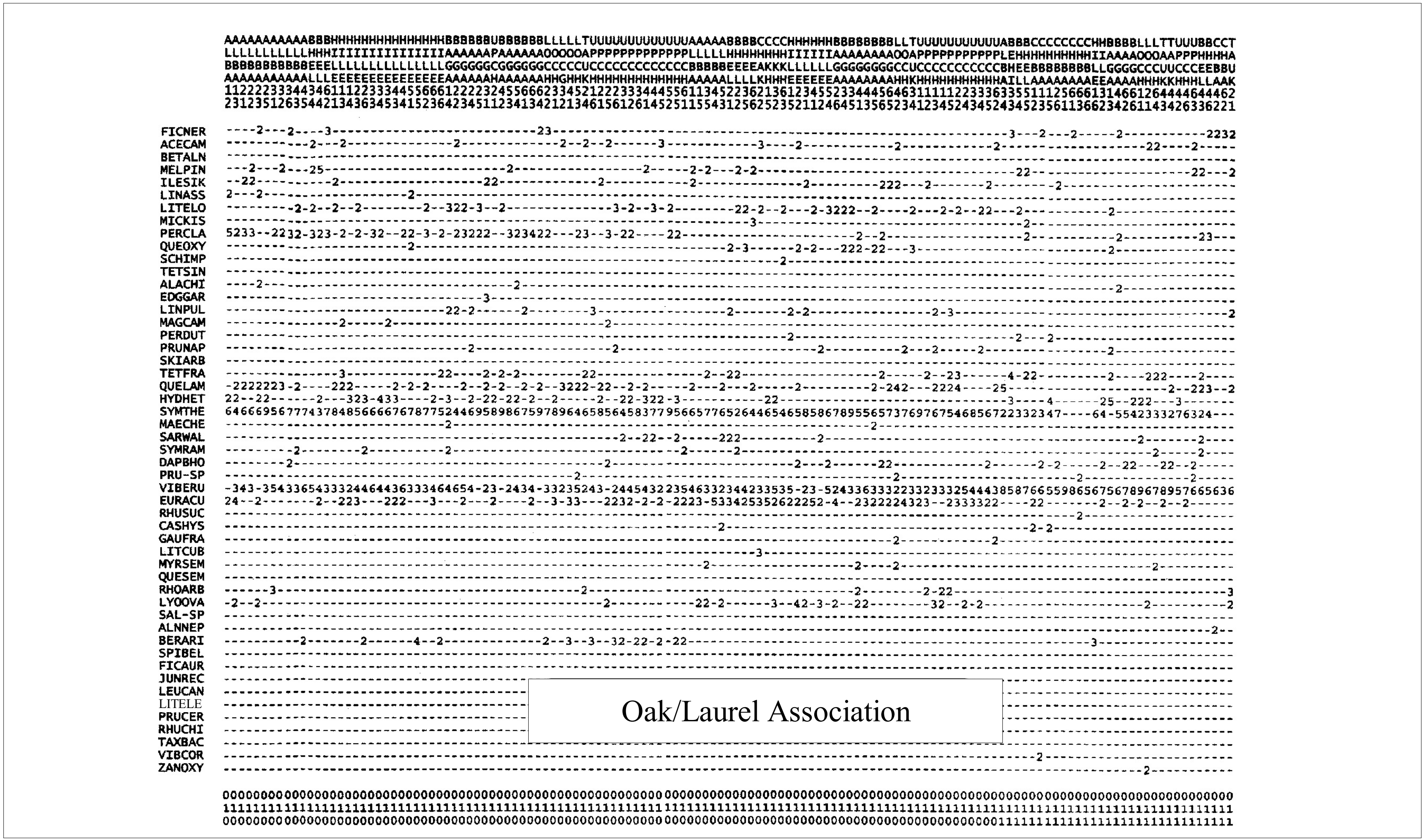
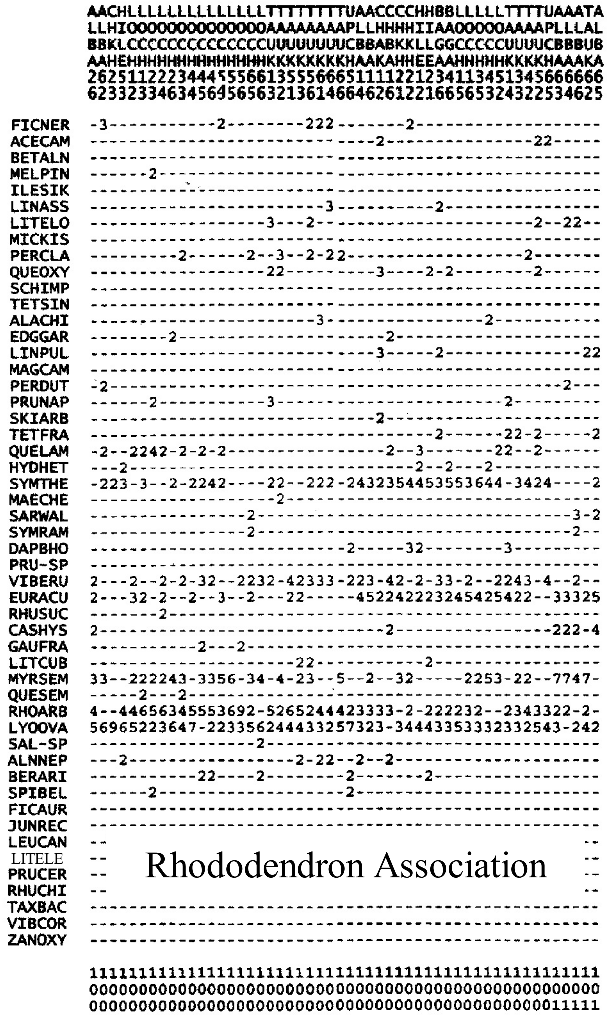


FIGURE 3.3.2. TWINSPAN ordered two-way table of tree species associations, part 2: oak/laurel association. Columns are 9-ha plots; rows, tree species (see Appendix 1.2 for species codes). Based on frequency of all size classes.



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FICNER  -3-----------2--------222-------2-------------------
ACECAM  -----------------------------2---------------22-----
BETALN  ----------------------------------------------------
MELPIN  ------2---------------------------------------------
ILESIK  ----------------------------------------------------
LINASS  ------------------------3----------2----------------
LITELO  ------------------3---2----------------------2--22--
MICKIS  ----------------------------------------------------
PERCLA  ---------2------2--3--2-22------------------2-------
QUEOXY  ------------------22---------3----2-2--------2------
SCHIMP  ----------------------------------------------------
TETSIN  ----------------------------------------------------
ALACHI  -----------------------3----------------2-----------
EDGGAR  --------2---------------------2---------------------
LINPUL  -----------------------------3-----2--------------22
MAGCAM  ----------------------------------------------------
PERDUT  -2----------------------------------------------2---
PRUNAP  ------2-----------3-----------------------2---------
SKIARB  -----------------------------2----------------------
TETFRA  -----------------------------------2------22-2-----2
QUELAM  -2--2242-2-2-2----------------2--3-------22--2------
HYDHET  ---2-----------------------------2--2---2-----------
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MAECHE  -------------------2--------------------------------
SARWAL  ----------------2--------------------------------3-2
SYMRAM  ----------------2--------------------------------2--
DAPBHO  --------------------------2-----32--------3---------
PRU-SP  ----------------------------------------------------
VIBERU  2---2--2-2-32--2232-42333-223-42-2-33-2--2243-4--2--
EURACU  2---32-2--2--3--2---22-----452242223245425422--33325
RHUSUC  -------2--------------------------------------------
CASHYS  2-----------------------------2----------------222-4
GAUFRA  -----------2---2------------------------------------
LITCUB  ---------------------22-----------2-----------------
MYRSEM  33--222243-3356-34-4-23--5--2--32-----2253-22--7747-
QUESEM  -----2---2------------------------------------------
RHOARB  4--44656345553692-5265244423333-2-222232--2343322-2-
LYOOVA  56965223647-223356244433257323-34443353332332543-242
SAL-SP  -----------------2----------------------------------
ALNNEP  ---2-----------------2-22--2--2---------------------
BERARI  -----------22----2--------2-------2-----------------
SPIBEL  ------2-------------------2-------------------------
FICAUR  ----------------------------------------------------
JUNREC  ----------------------------------------------------
LEUCAN  --                                                --
LITELE  --        Rhododendron Association                --
PRUCER  --                                                --
RHUCHI  --                                                --
TAXBAC  ----------------------------------------------------
VIBCOR  ----------------------------------------------------
ZANOXY  ----------------------------------------------------

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        0000000000000000000000000000000000000000000000000000
        0000000000000000000000000000000000000000000000011111
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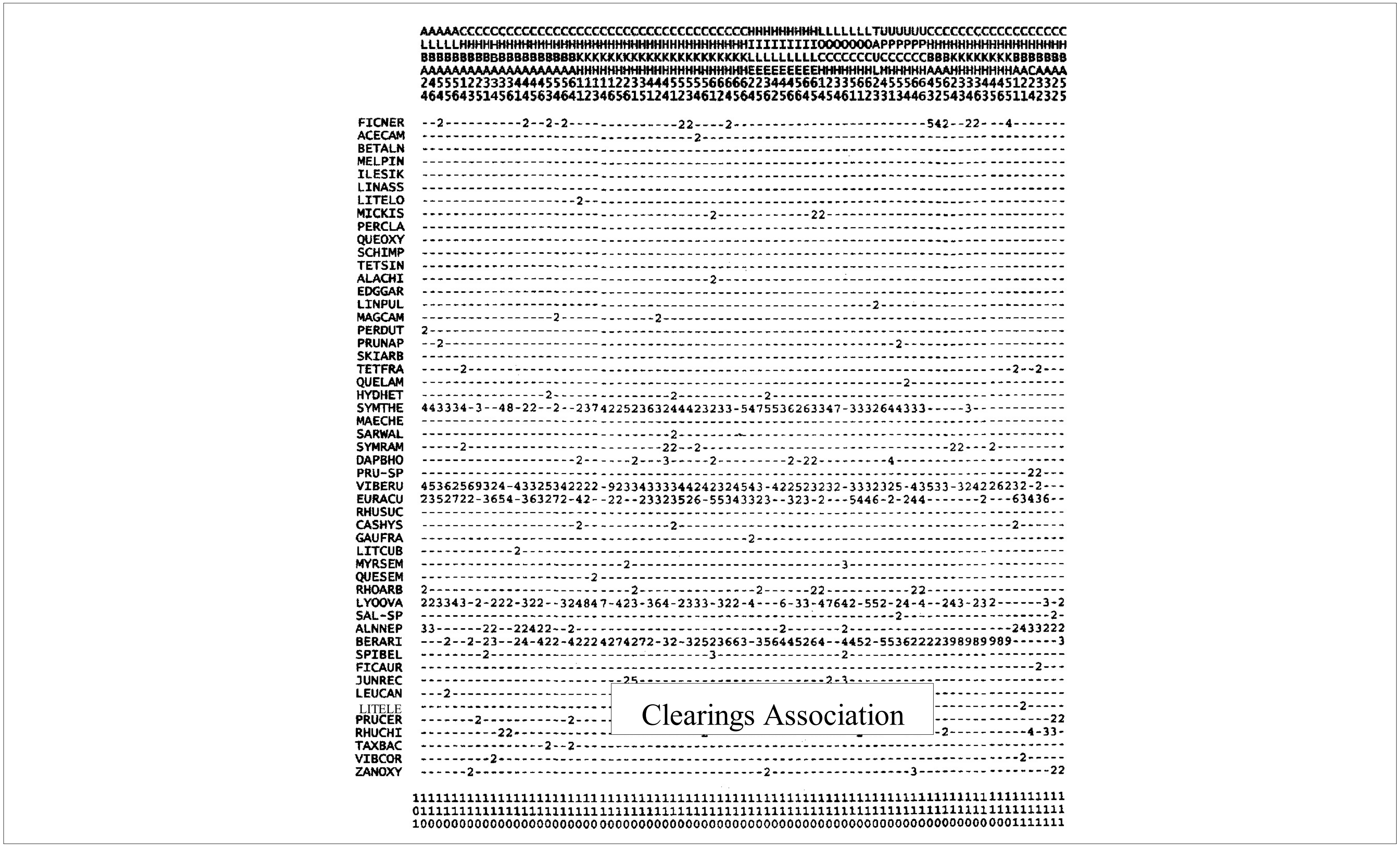
FIGURE 3.3.3. TWINSPAN ordered two-way table of tree species associations, part 3: rhododendron association. Columns are 9-ha plots; rows, tree species (see Appendix 1.2 for species codes). Based on frequency of all size classes.



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FICNER  --2----------2--2-2--------------22----2-------------------------542--22---4-------
ACECAM  -----------------------------------2-----------------------------------------------
BETALN  -----------------------------------------------------------------------------------
MELPIN  -----------------------------------------------------------------------------------
ILESIK  -----------------------------------------------------------------------------------
LINASS  -----------------------------------------------------------------------------------
LITELO  --------------------2--------------------------------------------------------------
MICKIS  -------------------------------------2------------22-------------------------------
PERCLA  -----------------------------------------------------------------------------------
QUEOXY  -----------------------------------------------------------------------------------
SCHIMP  -----------------------------------------------------------------------------------
TETSIN  -----------------------------------------------------------------------------------
ALACHI  -------------------------------------2---------------------------------------------
EDGGAR  -----------------------------------------------------------------------------------
LINPUL  ----------------------------------------------------------2------------------------
MAGCAM  -----------------2------------2----------------------------------------------------
PERDUT  2----------------------------------------------------------------------------------
PRUNAP  --2----------------------------------------------------------2---------------------
SKIARB  -----------------------------------------------------------------------------------
TETFRA  -----2----------------------------------------------------------------------2--2---
QUELAM  --------------------------------------------------------------2--------------------
HYDHET  ----------------2---------------2-----------2--------------------------------------
SYMTHE  443334-3--48-22--2--23742252363244423233-5475536263347-3332644333-----3------------
MAECHE  -----------------------------------------------------------------------------------
SARWAL  --------------------------------2--------------------------------------------------
SYMRAM  -----2-------------------------22--2--------------------------------22---2---------
DAPBHO  --------------------2------2---3-----2---------2-22---------4----------------------
PRU-SP  ------------------------------------------------------------------------------22---
VIBERU  45362569324-43325342222-92334333344242324543-422523232-3332325-43533-324226232-2---
EURACU  2352722-3654-363272-42--22--23323526-55343323--323-2---5446-2-244-------2---63436--
RHUSUC  -----------------------------------------------------------------------------------
CASHYS  --------------------2-----------2-------------------------------------------2------
GAUFRA  ------------------------------------------2----------------------------------------
LITCUB  ------------2----------------------------------------------------------------------
MYRSEM  --------------------------2---------------------------3----------------------------
QUESEM  ----------------------2------------------------------------------------------------
RHOARB  2--------------------------2---------------2------22-----------22------------------
LYOOVA  223343-2-222-322--324847-423-364-2333-322-4---6-33-47642-552-24-4--243-232------3-2
SAL-SP  -------------------------------------------------------------2-------------------2-
ALNNEP  33------22--22422--2--------------------------2-------2---------------------2433222
BERARI  ---2--2-23--24-422-42224274272-32-32523663-356445264--4452-55362222398989989------3
SPIBEL  --------2----------------------------3----------------2----------------------------
FICAUR  -------------------------------------------------------------------------------2---
JUNREC  --------------------------25------------------------2-3----------------------------
LEUCAN  ---2--------------------                                          -----------------
LITELE  ------------------------          Clearings Association           -----------2-----
PRUCER  -------2-----------2----                                          ---------------22
RHUCHI  ----------22------------                                          -2----------4-33-
TAXBAC  ----------------2--2---------------------------------------------------------------
VIBCOR  ---------2-------------------------------------------------------------------2-----
ZANOXY  ------2-------------------------------------2------------------3-----------------22

        11111111111111111111111111111111111111111111111111111111111111111111111111111111111
        01111111111111111111111111111111111111111111111111111111111111111111111111111111111
        10000000000000000000000000000000000000000000000000000000000000000000000000001111111
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FIGURE 3.3.4. TWINSPAN ordered two-way table of tree species associations, part 4: clearings association. Columns are 9-ha plots; rows, tree species (see Appendix 1.2 for species codes). Based on frequency of occurrence of all size classes.

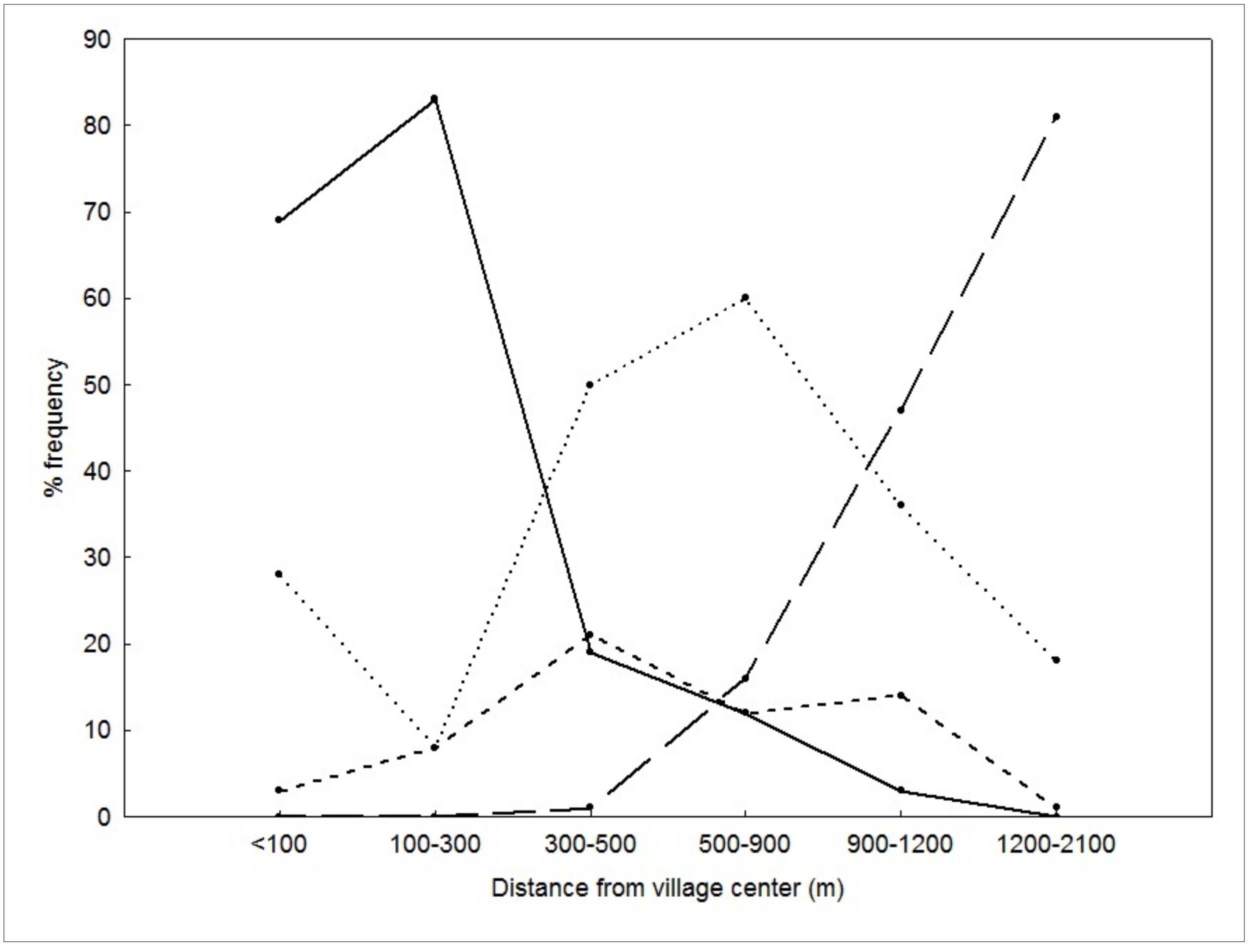

FIGURE 3.4. Relative frequency of sampling points classified as different TWINSPAN species associations at increasing distances from village center. Long-dashed line is the mixed broadleaved association; dotted line, oak/laurel association; short-dashed line, rhododendron association; solid line, clearings association. Horizontal axis is not to scale.

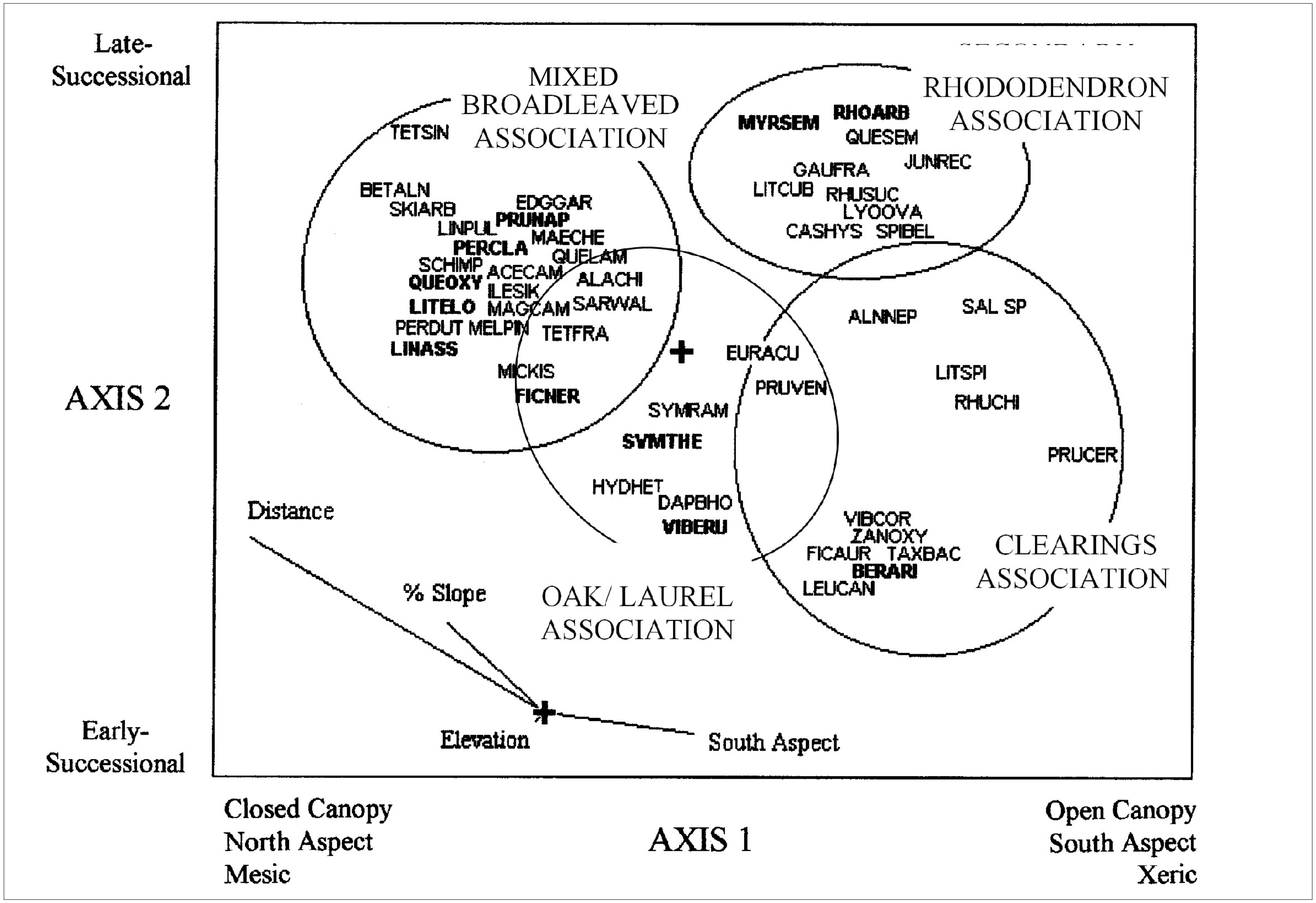

FIGURE 3.5. Ordination of tree species based on elevation, slope, aspect, and distance from village center. Association ellipses are positioned subjectively. Species in bold are TWINSPAN indicator species (see Appendix 1.2 for species codes). Vectors at lower left indicate relative influence of environmental factors. Large “+” is the centroid of ordination scores (centroid for environmental factors is displaced to lower left for clarity).

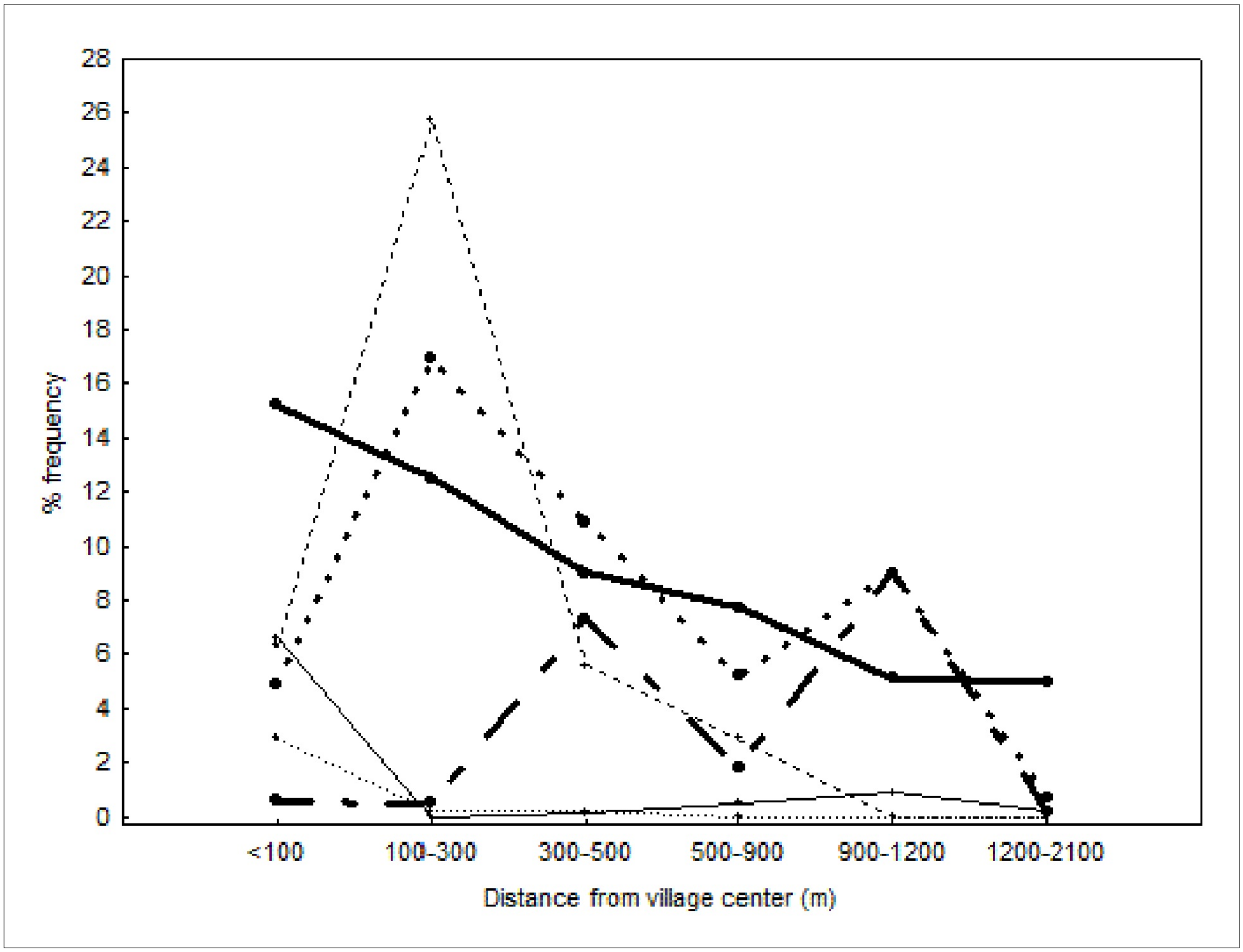

FIGURE 3.6. Relative frequency of xeric-habitat pioneer species at increasing distances from village center. Bold solid line is *Eurya acuminata*; bold dashed line, *Rhododendron arboreum*; bold dotted line, *Lyonia ovalifolia*; thin solid line, *Alnus nepalensis*; thin dashed line, *Berberis aristida*; thin dotted line, *Rhus chinensis*. Bold also indicates species that occur in forested habitats as undifferentiated canopy components. Horizontal axis is not to scale.

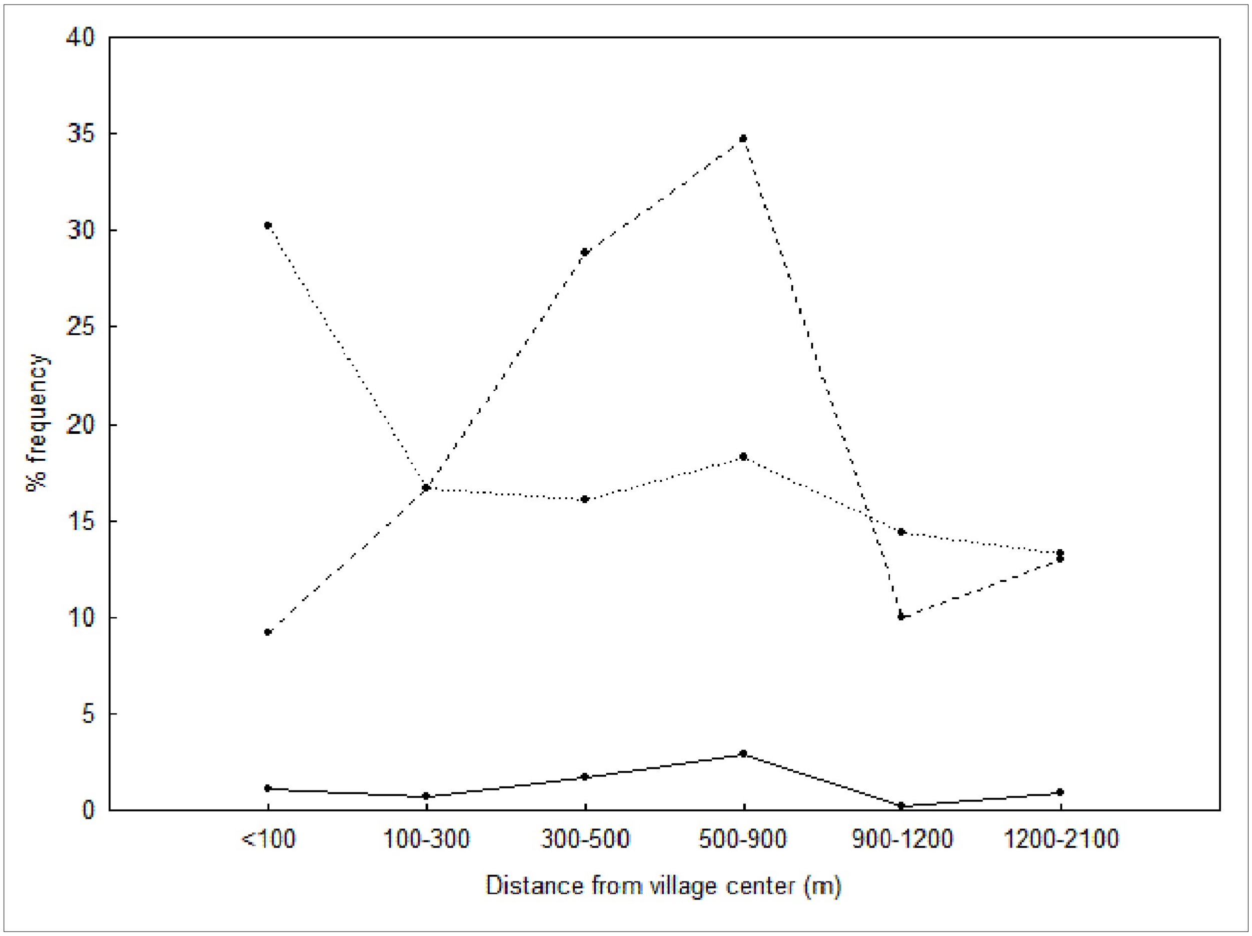

FIGURE 3.7. Relative frequency of mesic-habitat pioneer species at increasing distances from village center. Solid line is *Hydrangea heteromalla*; dashed line, *Symplocos theifolia*; dotted line, *Viburnum erubescens.* Horizontal axis is not to scale.

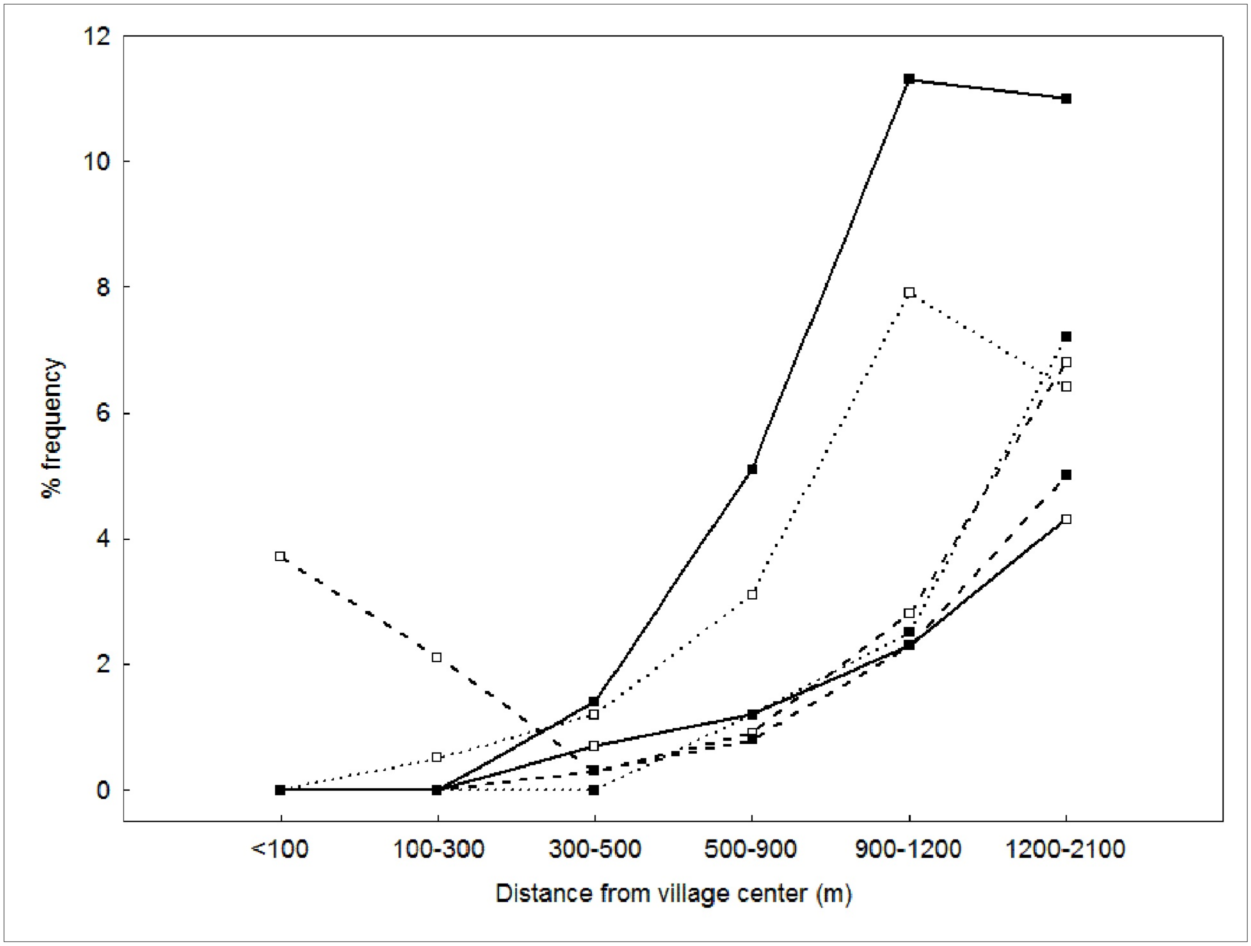

FIGURE 3.8. Relative frequency of six late-successional species that increase most with distance. Solid line with solid squares is *Persea clarkeana*; solid line with open squares, *Lindera pulcherrima*; dashed line with solid squares, *Meliosma pinnata*; dashed line with open squares, *Ficus neriifolia*; dotted line with solid squares, *Quercus oxyodon*; dotted line with open squares, *Litsea elongata*. Horizontal axis is not to scale.

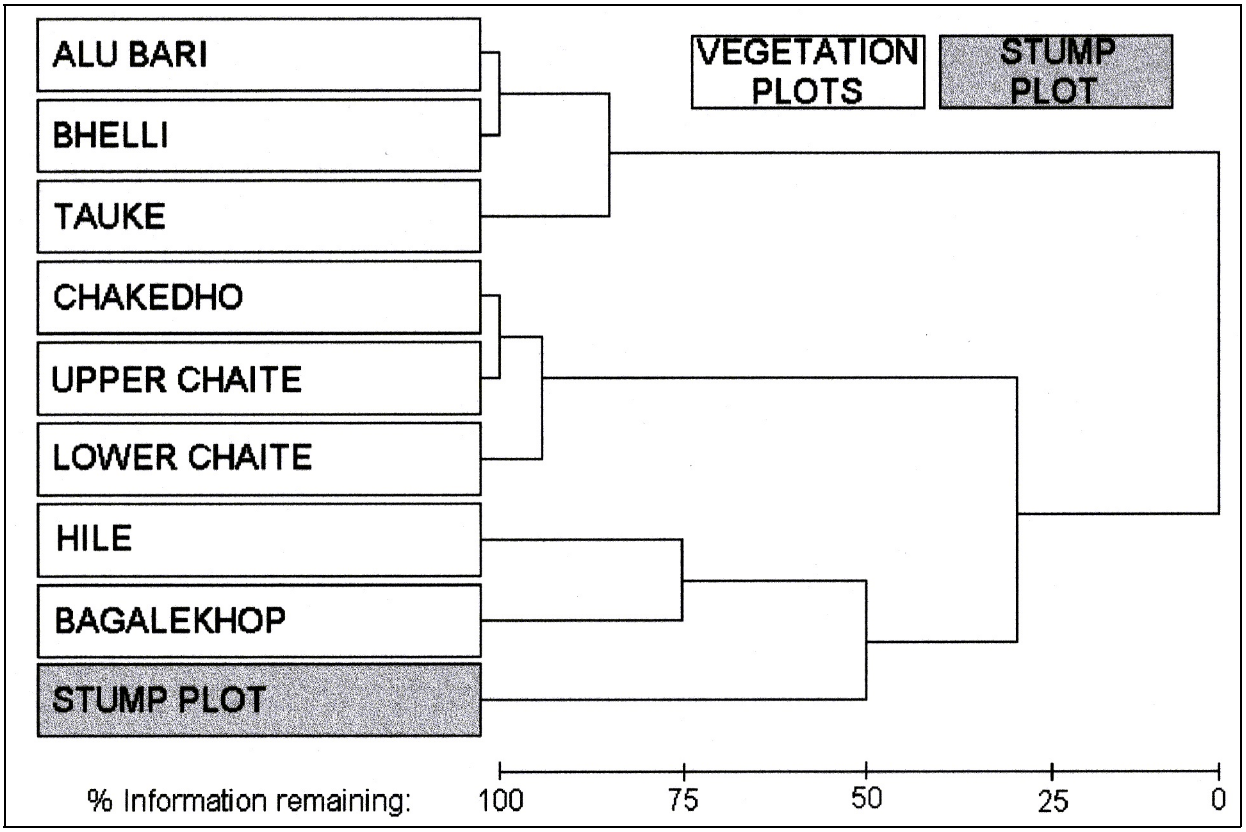

FIGURE 3.9. Nearest-neighbor cluster analysis of relativized Basal Area Ratios for *Persea*, *Quercus* and *Magnolia* stumps and living trees >50 cm diameter at eight vegetation plots and one stump plot (Chitre Bari was omitted because it had few trees >50 cm diameter; Chitre Kharka because it overlapped the stump plot).

APPENDIX 3.1. Density and basal area of stumps and living trees >50 cm diameter at one stump plot and eight vegetation plots.[A]

			Persea spp.		*Quercus* spp.		*Magnolia campbellii*	
Plot	Distance (m)	Effective sample area (m^2)[B]	No./ha	Basal area (cm^2)/ha	No./ha	Basal area (cm^2)/ha	No./ha	Basal area (cm^2)/ha
Stump Plot	350	500.0	0.81	5166	1.8	6107	0.6	3820
Upper Chaite	400	77.1	1.7	6374	8.4	40457	0	0
Lower Chaite	450	88.6	0	0	5.1	29829	0	0
Hile	600	82.8	7.3	31616	8.8	48762	2.9	21759
Alu Bari	700	86.1	21.6	82779	22.9	88065	0	0
Bagalekhop	800	85.0	15.2	58472	22.2	111265	1.4	24480
Tauke	1150	78.8	11.3	31481	4.8	18346	0	0
Chakedho	1750	79.9	7.8	22942	18.8	96709	1.6	4140
Bhelli	1900	98.4	16.5	92685	16.5	79415	0	0

[A] Chitre Bari was omitted because it had few trees >50 cm diameter; Chitre Kharka because it overlapped the stump plot. [B] Estimated at each sampling point with formulas provided by Muller-Dombois and Ellenberg (1974).