4. Plant species composition of verge meadows in relation to habitat conditions (landscape-element scale analyses)

A vegetation survey of the three study sites, which represented the three geomorphic locations, indicated that verge meadows not only have the highest agricultural management units but also have the highest abundance of unique species. This indicates the importance of considering the floristic diversity in verge meadows for the conservation and restoration of Yatsuda agro-ecosystem. However, differences in species number in potential habitat types were so complicatedly varied among the study sites that factors affecting species composition in verge meadows were not clarified. The present chapter, hence, focuses on verge meadows in detail. Chapter 4.1 clarifies the relationship between the habitat condition and the floristic composition of verge meadows, while Chapter 4.2 compares the floristic composition of upper slope areas by setting up cross-sectional transects from valley floor to neighbouring upland terrace or ridge.

4.1. Factors affecting plant species composition of the herbaceous layer on lowermost hillside slopes

4.1.1. Materials and methods

Measurement of habitat conditions

Floristic data should be sampled after taking account of minumum areas. In this study, however, due to the complexity of relief aspects and surface soil condition especially in Sites B and C, it is difficult to confirm minumum areas in each study study field. Hence the floristic data used in the analysis was sampled by 1 m around quadrat, which is the same as that used in Chapter 3.

To characterize the environment, light condition and soil moisture condition were measured in each quadrat. Relative light intensity was estimated by using the Gap Light Analyser (GLA) version 2.0 (Frazer, *et al.*, 1999). Hemispherical canopy photography was taken at approximately 1m above the ground level to understand the light transmission. Photographs were taken skyward with a 180° hemispherical (fisheye) lens. Digital scanners converted these hemispherical images into bitmaps, which were then analysed using the software. The period of estimation was May 1st to September 30th, which corresponds to the period where deciduous trees keep leaves.

Soil moisture was surveyed on a day which was not preceded by rain by less than 5 days in either 2004 or 2005. Soil moisture was measured in five replicates, one at the center and one 10 cm inside from each of the four corners of the quadrat.

Regarding the slope aspect, after the correction from magnetic north to geographic north, the angle of declination from geographic north was calculated.

Data analysis

At each study site, species compositional data was analysed by using the ordination method of Detrended Correspondence Analysis (DCA; Hill, 1979a; Hill & Gauch, 1980) and Two-Way Indicator Species Analysis (TWINSPAN; Hill, 1979b). Plant species that appeared in only one quadrat were excluded from the analysis to avoid ordination distortion by serendipitous species because of the use of presence/absence data. The relationships among DCA axis scores, environmental parameters, and species richness were compared with nonparametric statistical methods, Spearman's correlations with SPSS Base for Windows Version 10.0 (SPSS Inc., Chicago, Illinois, USA). To detect the representative species in each plant TWINSPAN group, Indicator Species Analysis (INSPAN; Dufrêne & Legendre, 1997) was used. In these multivariate analyses, the analytical program PC-ORD for Windows Version 4 (McCune & Mefford, 1999) was used.

To compare the species traits of detected groups among different study sites, compositions of each potential habitat were calculated based on the relative frequency of each species.

4.1.2. Results

Site A

The results of DCA ordination of quadrats are shown in Figure 4.1-1. The proportion of variance in the distance matrix of DCA ordination was substantially larger along axis 1 (0.384) and axis 2 (0.255) than along axis 3 (0.006). Spearman's correlations between DCA scores and habitat conditions are demonstrated in Table 4.1-1. They were correlated with light condition, slope aspect and adjacent land use, whereas not correlated with soil moisture condition. The scores of the first axis were well correlated with relative PPFD and slope aspect, while those of the second axis were substantially correlated with the land use of nearby upland terraces. Hence the left of the diagram indicates the north-facing darker and the right of the diagram the south-facing brighter conditions, while upper and lower location of the diagram implied adjacency to upland fields and secondary woodland, respectively.

The result of TWINSPAN classification is shown in Figure 4.1-2. 4 groups were classified by the second level divisions. In the DCA scattered diagram, Groups A_2, A_3 and A_4 were located from left to right, whereas Group A_1 is located towards the top of the diagram. Groups A_2, A_3 and A_4 were bordering woodland on the slopes, whereas Group A_1 was adjacent to either upland fields or abandoned upland fields where cultivation had been performed 20 years earlier. Relative light intensity and soil moisture condition are shown in Figure 4.1-3. Groups A_2, A_3 and A_4 had different light conditions. Group A_2 was brightest (40 %, on average), followed by Group A_3 (25 % on average), while group A_4 was the darkest (less than 20 %, on average). In terms of soil water contents, all groups were in mesic condition.

Figure 4.1-4 shows the total number of occurred species in terms of each potential habitat in each group. Table 4.1-2 showed averaged species number per quadrat in terms of each potential habitat in each group. Group A_1 is composed of a substantial number of upland or roadside species (UR species), which covers almost all species occurring in the verge meadows at Site A (see Figure 3.4-1). Groups A_2 and A_3 were composed of an abundant number of grassland species (G species). Forest margin species (FM species) were predominantly observed in number in Groups A_3 and A_4. When numbers of potential habitat types were compared in the same number of quadrats, similar trend was observed (Appendix 4).

Figure 4.1-5 illustrates dormancy forms of recorded species in each TWINSPAN group. Group A_1 has a larger proportion of therophyte, while Group A_4 was characterized by microphanerophyte (M) and mesophanerophyte (MM). Group A_2 and A_3 were characterized by large proportions of hemicryptophyte (H).

The number of indicator species in each group Is shown in Figure 4.1-6. Indicator species in Groups $A_{2\text{-}4}$ were mostly composed of unique species, whereas those of Group A_1 were composed of common species, which belonged mostly to UR species. This suggests that Groups $A_{2\text{-}4}$ contribute to the floristic diversity at landscape level, whereas Group A_1 does not. In Group A_2, indicator species were composed mostly of G species, including characteristic species belonging to Miscanthetea sinensis (*Potentilla fragarioides*, *Adenophora triphylla*, *Imperata cylindrica*, *Miscanthus sinensis* and *Sanguisorba officinalis*). In Group A_3, indicator species were composed of G species, FM species and FF species. Indicator species of Group A_4 were all unique species in the verge meadows. However, they were mostly composed of FM species and FF species.

Table 4.1-3 shows Spearman's correlates between the species number of each potential habitat type and habitat conditions. In the analysis, quadrats belonging to Group A_1 were excluded because adjacency to upland fields affected species composition markedly. UR species and G species were positively correlated with relative PPFD ($p < 0.01$). Conversely, FF species were negatively correlated with relative PPFD and slope aspect ($p < 0.05$). W species were significantly correlated with slope aspect ($p < 0.01$). No potential habitat types were significantly correlated to soil water contents, which is likely to be due to the lack of wet conditions compared to other study sites.

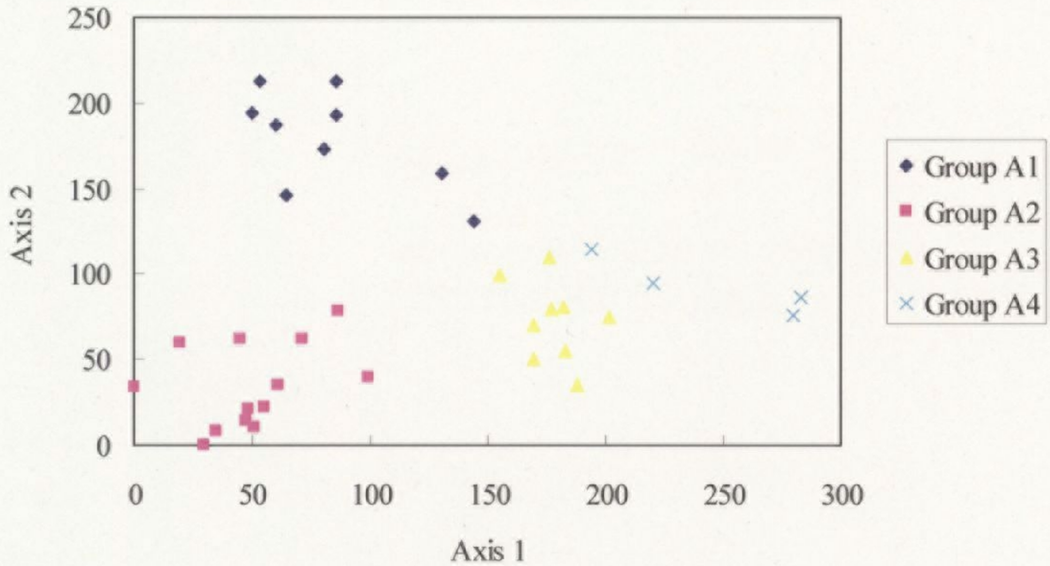


Figure 4.1-1 Scatter-plots of ordination scores for each quadrat by DCA in the first two dimensions at Site A.

Table 4.1-1 Spearman' s correlations between DCA scores and habitat conditions at Site A.

	Axis 1	Axis 2
Light	-0.614 **	0.081
Slope aspect	-0.650 **	0.112
Soil water content	0.250	0.146
Adjacent landuse	-0.146	0.728 **

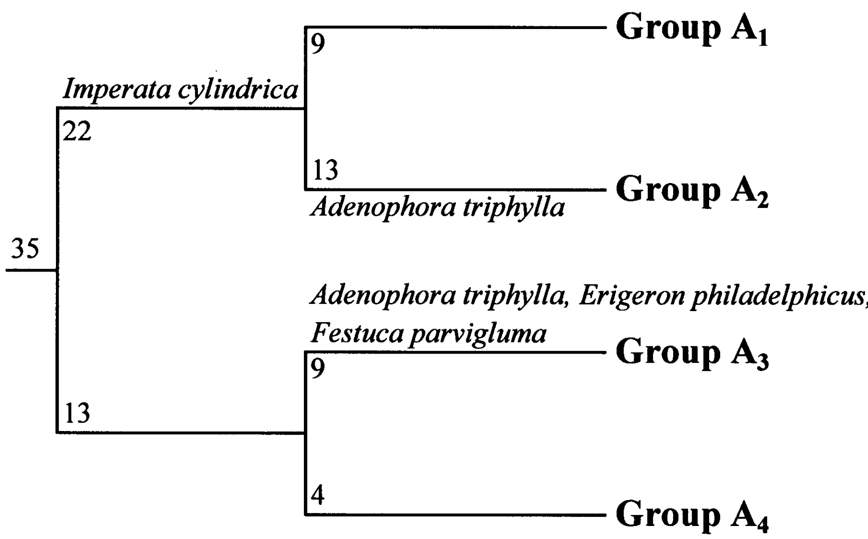


Figure 4.1-2 TWINSPAN classification dendrogram at Site A.

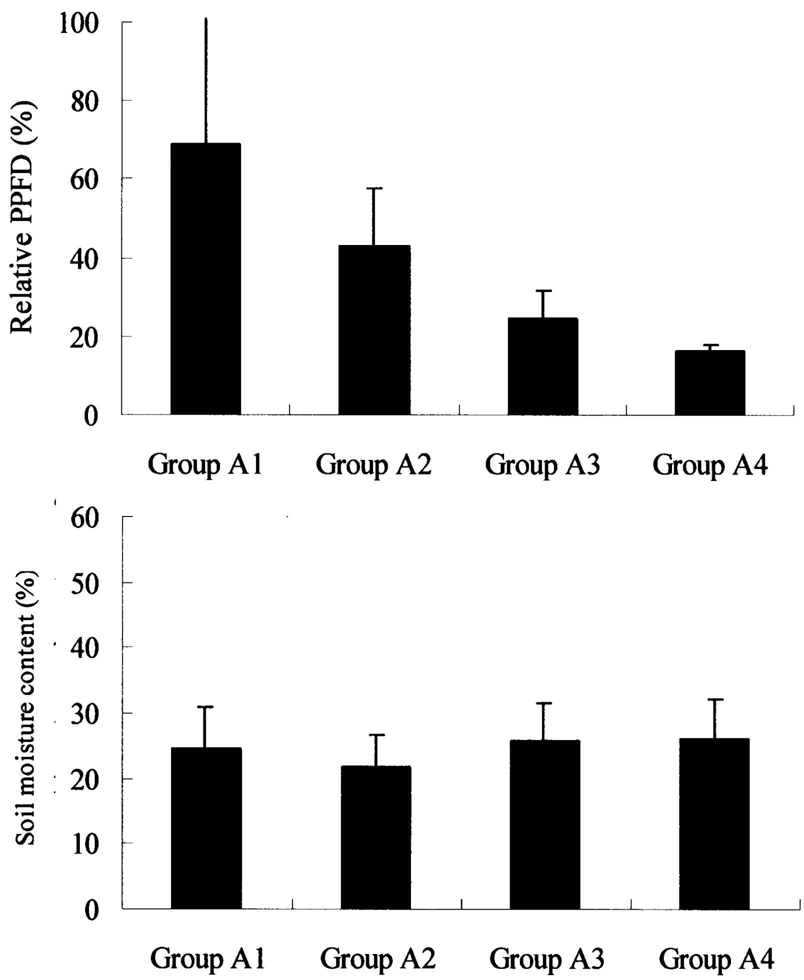


Figure 4.1-3 Environmental conditions in each TWINSPAN classification group at Site A ((a) Relative PPFD, (b) Soil moisture condition). Error bar indicates S.D.

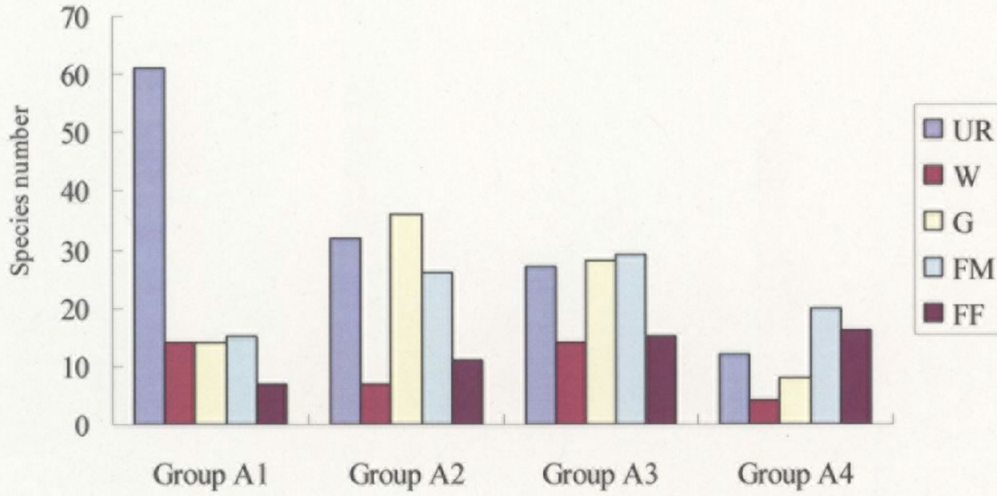


Figure 4.1-4 Potential habitat of occurring species in detected landscape elements at Site A.

Table 4.1-2 Number of potential habitat types in each group at a quadrat level (Site A).

	Group A_1	Group A_2	Group A_3	Group A_4
UR	19.6 ± 3.3	10.8 ± 3.1	11.6 ± 3.3	4.8 ± 2.8
W	2.3 ± 2.1	1.0 ± 0.8	3.8 ± 2.0	2.8 ± 1.3
G	3.9 ± 1.7	15.8 ± 3.8	11.6 ± 3.2	5.8 ± 0.5
FM	2.4 ± 1.6	4.8 ± 2.4	8.1 ± 4.7	7.8 ± 2.1
FF	1.3 ± 1.7	2.4 ± 1.9	4.0 ± 1.7	6.0 ± 2.4

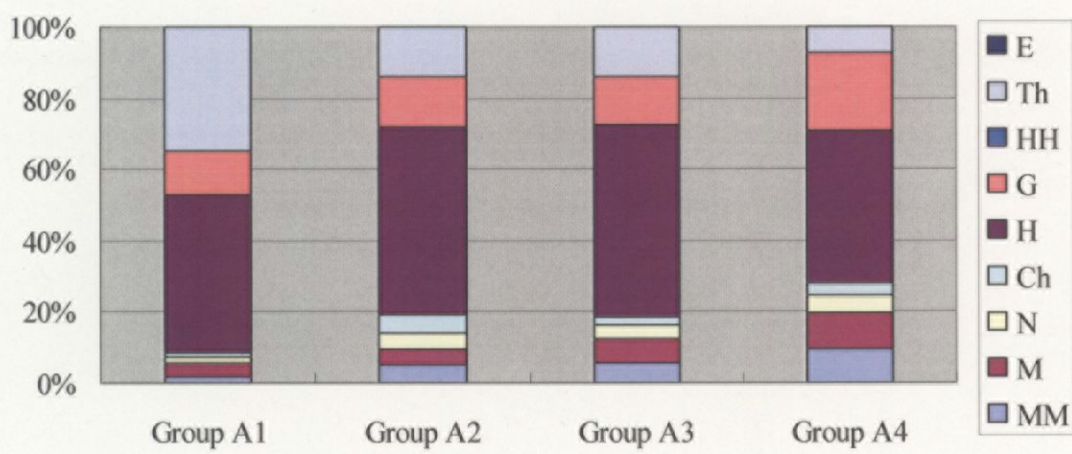


Figure 4.1-5 Dormancy form of occurring species in detected landscape elements at Site A.

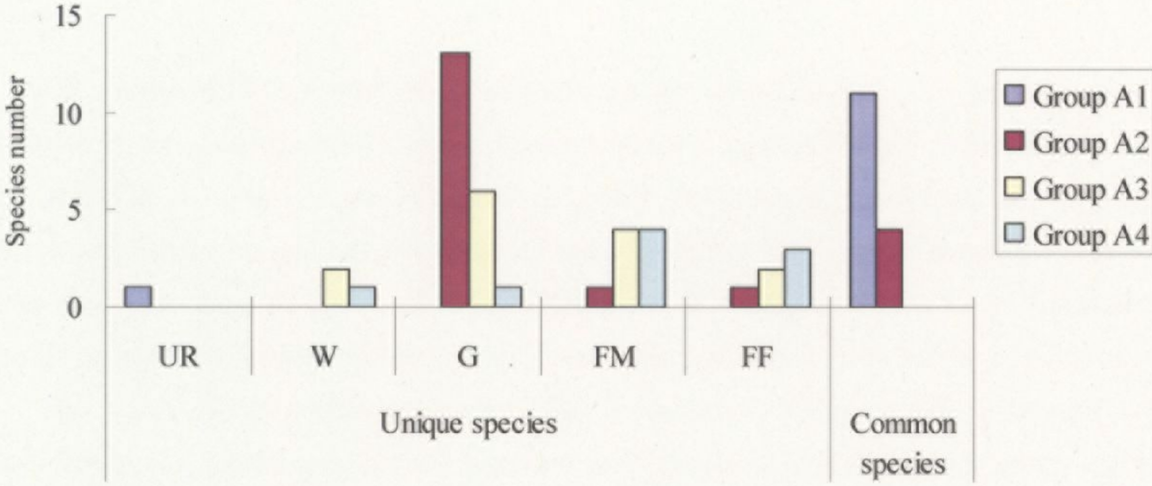


Figure 4.1-6 Number of indicator species in terms of unique/common species at Site A.

Table 4.1-3 Spearman's correlations between habitat conditions and the number of potential habitat types (Site A).

	Relative PPFD	Slope aspect	Soil water content
UR	0.501 **	0.053	0.143
W	-0.376	-0.754 **	0.299
G	0.642 **	0.346	-0.145
FM	-0.254	-0.383	0.335
FF	-0.429 *	-0.484 *	-0.198

Group A_1 was excluded from the calculation because of the adjacency to upland fields.

Site B

The results of DCA ordination of quadrats are shown in Figure 4.1-7. The proportion of variance in the distance matrix of DCA ordination was accumulatively 0.602; 0.312 along axis 1, 0.158 along axis 2 and 0.132 along axis 3. Spearman's correlations between DCA scores and habitat conditions are demonstrated in Table 4.1-4. The scores of the first axis were well correlated to relative PPFD, while those of the second axis were substantially correlated to soil moisture condition. Axis 3 was not correlated to these habitat conditions.

The result of TWINSPAN classification is shown in Figure 4.1-8. 6 Groups were classified by the second and partially the third level divisions. Relative light intensity and soil moisture condition are shown in Figure 4.1-9. Groups $B_{1\text{-}3}$ are located left in the DCA diagram, whereas Groups $B_{4\text{-}6}$ are located right in the diagram. Correspondingly, the former groups were observed to be in a darker condition, and the latter groups were in brighter conditions. Group B_1 and B_6 are located upper at the top of the diagram, correspondingly they are wetter than other groups. Groups B_3 and B_5 are located in the lower part on axis 3. Groups B_3 and B_5 were different of the adjacency to slopes. In Group $B_{3,}$ a concave slope borders the verge meadows, while in Group $B_{5,}$ well-managed meadows are located at relatively low relief heights of slopes.

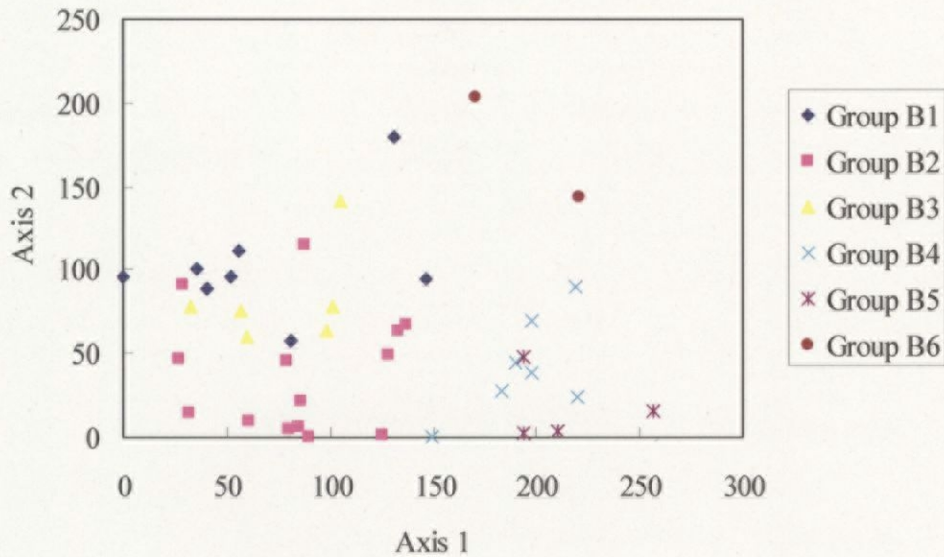
Figure 4.1-10 shows the total number of potential habitat types in each group. Table 4.1-5 shows the average species number per quadrat in each group. Group B_4 has a substantial number of G species, which is almost equal to the total number occurring in verge meadows (see Figure 3.4-1). In Groups B_1 and B_5, occurring species were predominantly composed of W species in number. Especially Group B_5 was composed of W species, which are only observed in this group. Group B_3 was substantially predominated by UR species. In Group B_1, the nationally threatened species *Parnassia palustris* was observed. When numbers of potential habitat types were compared in the same number of quadrats, similar trend was observed (Appendix 4).

Figure 4.1-11 shows the life forms of recorded species in each TWINSPAN group. Groups B_2 and B_4 had larger proportions relatively of microphanerophyte (M) and mesophanerophyte (MM), but smaller proportions of therophye (Th). Group B_5 was different from other groups. Only few geophyte (G) were observed and species of water-dispersed seeds were frequently observed. In terms of characteristic species, Group B_4 was observed to have a relatively large proportion of Miscanthetea sinensis. Group B_3 was observed to have a relatively large proportion of Rosetea multiflorae.

Since some groups were composed of a small number of quadrats, indicator species were not properly selected. Hence, to clarify the difference of occurrence in G species, Groups $B_{1\text{-}3}$ and Groups $B_{4\text{-}6}$ are compared in Figure 4.1-12. This division corresponds to the first division of TWINSPAN classification. As a result, abundant G species were uniquely observed in Groups $B_{4\text{-}6}$, whereas Groups $B_{1\text{-}3}$ were observed to have a smaller number of G species.

Table 4.1-6 shows Spearman's correlates between species number of each potential habitat type and habitat conditions. Groups B_3 and B_5 were excluded from the calculation because of the difference in slope condition (Group B_3) or the absence of the adjacency to woodland (Group B_5). Similarly to Site A, G species were positively correlated with relative PPFD, and in addition significantly with slope aspect. W species were positively correlated to soil water contents. FF and FM species were negatively correlated to soil water contents. This is not because these potential habitat types were correlated to soil water contents. These habitats are supposed to be characterized by thin surface soil condition, hence FF and FM species in which the ratio of woody species were high were small in species number.

(a)



(b)

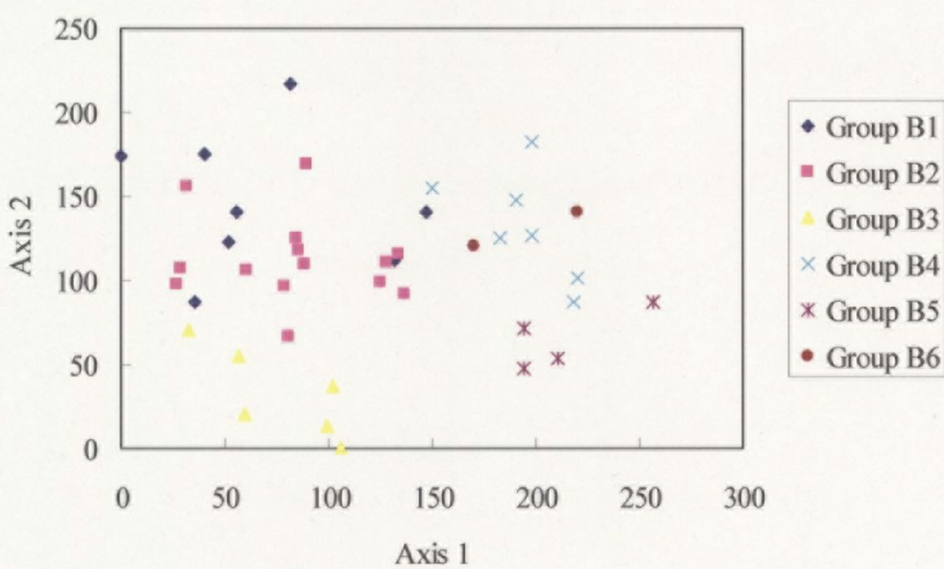


Figure 4.1-7 Scatter-plots of ordination scores for each quadrat by DCA in the first two dimensions in Site B ((a) axis 1 –axis 2, (b) axis 1 –axis 3).

Table 4.1-4 Spearman' s correlations between DCA scores and habitat conditions at Site B.

	Axis 1	Axis 2	Axis 3
Light	0.633 **	-0.161	-0.050
Slope aspect	0.566 **	0.051	-0.003
Soil water content	-0.152	0.696 **	0.130
Adjacency to concave/convex slope	-0.318 *	0.153	-0.099

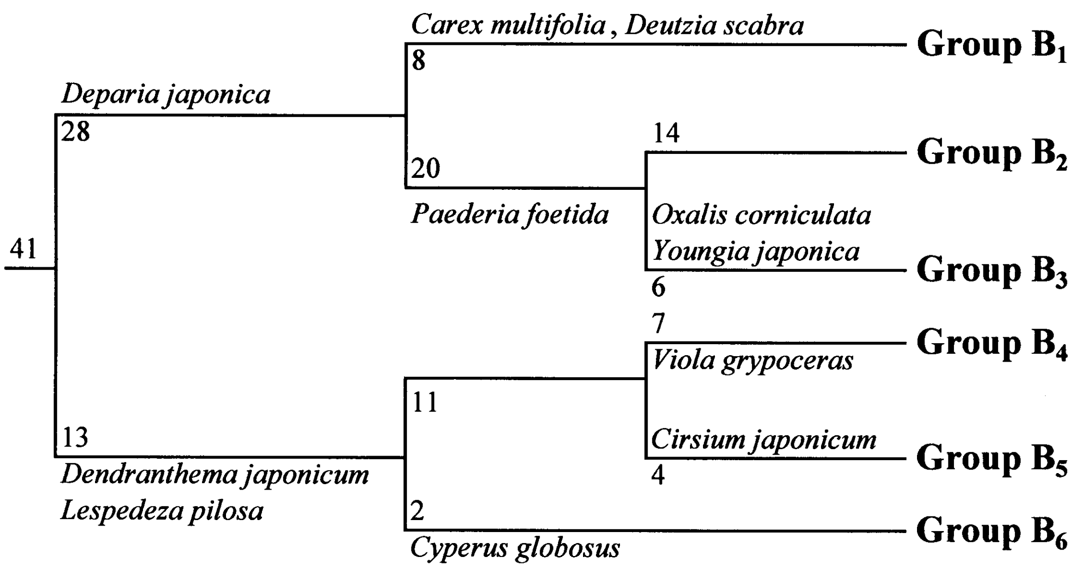


Figure 4.1-8 TWINSPAN classification dendrogram at Site B.

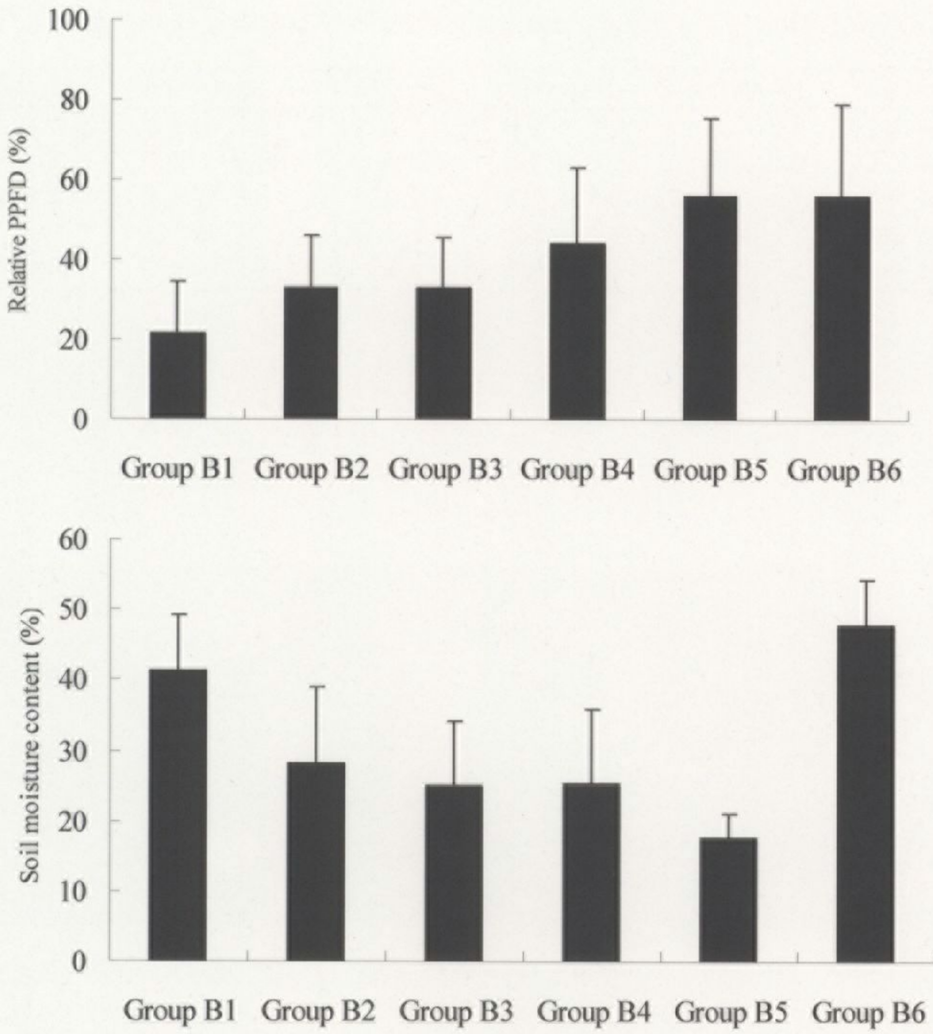


Figure 4.1-9 Environmental conditions in each TWINSPAN classification group in study area A ((a) Relative PPFD, (b) Soil moisture condition).

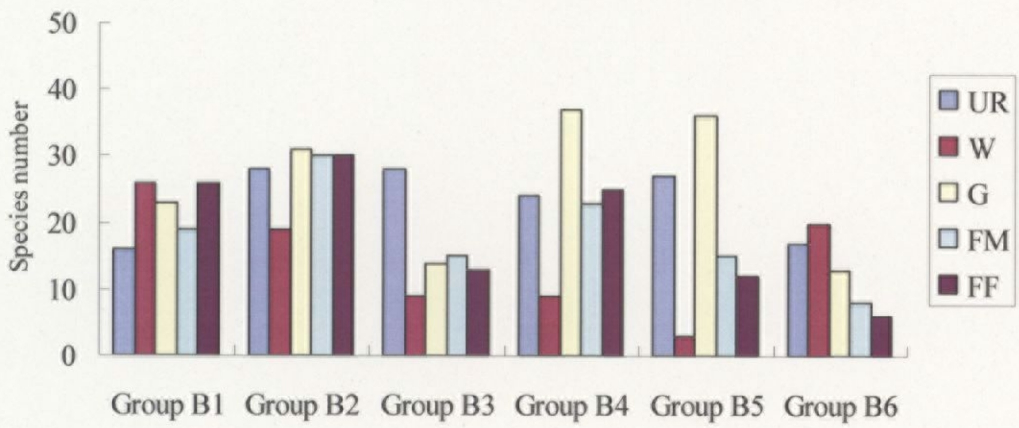


Figure 4.1-10 Potential habitat of occurred species in detected landscape elements at Site B.

Table 4.1-5 Number of potential habitat types in each group at a quadrat level (Site B).

	Group B_1	Group B_2	Group B_3	Group B_4	Group B_5	Group B_6
UR	4.5 ± 2.6	6.3 ± 3.0	11.8 ± 3.7	6.3 ± 3.4	9.8 ± 4.4	11.5 ± 0.7
W	7.3 ± 4.7	3.9 ± 3.0	3.5 ± 1.5	2.0 ± 1.3	1.0 ± 0.0	13.0 ± 2.8
G	6.6 ± 2.4	8.5 ± 2.9	5.3 ± 2.6	15.7 ± 5.5	19.5 ± 3.1	9.0 ± 0.0
FM	6.0 ± 1.7	8.7 ± 2.6	5.3 ± 1.0	6.4 ± 3.0	6.0 ± 2.4	4.5 ± 0.7
FF	6.8 ± 3.4	7.5 ± 2.8	4.5 ± 2.7	9.0 ± 4.5	5.0 ± 2.4	3.0 ± 1.4

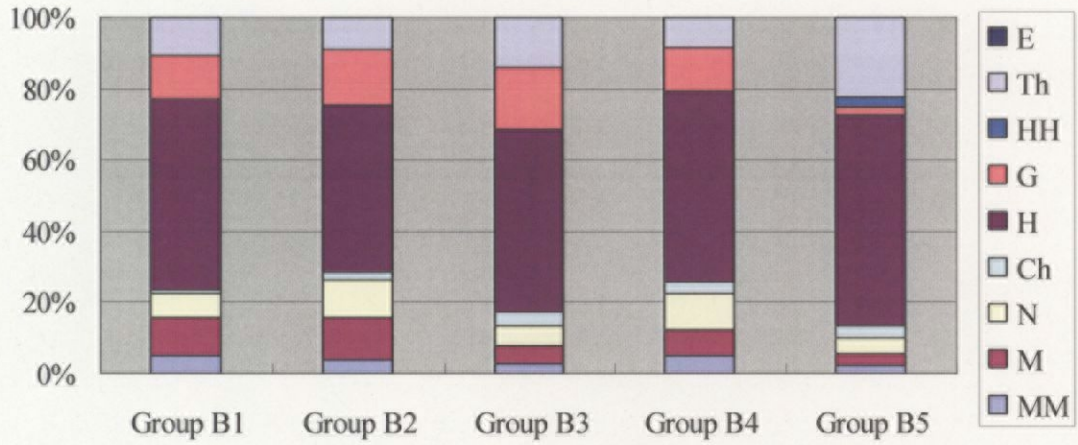


Figure 4.1-11 Dormancy form of occurred species in detected landscape elements at Site B.

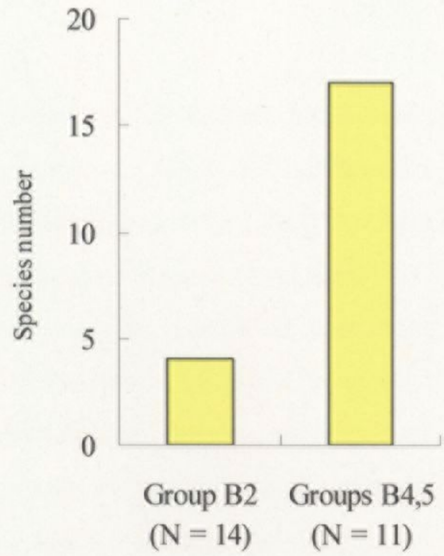


Figure 4.1-12 Number of unique species between Groups B_2 and Groups $B_{4,\,5}$.

Table 4.1-6 Spearman's correlations between habitat conditions and the number of potential habitat types (Site B).

	Relative PPFD	Slope aspect	Soil water content
UR	0.228	0.235	0.200
W	-0.063	-0.008	0.801 **
G	0.428 *	0.408 *	-0.074
FM	-0.196	-0.430 *	-0.417
FF	-0.228	-0.154	0.525 *

Groups B_3 and B_5 were excluded from the calculation because of the difference of slope condition (Group B_3) or the absence of the adjacency to woodland (Group B_5).

Site C

The results of DCA ordination of quadrats are shown in Figure 4.1-13. The proportion of variance in the distance matrix of DCA ordination was substantially larger along axis 1 (0.246) and axis 2 (0.259) than along axis 3 (0.054). Spearman's correlations between DCA scores and habitat conditions are demonstrated in Table 4.1-7. The scores of the first axis clearly divided two groups, which correlated with relative PPFD, slope aspect and soil moisture condition, whereas the scores of axis 2 were also correlated with relative PPFD.

The results of TWINSPAN classification are shown in Figure 4.1-14. Although Group C_3 includes a lot of quadrats, further classification did not show a reasonable correlation between species composition and habitat conditions. Relative light intensity and soil moisture condition are shown in Figure 4.1-15. Groups C_1 and C_2 are located left, correspondingly they had bright and relatively mesic condition. Group C_3 is located right, correspondingly they had darker and wetter conditions.

The potential habitat of occurring species is illustrated in Figure 4.1-16. Table 4.1-7 shows the averaged species number per quadrat in each group. Abundant G species were observed in Groups $C_{1\text{-}3}$. W species were abundantly observed in Group C_3. In Group C_4, although relative PPFD was observed to be quite high, FM species were observed to be predominant. Group C_4 was different in condition in terms of floristic condition of adjacent slope. Quadrats belonging to Group C4 were adjacent to non-wooded slopes, where coppicing was performed several years ago but the recovery of woody species was scarce. When numbers of potential habitat types were compared in the same number of quadrats, similar trend was observed (Appendix 4).

Figure 4-1-17 shows the life forms of recorded species in each TWINSPAN group. Although hemicryptophye was predominant in every group, group C_3 was observed to have a relatively higher proportion of nanophanerophyte (N) and microphanerophyte (M). Groups C_1 and C_4 frequently included therophyte (Th). In terms of characteristic species, larger proportions of Miscanthetea sinensis were observed in Groups $C_{1\text{-}3}$. Rosetea multiflorae were frequently observed in all groups.

Indicator species in each group are shown in Figure 4.1-18. Because of the similarity between Groups C_1 and C_2, as implied by the adjacency of plots in DCA ordination diagram, an abundant number of unique species was not observed. G species in unique species were observed in Groups $C_{1\text{-}3}$, indicating that these groups more or less functioned as unique habitats of G species. Only few W species were observed as unique species. Uniquely observed G species between Groups C1-2 and Group C3 are shown in Figure 4.1-19. Both groups included abundant G species, indicating the importance in terms of both groups for the occurrence of G species at Site C.

Table 4.1-9 shows Spearman's correlates between the species number of each potential habitat type and habitat conditions. Group C4 was excluded from the calculation because of the adjacency to non-wooded slopes. UR species were positively correlated with relative PPFD and slope aspect. W species were significantly correlated to soil water contents and slope aspect. G species were significantly correlated with relative PPFD.

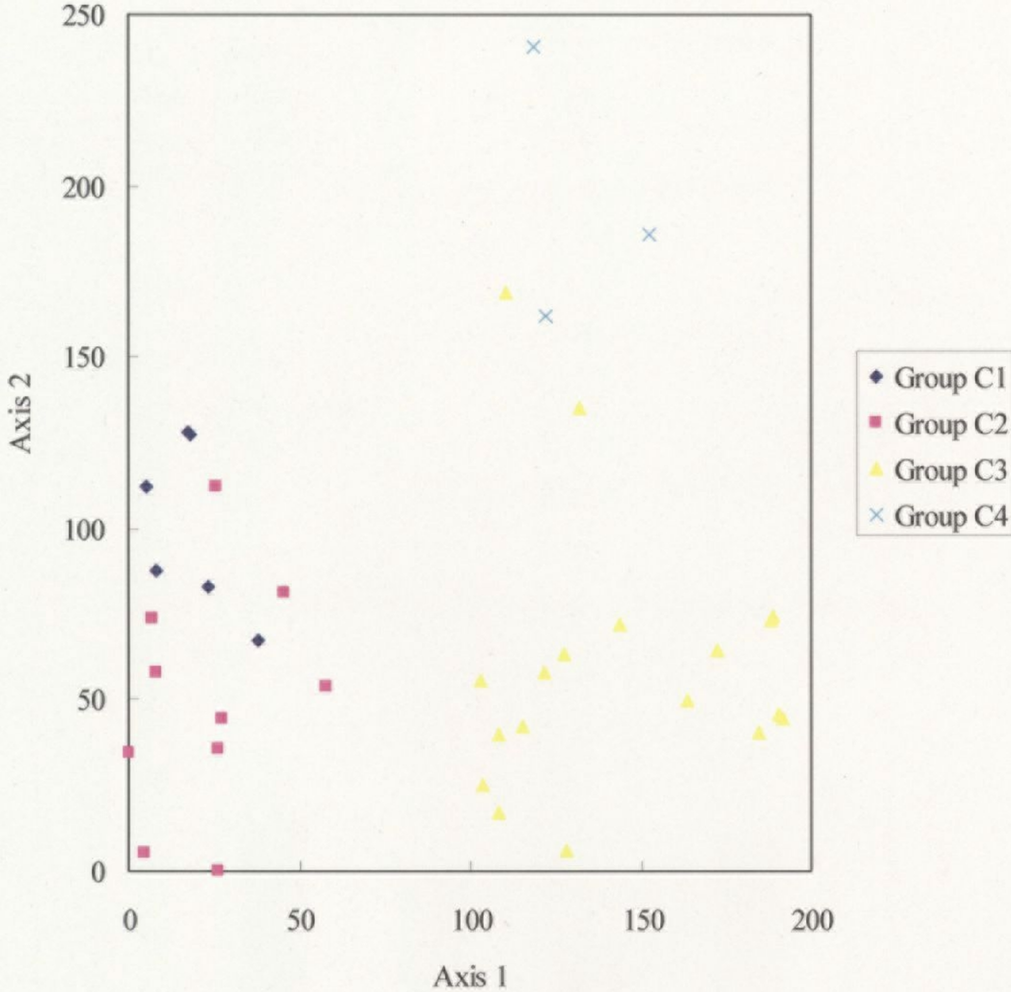


Figure 4.1-13 Scatter-plots of ordination scores for each quadrat by DCA in the first two dimensions in study area C.

Table 4.1-7 Spearman' s correlations between DCA scores and habitat conditions at Site C.

	Axis 1	Axis 2
Light	-0.444 **	0.672 **
Slope aspect	-0.882 **	-0.251
Soil water content	0.330 *	0.193
Adjacent landuse	0.103	-0.137

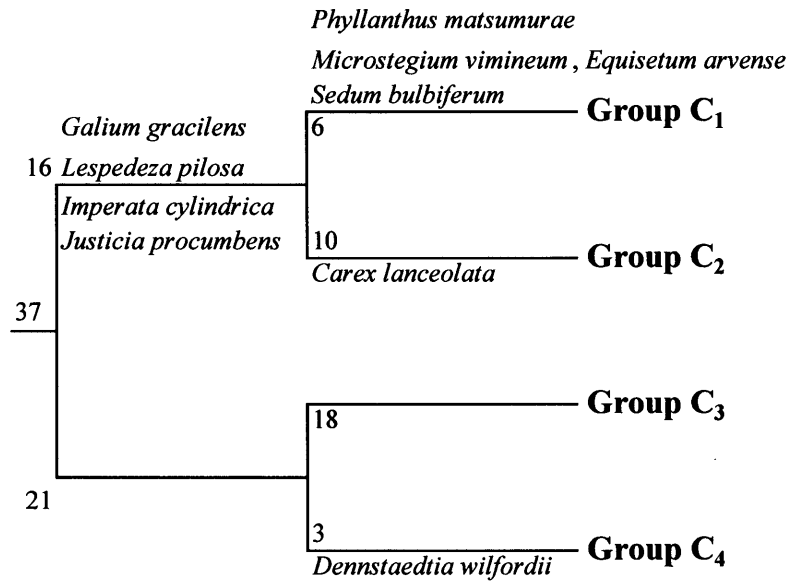


Figure 4.1-14 TWINSPAN classification dendrogram at Site C.

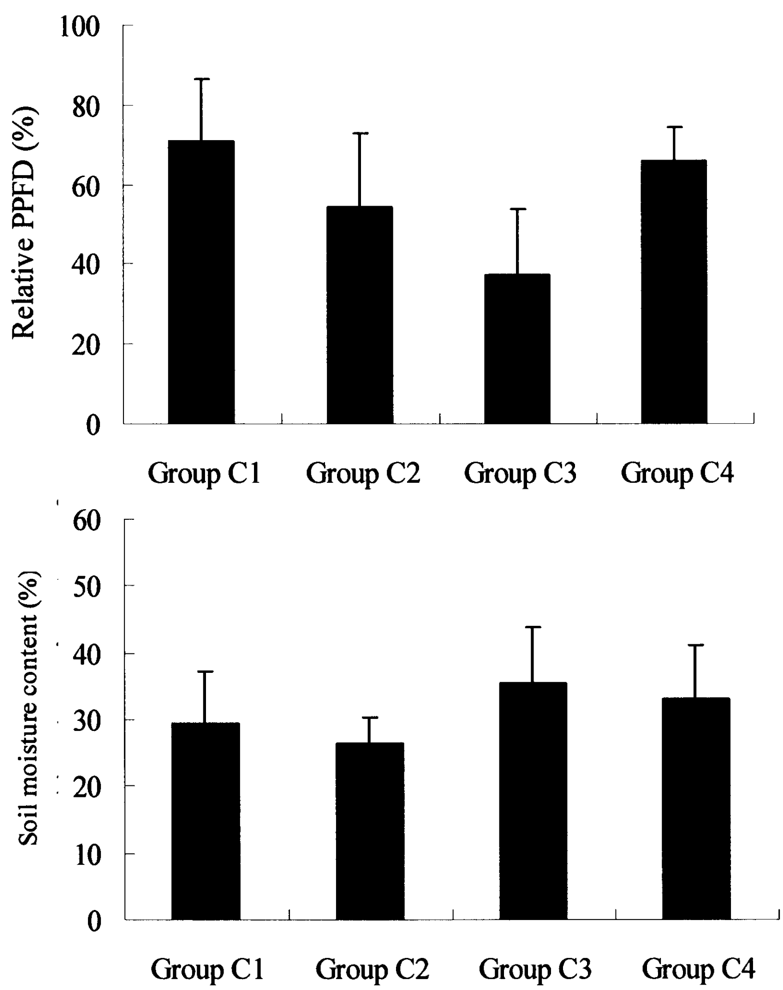


Figure 4.1-15 Environmental conditions in each TWINSPAN classification group at Site C ((a) Relative light intensity, (b) Soil moisture condition).

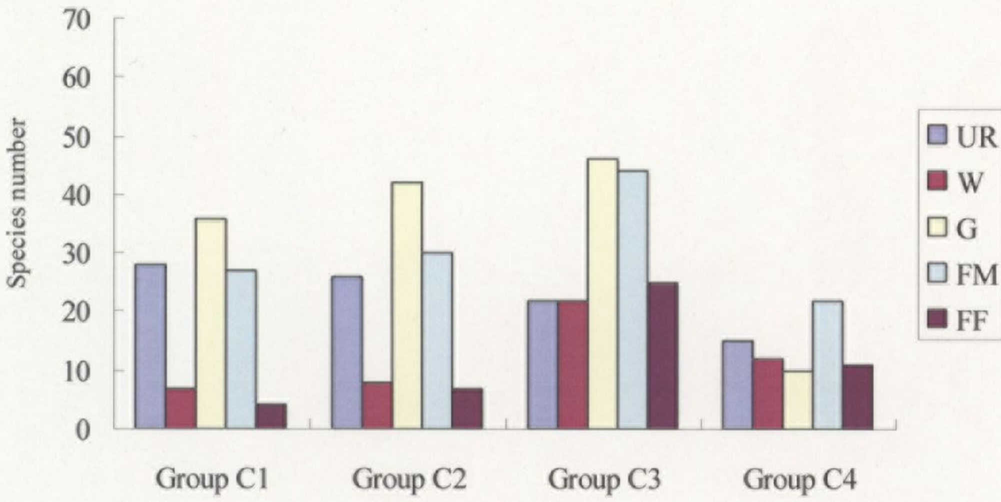


Figure 4.1-16 Potential habitat of occurred species in detected landscape elements at Site C.

Table 4.1-8 Number of potential habitat types in each group at a quadrat level (Site C).

	Group C_1	Group C_2	Group C_3	Group C_4
UR	11.0 ± 3.3	5.5 ± 2.3	4.7 ± 2.4	7.7 ± 0.6
W	2.5 ± 0.8	1.5 ± 0.7	3.8 ± 1.8	5.7 ± 2.1
G	14.7 ± 3.3	16.3 ± 4.1	10.6 ± 4.6	5.0 ± 2.0
FM	8.3 ± 2.3	8.4 ± 1.8	10.5 ± 2.8	10.0 ± 1.7
FF	0.8 ± 1.0	2.1 ± 1.1	4.3 ± 1.6	5.0 ± 2.6

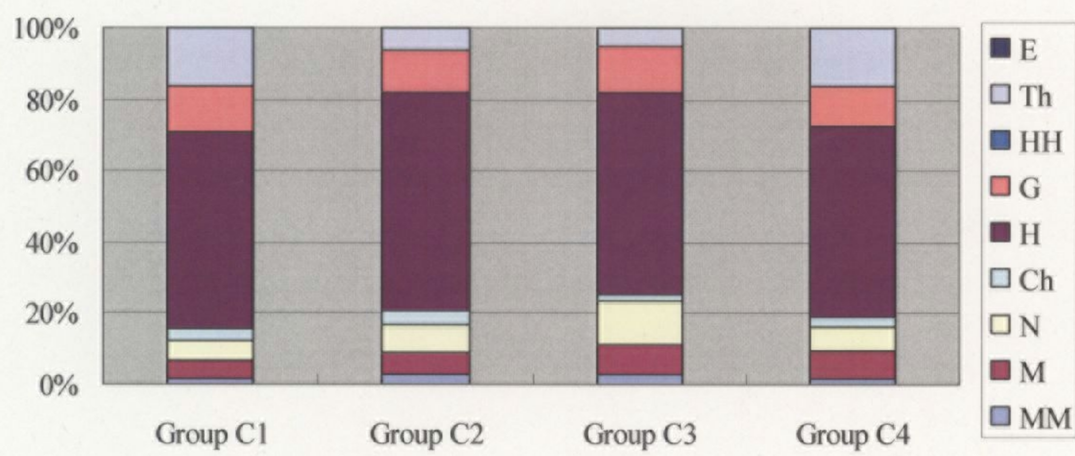


Figure 4.1- Dormancy form of occurred species in detected landscape elements at Site C.

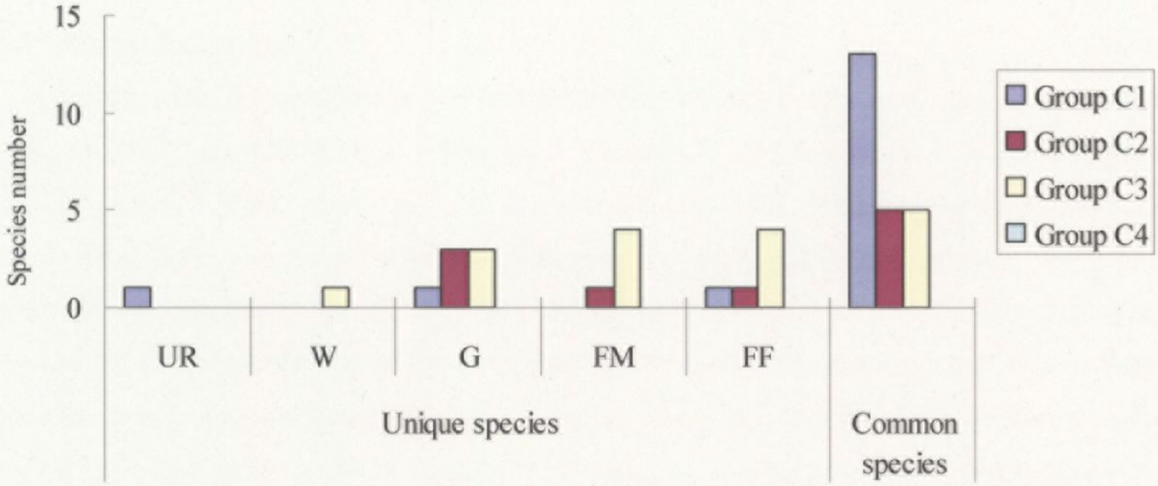


Figure 4.1-17 Number of indicator species in terms of unique/common species at Site C.

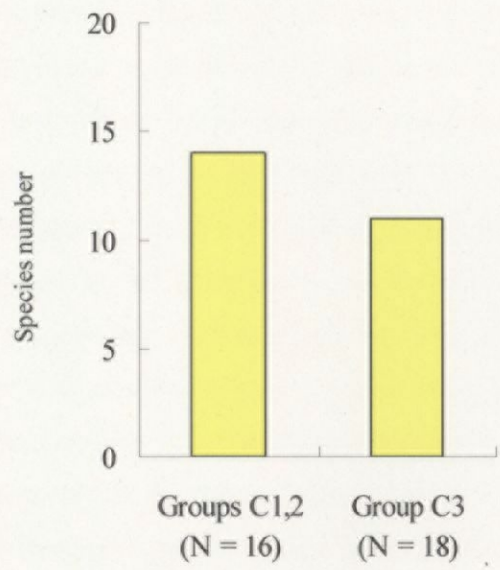


Figure 4.1-18 Number of unique species between Groups C_{1-2} and Group C_3.

Table 4.1-9 Spearman's correlations between habitat conditions and the number of potential habitat types (Site C).

	Relative PPFD	Slope aspect	Soil water content
UR	0.497 **	0.370 *	-0.269
W	-0.137	-0.642 **	0.495 **
G	0.433 *	0.262	-0.076
FM	-0.024	-0.210	-0.170
FF	-0.533 **	-0.554 **	-0.183