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The Distribution of Vegetation in the Perched Basins of the Peace-Athabasca Delta

by

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This thesis is submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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Abstract

This study was conducted to assess the general pattern of the distribution of vegetation in the perched basins of the Peace-Athabasca Delta (PAD).

Six hundred plots along 32 transects were sampled for species presence or absence and several environmental variables. Two ordination methods showed a clear wet-to-dry gradient among the species, and water-related variables were highly correlated with the primary axes of variation. However, both also indicated a secondary trend among species attributed primarily to the effects of small-scale bison disturbance.

Species were grouped into seven classes, which were then assessed statistically against two components of the water-regime gradient: elevation and water table. Logistic regression models were used to analyze transects individually, and results were then combined using random effects models. The individual transect results showed a statistically significant relationship between the species groups and both variables for a small number of transects, and showed a wide range among p-values. The combined analysis of transect results showed both elevation and water table not to be significant across two large geographic areas of the PAD.

These results show that the distribution of vegetation in the perched basins is dependent on variables besides elevation and water table. Small and large-scale disturbance characteristics, pre-emption of resources, wave action, wind-driven seiches and longer-term water-related variables all may be important, but shift in importance from region to region within the PAD.

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GENERAL INTRODUCTION

1. Introduction

The Peace-Athabasca Delta (PAD) is the largest boreal freshwater delta on the planet (Griffiths and Townsend 1985), occupying the southeast portion of Wood Buffalo National Park. It supports the majority of the largest free-ranging bison herd on earth (Timoney 1996a) and is situated at the confluence of four flyways for migratory birds in North America. In 1982, it was designated a Ramsar Wetland of International Significance, and it was a major factor in having Wood Buffalo National Park designated a UNESCO World Heritage site in 1983 (Timoney 1996a).

The vegetation of the marshes and wet meadows of the perched basins of the PAD are especially important in that they comprise a major portion of the habitat essential for wildlife populations (PADTS 1996). Bison forage on sedges in the wet meadows (Timoney 1996a) and the basin wetlands provide important staging and nesting habitat for millions of waterfowl and shorebirds (Timoney 1995) and support abundant emergent and submergent aquatic vegetation essential for muskrats (PADTS 1996). Many of the indigenous people living in and around the delta still rely on these and other biological resources for subsistence and livelihood.

During the past 70 years, several vegetation studies have been conducted in the Peace-Athabasca Delta (e.g. Raup 1935, Fuller and LaRoi 1971, Dirschl *et al.* 1974, Cordes and Pearce 1979). All have been descriptive in nature and have recognized the heterogeneity of the PAD mosaic in landform, hydrology and vegetation. However, there has been no analytical research aimed at specific components of this heterogeneity, either in limiting the study area to a particular feature of the PAD complex, or in identifying specific environmental variables and quantifying their relationship with vegetation.

To further understanding of the ecology of the PAD, this thesis focused on the vegetation distribution of a specific landform component of the ecosystem, the perched basins. The objectives were to identify important environmental variables contributing to the distribution of vegetation and to test these relationships statistically. Variables were identified using descriptive gradient analyses, and were tested using an inferential gradient analysis. These results were used to examine processes influencing the distribution of plant species.

2. Study Site

2.1 General Description

The PAD spans over 3900 km^2 across the Peace River Lowlands of northeastern Alberta (PADTS 1996) (Fig 1-1). The area is bounded by the Peace River to the north and the Birch Mountains to the southwest. To the east is Lake Athabasca, the north shore of which represents the southern margin of the Precambrian bedrock of the Canadian Shield in Alberta (Dirschl *et al.* 1974). Eighty percent of the area of the PAD lies within Wood Buffalo National Park; the remainder includes the Athabasca Chipewyan Reserve and Alberta crown lands (PADTS 1996).

The PAD lies at the confluence of the Peace, Athabasca and Birch River basins. The delta is the assembly of these three river deltas and several large, shallow lakes interconnected with Lake Athabasca by a network of active and inactive channels (PADTS 1996). Surrounding this main flow system are 1200 km^2 of sedge and grass wet meadows contained primarily in shallow perched basins (PADTS 1996). In the northeast portion of the PAD, Precambrian bedrock outliers occasionally protrude from the delta plain (Dirschl *et al.* 1974).

The PAD has been partitioned into two ecological units: regions where water levels are directly controlled by Lake Athabasca, and the Mamawi-Lake Claire system; and perched basins which at low to medium water levels do not have direct surface water connections with the delta lakes and channels (Cordes and Pearce 1979). The latter provides the definition of 'perched basin' used in this study.

The ecosystem is shaped by active deltaic, fluvial and lacustrine processes (Timoney 1996a) but is driven primarily by seasonal and annual water level fluctuations (PADTS 1996). Yearly flooding in the PAD occurs with peak water levels on the Peace and Athabasca Rivers resulting from spring break-up in late April-early May, and high runoff from mountain snowmelt in June or July (Peterson 1995). Although many of the low elevation basins are recharged with water, the high elevation basins are not. However, under special circumstances of spring break-up, ice jams severely restrict the river channels causing backwater to overflow the banks and recharge the higher elevation basins (PADTS 1996). These large-scale overland floods occur with a long-term frequency of one flood in 6.25 years (Timoney *et al.* 1997).

2.2 Physical Development

Deltas grow downstream and mature upstream (Dirschl *et al.* 1974). The Peace and Athabasca deltas began their development after the last continental glacier receded from the area about 10 000 years ago (Bayrock and Root 1972). Eventually the two deltas converged, cutting off the eastern tip of Lake Athabasca and creating several large shallow lakes (PADPG 1973). Development of the Birch Delta then began on the west shore of Lake Claire. The

Peace Delta has now ceased active growth, and sediment is deposited only during extreme flood events (Cordes and Pearce 1979). However, the Athabasca and Birch Deltas are continually depositing sediment (PADTS 1996), and are advancing into the western end of Lake Athabasca, and into Lake Claire, respectively (PADSR 1972).

The prevalence of perched basins in each of the three sub-deltas is typical of a bird's foot delta (PADPG 1973), and is a consequence of low levees, abundant alluvium and limited wave erosion (Selby 1985). The development of a perched basin begins with the build-up of levees along the channel distributaries to a height above flood water levels. Often, these tributaries divide then reunite to enclose depressions between them. During flood periods water in the tributaries overflows the banks depositing coarser materials on the levees, and silt and clay in the intervening depressions (PADPG 1973). Maturation is marked by continued accumulation of sediments, an increase in elevation with levees maintaining an elevated position over the depressions, and a decline in flood frequency. Eventually, the river channel is abandoned in favour of a shorter and steeper gradient, and the process begins anew (PADPG 1973).

This dynamic cycle of channel bifurcation, flooding, deposition and abandonment has continued since deglaciation, producing an immense mosaic of abandoned and openly-drained channels, frequently flooded basins with restricted drainage, and perched basins with closed drainage.

2.3 Vegetation Development

The development of biological ecosystem components in the PAD parallels the evolution of the physical environment (Dirschl 1973). Over centuries, there is allogenic succession from the aquatic communities of open water ponds to emergent wetlands, wet meadows, and finally to shrub and forest communities (PADSR 1972). Superimposed on this general successional pattern are shorter-term vegetation changes which may be caused by periodic droughts and floods, fires, animals, and the vegetation itself (Dirschl 1973).

Water is probably the primary agent of short-term vegetation change in the perched basins. Periodic large-scale flooding slows the normal long-term development by temporarily arresting the successional sequence, or setting it back to an earlier successional stage (Dirschl 1973, Fuller and LaRoi 1971). These floods recharge the basins with nutrient-rich waters, deposit silt and plant seeds, and flush out or bury plant debris (Dirschl *et al.* 1974). Following flooding, water in the basins recedes to the level of the lowest point of the surrounding levee through outflow into the rivers and lakes. Any subsequent decline in the water level in the basins is gradual and due almost exclusively to evapotranspiration (PADTS 1996). This period of gradual water recession is accompanied by succession as the vegetation adjusts to the new conditions, the successional sequence continuing until the next flood event.

2.4 Prior Research on Plant Communities in the Peace-Athabasca Delta

There has been a long history of written accounts of the vegetation of the PAD. Each author has referred to the impact of the water regime on vegetation and most have also commented on the dynamic nature of the vegetation and its pattern on the landscape.

The first written reference to the region and its vegetation was by MacKenzie (1801). He wrote: "The last two lakes (Baril and Mamawi) are now so shallow... that in a few years, they will have exchanged their character and become extensive forests...the country is so level, that, at some seasons, it is entirely overflowed, which accounts for the periodic influx and reflux of the waters between the Lake of the Hills and the Peace River".

When traveling through the upper Athabasca Delta in 1875, John Macoun, botanist with the Geological Survey of Canada, described the vegetation as follows: "willow, balsam poplar and spruce make up the forest in the above order, corresponding to the age of the land" (Macoun 1875).

The first botanical study of the PAD was conducted by Raup (1935). Although he did not specifically address the vegetation of the perched basins, his detailed accounts provide useful descriptions. He writes: "Lands subject to inundations, or at most only a few inches above the water-table, have an herbaceous vegetation ranging from semi-floating aquatic plants to sedges and grasses. Large areas in the lower deltas have nearly pure stands of the (marsh) sedge *Carex atherodes* or bluejoint grass *Calamagrostis canadensis*. On the margins of the stream channels, abandoned or otherwise, are long lines of willow *Salix* spp., which are limited to the slightly elevated ridges peculiar to such areas. The farther towards the margins of the basin the more land is covered by shrub and tree growth, so that the upper deltas and the banks of the larger channels support a forest of (white) spruce and balsam poplar."

Fuller and LaRoi (1971) delineated three categories of habitat in the perched basins: aquatic, wetland, and terrestrial. The aquatic vegetation included submerged macrophytes in deep water and floating macrophytes in shallow water. Wetland habitat supported, in ascending elevation, rushes in deep water, sedges in shallow water, herbs, and scrub savanna. The terrestrial vegetation on alluvium was described as willow-alder scrub, poplar forest, and spruce forest at the highest elevations.

Dirschl *et al.* (1974) conducted a land facet classification of the PAD, rendering six classes. Each land facet was then partitioned into vegetation units. The 'Semi-active delta' facet corresponded to perched basins and the backslopes of levees. It differed from the 'Backswamp (wet depression)' facet in that basins were frequently flooded, thereby being wetter, richer in nutrients and possessing different communities. The communities were named after the dominant species and were arranged in ascending elevation. They were: *Potamogeton - Nuphar*, *Scirpus - Typha*, *Senecio*, *Equisetum*, *Scolochloa*, *Eleocharis - Carex*, *Carex*, *Calamagrostis*, *Salix*.

Cordes and Pearce (1979) delineated the following 'perched basin and levee backslope' communities, in no clear order: *Potamogeton - Nuphar*, *Scirpus*, *Sparganium*, *Scolochloa*, *Scolochloa - Carex*, *Eleocharis - Carex*, *Equisetum*, *Carex*, *Salix - Carex*, *Senecio*, Immature fen, *Calamagrostis*.

Although most of these studies recognized a general wet-to-dry gradient, the classifications of vegetation along it were subjective. Each successive account built upon previous ones and described the vegetation in greater detail. However, this has not always generated a clearer understanding of the perched basins ecosystem, only a proliferation of vegetation type designations. The underlying causes of vegetation heterogeneity have not been investigated. As a result, an objective and statistical treatment of vegetation and the variables influencing its distribution was needed.

The objective of this thesis was to identify the primary environmental gradients influencing the distribution of vegetation, and to test their relationship with the vegetation in a statistical manner.

3. Analytical Tools

Gradient analysis is a research approach for the study of spatial patterns of vegetation (Whittaker 1967). There are two general categories of gradient analysis. Descriptive methods are used to summarize data, to identify pattern and to generate hypotheses while inferential methods are able to test relationships statistically by explicitly accepting or rejecting a null hypothesis. We used descriptive methods to identify variables contributing to vegetation pattern in the perched basins of the PAD. These variables were then tested statistically using inferential methods. By determining how environmental variables are related to vegetation distribution, we can better understand the forces that dictate its pattern.

3.1 Descriptive Methods

Descriptive analysis methods can be of two general types. Direct gradient analyses involve the analysis of species distributions on recognized, easily-measured environmental gradients (Whittaker 1967), and indirect gradient analyses use the vegetation data to generate axes of variation, or 'community' gradients. These axes can then be interpreted in light of measurable environmental variables (ter Braak, in Jongman *et al.* 1987, Mueller-Dombois and Ellenberg 1974).

In ecology, ordinations are useful for descriptive analysis because they identify structure in the data and can be used to generate hypotheses. This thesis used ordination techniques as an indirect method to show patterns of variation in composition. These were then interpreted using the available environmental data. Ordination techniques were also used as a direct analysis method. Together, the results assisted in identifying which variables were the most important determinants of vegetation pattern.

3.2 Inferential Methods

Although descriptive techniques provide valuable insight, they are considered preliminary. Inferential methods, however, are able to yield statistically-tested results by explicitly accepting or rejecting a null hypothesis. Once testable environmental variables were identified, inferential methods were used to test two null hypotheses.

4. Data

Data for this project were from transects established as part of a long-term vegetation monitoring plan (Timoney, 1996b). Timoney established 36 permanent transects in perched basins across the PAD, each having a number of plots situated along its length. Thirty-two transects were established in 1993, two in 1994, and two more in 1995 (Fig. 1-2 - transects are denoted by Dtxx-yy: DT=Delta Transect, xx denotes year of sampling, yy denotes transect number; transects are hereinafter referred to as DTyy).

The dataset was compiled over a four year period by sampling from a total of 673 plots. The first three years of data were collected by Timoney (with assistance by me during 1994 and 1995) and the fourth by me. In all years, data were taken over three weeks in late July and early August to reduce the effect of seasonal vegetation growth and water changes.

Thirty-two transects were sampled in 1993 by Timoney; nine were sampled in 1994 by Timoney and me (of which 2 were newly-established transects); and eight were sampled in

1995 by Timoney with my assistance (again, two of these were newly-established). In 1996, we resampled 34 of the transects, and collected elevation data for 29.

The transects were placed widely across the PAD complex to represent vegetation types in various basins in the semi-active delta. Transect length was dictated by basin size, and varied from 176m to 926m. Each transect was situated to cross vegetation zones, typically beginning on a dry levee and ending in a wet basin.

The plots along each transect varied in number from 8 to 23, and were sufficiently spaced to represent all vegetation types. The method of plot placement along transects was semi-random, and required a detailed description (Fig. 1-3). A plot spacing interval (x) for each transect was predetermined based on transect length (for example, x=15 for the shortest transect, length = 176m; x=40 for the longest transect, length = 926m). For a given transect (t), a random number (r_n) between 1 and 20 was selected for each plot (n). The sum of r_n and x_t was the distance in meters to the next plot. For example, the first plot along transect t was located at x_t+r_1 meters from the start post. The second plot was situated x_t+r_2 meters from the first plot. The third was situated x_t+r_3 meters from the second plot, etc.

Each plot consisted of two subplots. The first was a 0.5m x 0.5m quadrat used for estimating cover of all vascular plants, not including willows, alders and trees. The second was a 10 m^2 circular plot used for estimating the cover of willows, alders and trees. The smaller subplot was located at the center of the larger subplot.

4.1 Environmental Data

Environmental variables were assessed at each plot. The level of the water table was measured; positive values represented the depth of standing water and negative values represented the depth to wetting in the soil profile. Soil texture and soil drainage were assessed; there were seven possible classes of soil drainage ranging from very rapidly to very poorly. There were nine classes of ecological moisture regime (EMR), ranging from very xeric to hydric. The factors influencing stand establishment were nominal class data and represented one of the following: tree cutting and soil disturbance, fire, plant/animal effects, terrain effects, or flood effects. Successional status was quantified using ordinal class data ranging from a pioneer seral category to a disclimax category. Except for water table and texture, all of these variables were from a site description manual provided by the Government of Alberta (Resource Information Branch, 1990).

Several plot attributes were also assessed at each plot. The number of live stems greater than 1m in height was counted; the number of dead stems was counted, the woody basal area per hectare was estimated with a factor 2 metric prism; and the dominant height of the non-woody species at plot centre was estimated.

In 1996, 29 transects were surveyed to determine the elevation of each plot.

5. Conclusion

In Chapter 2, Detrended Correspondence Analysis and Detrended Canonical Correspondence Analysis were used to identify the water regime as the most important environmental variable in the perched basins of the PAD.

In Chapter 3, two components of the water regime were tested statistically. Analysis was first conducted by transect; results were further examined by meta-analysis to draw conclusions on a larger geographic scale. Results were discussed in the context of ordination results from Chapter 2.

In Chapter 4, recommendations and directions for future research were suggested.

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Figure 1-1. Location of the Peace-Athabasca Delta, modified from PADTS 1996.

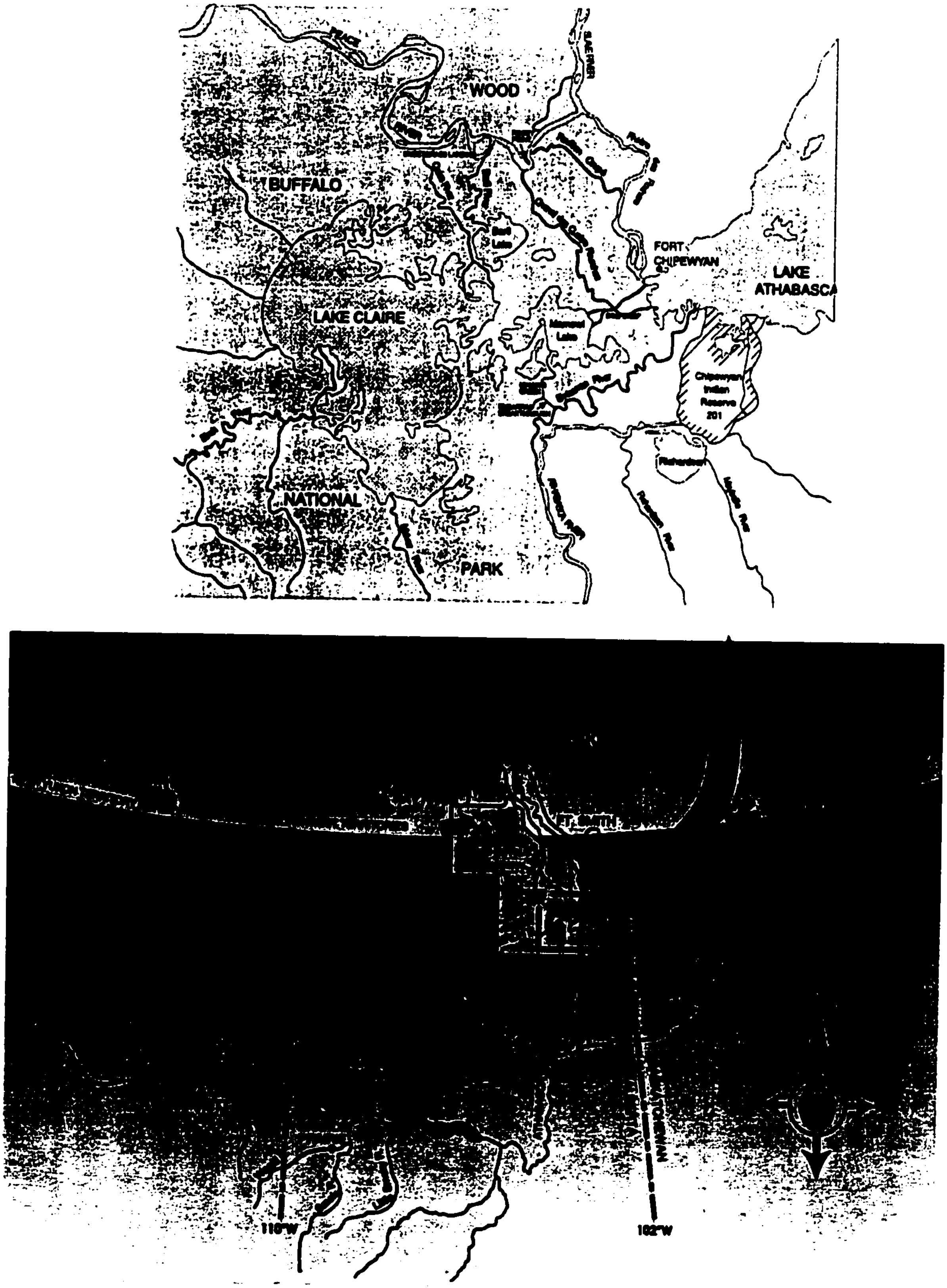


Figure 1-2. Map of the Peace-Athabasca Delta showing locations of 36 vegetation transects, modified from PADTS 1996.

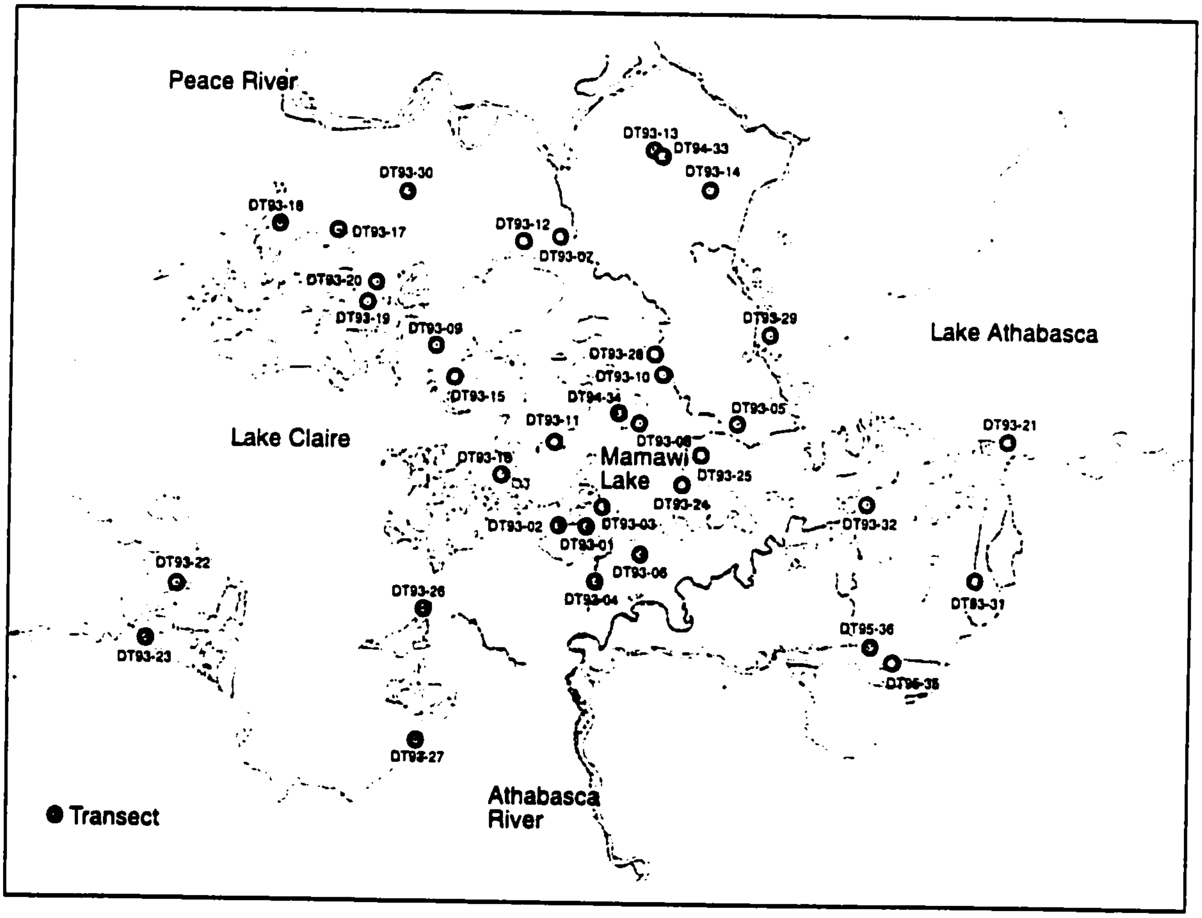
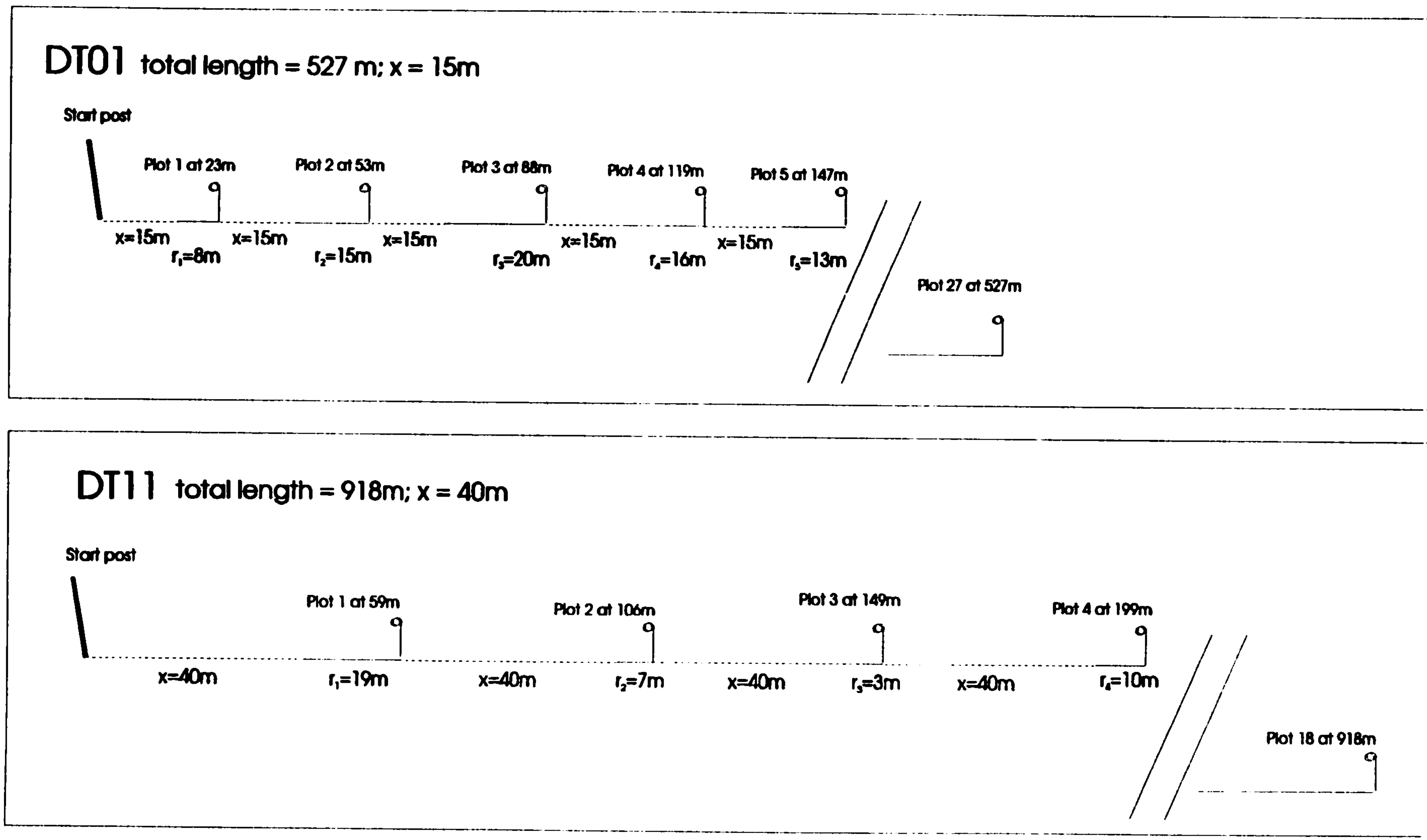


Figure 1-3. Two transects illustrating the method of plot placement along 36 transects in the Peace-Athabasca Delta; x = predetermined spacing interval, r = random number spacing interval (between 1 and 20).



Chapter 2

IDENTIFYING IMPORTANT ENVIRONMENTAL VARIABLES

1. Introduction

Marsh and meadow ecosystems in the Prairie provinces and north-central United States are similar in biological structure and composition (Fuller and LaRoi 1971). The wetland plant communities in the Peace-Athabasca Delta (PAD) as described by Raup (1935), and those of northern Wisconsin (Curtis 1959), northern Minnesota (Harris and Marshall 1963), central Saskatchewan (Walker and Coupland 1968, 1970), and northwestern Alberta (Moss 1953) have a high degree of similarity in dominant species and species composition among equivalent habitats (Fuller and LaRoi 1971).

In a review of papers pertaining to wetland vegetation in the Grassland biome of Canada and the northern United States, Walker and Coupland (1970) identified five important environmental gradients: water regime, salinity, the edaphic complex, plant competition, and disturbance. They suggest that, of these, water regime has an overriding importance in controlling vegetation composition and distribution. However, there is a growing body of more recent literature on the importance of exposure gradients in shoreline wetlands (Day *et al.* 1988). Pre-emption of resources is a form of competition, and is also known to have significant impacts on wetland community structure (Ellison and Bedford 1995).

Økland (1996) recommends parallel application of ordination and constrained ordination to explore different aspects of plant species composition and vegetation-environment relationships. The objectives of this chapter were to use two analytical techniques to identify patterns in the composition of vegetation in the perched basins of the PAD, and identify the primary environmental variables contributing to this pattern. The first is an ordination technique, Detrended Correspondence Analysis (DCA), and the second is a constrained ordination technique, Detrended Canonical Correspondence Analysis (DCCA) (ter Braak and Prentice 1988).

1.1 Peace-Athabasca Delta

Of the five gradients cited by Walker and Coupland (1970), two have little influence in the PAD. There are few halophytes in the delta (Fuller and LaRoi 1971), and the alluvial parent materials are virtually the same throughout the region (Fuller and LaRoi 1971). Thus, neither salinity nor edaphic differences likely account for the variety of biotic communities found there. Although competition and disturbance cannot be discounted as influential processes in the perched basins, they cannot be addressed explicitly with the data currently available. Therefore, water regime is the variable of primary interest. However, conclusions regarding disturbance and competition may potentially be inferred from results of this analysis.

Although the conventional understanding of the ecology of the perched basins in the Peace-Athabasca Delta recognizes water as primary in affecting vegetation patterns through its manifestation along an elevational gradient, there is little data to support this view. Dirschl *et al.* (1974) recognized three vegetation types, each distinguished by elevation which determines the effect of water on the plant communities. Fuller and LaRoi (1971) described nine vegetation zones in the perched basins arranged according to elevation. Although Raup (1935) did not specifically address perched basins, he attributes the arrangement of plant cover in the PAD to differences in elevation. This view is well-established and visible changes in vegetation have been used as an indicator of topography for large-scale mapping (Dirschl *et al.* 1974). Although a strong relationship between vegetation and elevation/water regime seems obvious, there is little direct support for it.

Dirschl *et al.* (1974) used an agglomerative classification approach to produce 15 vegetation types, which were then ordered along a gradient of relative moisture as indicated by elevation above the Lake Athabasca water level. He concluded that species aligned themselves in a predictable manner, ranging from the emergent aquatics of shallow water and immediate lakeshores through fen species to those typical of tall shrub and forested communities on high levees (Table 2-1). Such a description has three shortcomings. It is general, offers little insight into processes affecting vegetation, and is simply a visual interpretation of a table. Timoney (1996) determined that correlations between plant cover and water depth are low, and suggested that factors other than water are acting to depress or elevate species cover.

2. Data

Data used for the two analyses were a subset from the Timoney (1996) database, determined as follows. First, to eliminate the effect of interannual water fluctuations, the dataset was limited to those collected in 1993. Although there were ample 1996 data, it was a flood year, and water levels were rising during the sampling period. This prevented the standardization of water level data as some basins were flooded and some were not. Many of the inundated plots contained species with poor vigour, and many were completely submerged.

Second, only species present in at least 1% of the 600 plots were used. This was needed to reduce ordination distortion caused by 'similarity' among plots being based on their mutual absence of infrequently-occurring species (Hill 1979). Although the original data were species cover values, they were converted to presence/absence. This both eliminated the subjectivity of coverage values, and addressed the heterogeneity of plant cover that occurs from site to site, even within a small area (Barbour *et al.* 1987). Consequently, the ordination used presence/absence of 59 species from 597 plots (in excluding rarely-occurring species, 3 plots became 'empty'). To facilitate data handling, scientific names were coded (Table 2-2).

Data for the following environmental variables and plot attributes were included in this analysis: water table, soil texture, soil drainage, ecological moisture regime (EMR), successional status, a count of the live stems in the plot greater than 1m in height (livetally), a count of the dead stems in the plot (deadtally), the woody basal area per hectare (BAF), and the dominant height of the non-woody species at plot centre (dom.ht.) (Timoney 1996). Summary statistics for these variables are in Table 2-3. In addition, the factors influencing stand establishment were included, and were class data representing one of the following: tree cutting and soil disturbance, fire, plant/animal effects (animal), terrain-related effects (terrain), or water-related effects (flood). Due to their nominal nature, each of the factors for which there were data had to be considered independently (ter Braak 1987). These categories were 'fire', 'animal', 'terrain', and 'flood'.

3. Methods

The DCA was performed without data transformation or downweighting of rare species or samples. Detrending was done by segment (26 segments), and there was no rescaling of axes. Correlations of the environmental variables/plot attributes with axes of variation were determined.

The DCCA included all environmental variables and plot attributes (a total of thirteen when the factors influencing succession are included independently). The analysis options used were the same as with the DCA. Both analyses were performed using CANOCO (ter Braak 1987).

4. Results

4.1 Detrended Correspondence Analysis

The primary axis of variation (Axis 1) had an eigenvalue of 0.78 and explained 5.9% of the total variance in species data, and the secondary axis of variation (Axis 2) had an eigenvalue of 0.67 and explained 5.1% of the total variance. Axis 3 had an eigenvalue of 0.44 and explained 3.4% of the total variance, and Axis 4 had an eigenvalue of 0.36 and explained 2.7% of the total variance. Because eigenvalues represent the dispersion of species scores along that axis (ter Braak 1985), axes with higher eigenvalues had species scores covering a greater range along that axis and thus accounted for more variation among the species data.

The aquatic species were located near the low end of the x axis, with emergents below and to the right (Fig. 2-1). Meadow species occupy a central location, and at the lower right edge are species typical of disturbed meadows. Toward the upper right are the levee species, ranging from pioneer woody species (*Salix exigua*) near the center to boreal understory species at the extreme top.

With respect to a wet-to-dry gradient, the general trend among species is from aquatics to emergents, then to meadow species (including disturbed meadow species), and finally through levee species toward the upper right of the figure. This differentiation occurs primarily along Axis 1, but exhibits neither a clear nor unidirectional relationship with either axis.

The weighted correlations between each of the environmental variables/plot attributes and each of the DCA ordination axes indicate strong relationships between Axis 1 and soil drainage, and Axis 1 and water table (Table 2-4). All other correlation values are small. The variable of highest correlation with Axis 2 is basal area of woody stems, followed by successional status and live stem tally. Correlations with third and higher axes are less than 0.30 for all environmental variables and plot attributes.

4.2 Detrended Canonical Correspondence Analysis

Eigenvalues were lower than for the DCA: Axis 1 eigenvalue was 0.51 and explained 3.9% of the total variance in species data, and Axis 2 eigenvalue was 0.32 and explained 2.4% of the total variance in species data. The eigenvalues for Axis 3 and Axis 4 are 0.15 and 0.10, respectively. Because the DCCA axes were 'constrained' to be linear combinations of the environmental variables, eigenvalues were expected to be lower.

The arrangement of species in the DCCA ordination is similar to that of the DCA (Fig. 2-2a). The most obvious difference is that emergent species are now located between aquatics and meadow species, resulting in a clearer arrangement of species along the water gradient. A notable emergent outlier is *Sparganium eurycarpum*, situated amongst the disturbed meadow species.

The DCCA also presents a clear secondary trend among species. In moving along Axis 1 from aquatic species, we encounter emergents, then meadow species. At this point, species diverge into levee species toward the upper right of the figure, and disturbed meadow species to the lower right. Although disturbed meadow species still occupy a region adjacent to the mid-range of the wet-to-dry gradient, and are removed from the general trend.

The variables with the highest correlation with Axis 1 are: soil drainage, water table, ecological moisture regime, and flood effects (Table 2-5). Those with highest correlation with Axis 2 were successional status, animal effects, basal area of woody stems, and live stem tally.

5. Discussion

5.1 Detrended Correspondence Analysis

There is a wet-to-dry trend among the data, but it is neither simple nor strong. The eigenvalue for Axis 1 is high, as are the eigenvalues for the other axes. Although soil drainage and water table have high correlations with Axis 1, they show low correlations with Axis 2. This suggests that although water-related variables may be the most important in influencing vegetation distribution, much of the variation among the data remains unexplained. This is surprising considering the purported overwhelming influence of water on vegetation distribution. Either the influence of water on the vegetation is complex, or other factors are important.

All meadow species would be expected to exist together near the midrange of a water gradient, yet a large spread is evident among them. To the lower right of the figure are disturbed meadow species: *Plantago major*, *Cirsium arvense*, *Taraxicum officinale*, *Sonchus arvensis*, described as introduced weeds, and *Hordeum jubatum*, *Anemone canadensis*, *Beckmannia syzigachne*, *Potentilla norvegica*, *Ranunculus sceleratus*, *Achillea sibirica*, *Epilobium angustifolium*, *Poa palustris*, described as disturbance species or found in ditches (Johnson *et al.* 1995). Although their habitat with respect to water would be similar to that of the other meadow species, the DCA analysis shows clear separation. Several of these species are prevalent in the basins adjacent to the north shore of Lake Claire where bison calve and raise their young (Allison 1973). Thus, these species may be adapted to the periodic small-scale disturbances of bison trails, wallows, droppings and herbivory. If this is the case, adaptive strategies may be based on rapidly colonizing these disturbed areas and pre-empting resources.

5.2 Detrended Canonical Correspondence Analysis

The DCCA ordination provides a poorer representation of variation among the species data, as indicated by lower eigenvalues for the axes. However, more information was used in this analysis, and it is inherently more complicated. As with the DCA results, total variation among the data is distributed more evenly among axes than would be expected for a system driven by the water regime alone.

The general similarity between the DCCA and the DCA ordinations may indicate that the environmental variables used in the analyses were important driving variables of plant community composition. Congruent configurations are an indication (but not proof) that optimal environmental variables have been found (Økland 1996).

Several axes correlation values for the environmental variables are high. Again, water-related variables are associated with Axis 1, and are the most important. However, it should be considered that there are four water-related variables, and some are highly correlated: drainage and water (-0.86), drainage and EMR (0.63) and water and EMR (-0.60). Thus, a water bias in the data collected may explain why the water-related gradient is stronger than in the DCA ordination.

If there is a water bias in the DCCA, disturbed meadow species are strongly resisting that bias. Animal effects show a high correlation with Axis 2. This is not surprising because many of the disturbed meadow species are prevalent where bison range in the northern portion of the PAD. Other highly correlated variables are successional status, BAF, and live stem tally. It should be noted that both BAF and live stem tally, as well as dead stem tally, are plot attributes, and can only be considered in a correlative sense, not an explanatory sense. BAF and live stem tally increased toward the top of the diagram. A possible explanation is that constant bison activity in the area may prevent the establishment of larger woody species. The fact that the aquatic species are situated higher along Axis 2 may be due to the presence of flooded plots along several transects (DT01, 02, 03). Here, willows that established in the low-water years of the late 1960's have persisted through several years of flood during which aquatic species were introduced (Timoney 1996).

The water regime gradient and the disturbance component may together explain the divergence in species along Axis 1. With drying of the basins, aquatics are succeeded by emergents, then meadow species. Continued drying may lead to the establishment of willow and eventually, forest species. However, if the region is frequented by bison, meadow species may be replaced by disturbed meadow species. Because the two paths show no subsequent sign of convergence, further drying may not lead to the establishment of woody species in disturbed areas because continual use by bison may prevent the establishment of shrub and tree species.

Because the disturbed species are generally found in the basins on the northern margins of Lake Claire, and this is the region of habitual bison activity, there may be a spatial component to vegetation distribution in the basins.

Although competition among plant species was identified as a possible influence on the distribution of vegetation, these ordination results offer no conclusions in this regard.

6. Conclusion

These results may contrast with the conventional understanding of the predominant influence of water on vegetation distribution in the PAD, but still show clear wet-to-dry trends. Of the five variables cited by Walker and Coupland (1970), my results find water regime to be the most influential, with small-scale disturbance secondary in importance.

These results direct further research in one of two directions. With respect to the water regime, the next step is assessing how water influences species distributions. Water regime is a complex variable with many possible interpretations including water depth (or depth to water table where the water level lies below the soil surface), flood frequency, flood depth, flood duration, hydroperiod, and amplitude of water fluctuation, among others. Water regime can be further complicated when the related processes of silt deposition and wave action are considered.

Variables that are unrelated to the water regime may also be necessary to explain the distribution of species in the perched basins. The disturbance regime also appears to be important, particularly with respect to the small-scale effects of bison.

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Table 2-1. Matrix representing major species occurrence along a gradient of relative moisture as indicated by elevation above lake level. Only species cover values of 5 percent or greater are included (from Dirschl et al. 1974)

	Stand																																						
Species	27	11	22	13	12	21	28	6	16	3	2	1a	1b	35	26	4	14	17	43	42	36	30	25	29	20	9	37	8	24	44	41	18	19	31	40	38	34	32	33
	Wet —																																						> Dry
Senecio congestus	33																																						
Scirpus validus	6																																						
Typha latifolia																15																							
Eleocharis palustris	24	21	8		6	21	20	35				5	6	21							15																		
Beckmannia syzigachne		9						7			6																			27									
Salix interior			11	6	11	7																																	
Carex atherodes						8		21							22	10	27			81	22	21	11	16		9							66						
Chenopodium glaucum			7																																				
Salix planifolia				10		6			11				9			8																27							
Sium suave							6			14																													
Juncus nodosus								6																															
Rorippa islandica									9																														
Phragmites communis									16										73											5									
Chenopodium album									6																														
Puccinella nuttaliana									9																														
Carex aquatilis										17	21	27	11													43		37											
Deschampsia caespitosa										6																													
Juncus brevicaudatus											9																												
Salix rigida													8													7						12							
Glyceria grandis														23							5																		
Eleocharis acicularis														9																									
Equisetum scirpoides																14																							
Scolochloa festucacea															51			53				64																	
Equisetum fluviatile																			7						76						51	47							
Calamagrostis inexpansa																					11					7	88		80				86						
Galium trifidum																							33																
Calamagrostis canadensis																																			45				
Rosa woodsii																																			3	13			
Equisetum pratense																																			23	19		9	
Maianthemum canadense																																			12				
Salix discolor																																			17	10			
Salix bebbiana																																				57			
Populus balsamifera																																					34		
Betula papyrifera																																					7	12	
Rubus pubescens																																						8	
Cornus canadensis																																						17	
Picea glauca																																						64	58
Abies balsamea																																							7
Mitella nuda																																							6
Hylocomium splendens																																							81

Table 2-2. Species codes, frequencies, median water tables, and scientific names for 59 species occurring in at least 10% of 597 plots, Peace-Athabasca Delta, 1993. Species are arranged according to median water table from wet to dry; 130cm was the maximum value recorded.

Species Code	Frequency (total plots=597)	median water table (cm)	Scientific Name
acor cal	7	-50	*Acorus calamus*
utri vul	18	-50	*Utricularia vulgaris*
cera dem	8	-36	*Ceratophyllum demersum*
lenm tri	45	-31	*Lemna trisulca*
lemn min	112	-20	*Lemna minor*
utri min	51	-18	*Utricularia minor*
typhlat	12	-13	*Typha latifolia*
epil cil	10	-7	*Epilobium ciliatum*
care ros	18	-3	*Carex rostrata*
equi flu	28	-3	*Equisetum fluviatile*
phra com	14	-3	*Phragmites communis*
scol fes	101	-2	*Scolochloa festucaceae*
care aqu	45	-1	*Carex aquatilis*
gali trf	64	0	*Galium trifidum*
spar eur	11	1	*Sparganium eurycarpum*
ranu scl	16	3	*Ranunculus sceleratus*
care ath	317	4	*Carex atherodes*
sali pla	141	5	*Salix planifolia*
scir val	11	5	*Scirpus validus*
sali lut	10	7	*Salix lutea*
rori pal	7	7	*Rorippa palustris*
geum ale	12	10	*Geum aleppicum*
aste pun	15	17	*Aster puniceus*
ment arv	23	24	*Mentha arvensis*
sali exi	85	24	*Salix exigua*
cala can	202	25	*Calamagrostis canadensis*
sali dis	62	27	*Salix discolor*
pice gla	9	31	*Picea glauca*
agro sca	23	33	*Agrostis scabra*
pote nor	15	39	*Potentilla norvegica*
sali beb	84	45	*Salix bebbiana*
geum mac	36	55	*Geum macrophyllum*
beck syz	9	70	*Beckmannia syzigachne*
rume mar	80	75	*Rumex maritimus*
vice ame	7	77	*Vicea americana*
sonc arv	69	83	*Sonchus arvensis*
cala str	32	90	*Calamagrostis stricta*
orth sec	6	105	*Orthilia secunda*
cirs arv	14	115	*Cirsium arvense*
achi sib	14	130	*Achillea sibirica*
agro rep	8	130	*Agropyron repens*
alnu inc	10	130	*Alnus incana*
anem can	21	130	*Anemone canadensis*
corn sto	12	130	*Cornus stolonifera*
epil ang	26	130	*Epilobium angustifolium*
equi arv	76	130	*Equisetum arvense*
hord jub	27	130	*Hordeum jubatum*
plan maj	14	130	*Plantago major*
poa int	10	130	*Poa interior*
poa pal	23	130	*Poa palustris*
pote ans	35	130	*Potentilla anserina*
ranu cym	6	130	*Ranunculus cymbalaria*
rosa aci	7	130	*Rosa acicularis*
rubu ida	20	130	*Rubus idaeus*
rubu pub	6	130	*Rubus pubescens*
scut gal	10	130	*Scutellaria galericulata*
stac pal	10	130	*Stachys palustris*
tara off	19	130	*Taraxacum officinale*
urti dio	12	130	*Urtica dioica*

Table 2-3. Summary statistics for environmental variables measured from 597 plots along 32 transects in the perched basins of the Peace-Athabasca Delta

	mean value/class	minimum	maximum	range
water table (cm)	34	-130	86	216
soil texture	silt/silt loam	sand	silty clay	n/a
soil drainage	poorly	very poorly	moderately well	n/a
ecological moisture regime	hygric	xeric	hydric	n/a
sucessional status	old seral	pioneer seral	mature climatic climax	n/a
number of live stems	2	0	25	25
number of dead stems	2	0	25	25
basal area factor	3	0	40	40
dominant height (cm)	77	0	589	589

Table 2-4. Weighted correlation matrix of Detrended Correspondence Analysis ordination axes and environmental variables, Peace-Athabasca Delta, 1993; succ. st. = successional status; emr = ecological moisture regime; deadtally = count of dead stems per plot; baf = basal area factor of the living stem count; livetally = count of live stems in plot >1m in height; dom.ht.= dominant height of non-woody species.

	Axis 1	Axis 2	Axis 3	Axis 4	texture	fire	animal	terrain	flood	succ. st.	drainage	emr	dtally	baf	ltally	water	dom. ht.
Axis 1	1.00																
Axis 2	0.23	1.00															
Axis 3	0.03	0.22	1.00														
Axis 4	0.04	0.01	-0.11	1.00													
texture	0.03	-0.05	0.15	0.01	1.00												
fire	0.09	0.21	0.02	-0.02	-0.01	1.00											
animal	0.32	-0.32	-0.19	0.03	-0.01	-0.02	1.00										
terrain	-0.01	0.00	-0.01	0.01	0.00	0.00	-0.01	1.00									
flood	-0.33	0.25	0.17	-0.02	0.02	-0.27	-0.96	-0.08	1.00								
succ. st.	0.11	-0.42	-0.24	0.06	0.05	-0.02	0.56	0.01	-0.53	1.00							
drainage	-0.73	-0.10	0.02	-0.11	-0.01	-0.14	-0.26	0.00	0.29	-0.09	1.00						
emr	-0.49	-0.10	-0.11	-0.06	0.07	-0.08	-0.06	-0.01	0.08	0.13	0.63	1.00					
deadtally	0.02	0.29	0.30	-0.06	0.25	-0.03	-0.11	-0.01	0.11	-0.20	0.12	0.09	1.00				
baf	0.20	0.51	0.06	-0.01	-0.04	0.05	-0.11	-0.01	0.09	-0.21	-0.14	-0.09	0.29	1.00			
livetally	0.15	0.42	0.24	0.09	0.00	-0.04	-0.15	-0.01	0.15	-0.38	0.02	0.00	0.50	0.53	1.00		
water	0.71	0.11	0.00	0.08	-0.05	0.10	0.29	-0.01	-0.31	0.12	-0.86	-0.60	-0.14	0.16	-0.03	1.00	
dom. ht.	-0.28	0.00	0.15	0.11	-0.02	-0.04	-0.20	0.01	0.21	-0.12	0.27	0.08	-0.03	-0.23	-0.11	-0.27	1.00

Table 2-5. Weighted correlation matrix of Detrended Canonical Correspondence Analysis ordination axes and environmental variables, Peace-Athabasca Delta, 1993; succ. st. = successional status; emr = ecological moisture regime; deadtally = count of dead stems per plot; baf = basal area factor of the living stem count; livetally = count of live stems in plot >1m in height; dom. ht. = dominant height of non-woody species.

	Axis 1	Axis 2	Axis 3	Axis 4	texture	fire	animal	terrain	flood	succ. st.	drainage	emr	dtally	baf	ltally	water	dom. ht.
Axis 1	1.00																
Axis 2	-0.16	1.00															
Axis 3	-0.11	0.07	1.00														
Axis 4	-0.20	-0.18	-0.19	1.00													
texture	0.00	-0.01	0.27	0.27	1.00												
fire	0.11	0.20	-0.10	-0.09	-0.01	1.00											
animal	0.35	[illegible]	-0.19	0.15	-0.01	-0.02	1.00										
terrain	-0.01	0.00	0.02	-0.02	0.00	0.00	-0.01	1.00									
flood	-0.57	0.44	0.20	-0.12	0.02	-0.27	-0.96	-0.08	1.00								
succ. st.	0.09	[illegible]	-0.16	0.17	0.05	-0.02	0.56	0.01	-0.53	1.00							
drainage	[illegible]	0.15	0.06	0.22	-0.01	-0.14	-0.26	0.00	0.29	-0.09	1.00						
emr	-0.54	0.01	-0.03	0.37	0.07	-0.08	-0.06	-0.01	[illegible]	0.13	0.63	1.00					
deadtally	-0.01	0.33	0.22	0.16	0.25	-0.03	-0.11	-0.01	0.11	-0.20	0.12	0.09	1.00				
baf	0.22	0.47	-0.20	0.05	-0.04	0.05	-0.11	-0.01	0.09	-0.21	-0.14	-0.09	0.29	1.00			
livetally	0.13	0.39	0.21	0.12	0.00	-0.04	-0.15	-0.01	0.15	-0.38	0.02	0.00	0.50	0.53	1.00		
water	0.78	-0.12	-0.11	-0.23	-0.05	0.10	0.29	-0.01	-0.91	0.12	-0.86	-0.80	-0.14	0.16	-0.03	1.00	
dom. ht.	-0.29	0.12	0.37	-0.43	-0.02	-0.04	-0.20	0.01	0.21	-0.12	0.27	0.08	-0.03	-0.23	-0.11	-0.27	1.00

Figure 2-1. Detrended Correspondence Analysis ordination of 59 species, Peace-Athabasca Delta, 1993; (Axis 1 eigenvalue = 0.780, Axis 2 eigenvalue = 0.667). Five general species groups are shown; for complete species names, see Table 2-2.

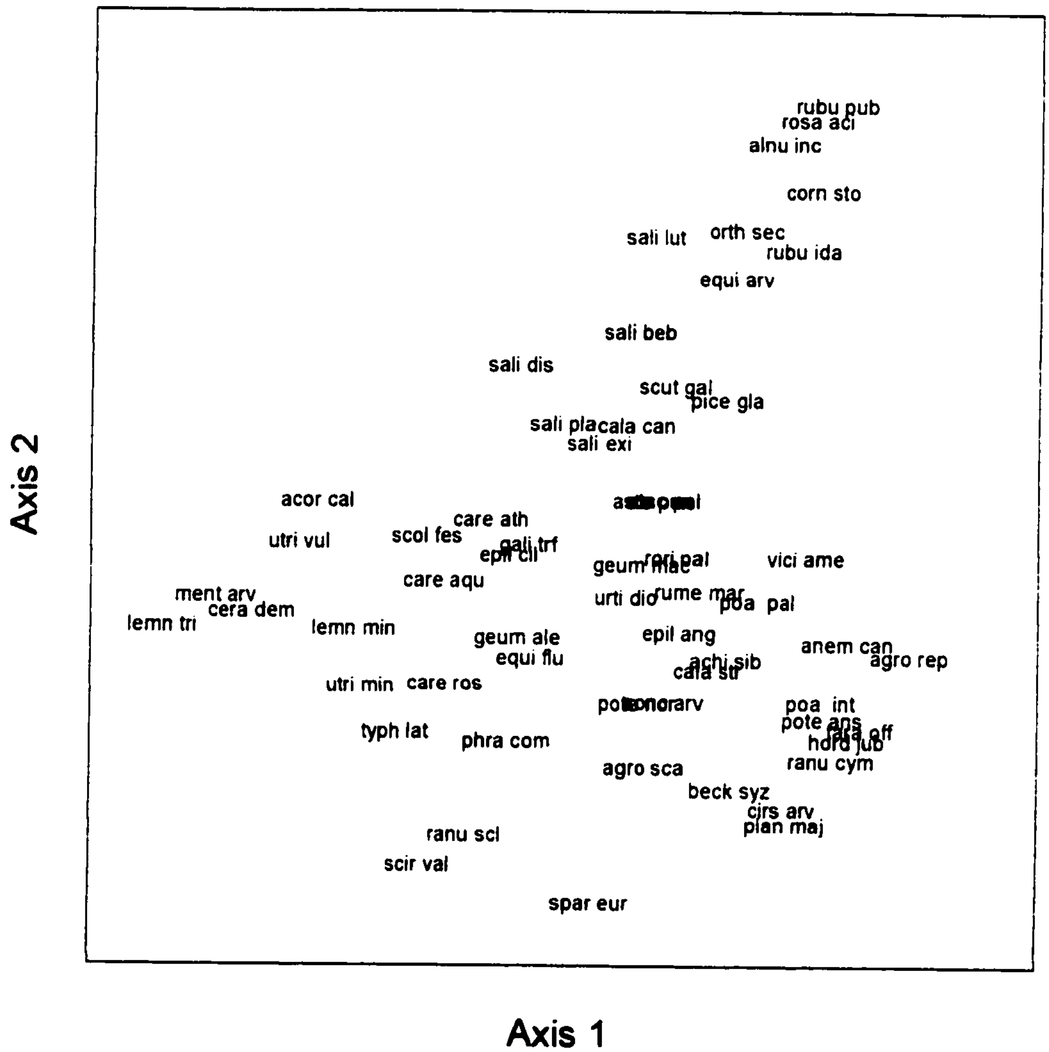


Figure 2-2a. Detrended Canonical Correspondence Analysis ordination of 59 species, Peace-Athabasca Delta, 1993 (Axis 1 eigenvalue = 0.508; Axis 2 eigenvalue = 0.320). Five general species groups are shown; for complete species names, see Table 2-2.

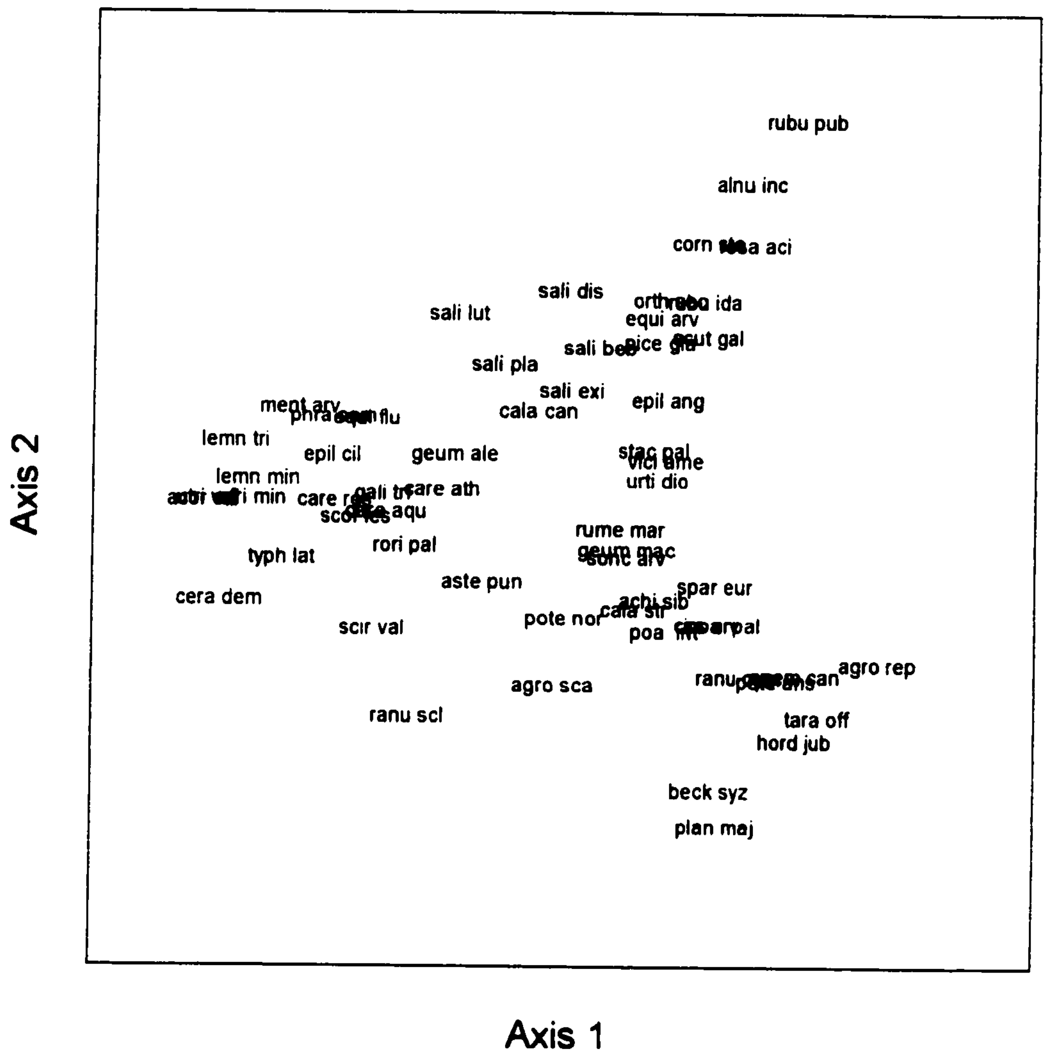
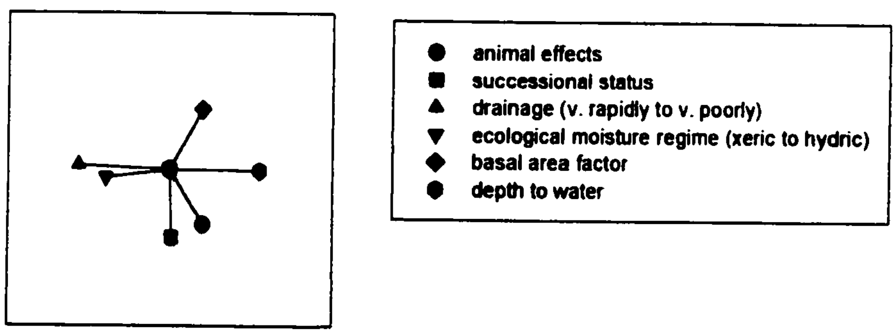


Fig. 2-2b. Biplot score for environmental variables and plot attributes; symbol indicates high value for that variable. Plot scale is identical to scale for Fig. 2-2a above.



Chapter 3

ELEVATION AND WATER TABLE

1. Introduction

Chapter 2 provided evidence of arrangement of species in the perched basins of the Peace-Athabasca Delta (PAD) along a wet-to-dry gradient. The primary objective of this chapter was to explore this relationship further. Analysis was first conducted by transect and results were then combined using meta-analysis to yield conclusions across perched basins of the PAD. Elevation and water table were two components of the water regime gradient used for these analyses. Results were discussed in the context of the ordination results from the Detrended Correspondence Analysis in Chapter 2.

1.1 Justification for Gradients

There are many ways in which water influences plant distribution, and the 'water regime' gradient can be interpreted in many ways. Day *et al.* (1988) found water depth to be one of three factors controlling vegetation composition in a riverine marsh while David (1996) examined plant species distributions in relation to hydroperiod (i.e. depth and duration of flooding). Vince and Snow (1984) assessed vegetation relationships to frequency, depth and duration of tidal flooding. Franz and Bazzaz (1977) modeled species distributions using 'stage probability', or the probability of flooding. Other important water-related variables are soil depth to the permanent water table and amplitude of water level fluctuation.

Although hydrologic changes may occur on several time-scales, elevational position remains relatively fixed. As such, many hydrological effects are inextricably linked to elevation within the basin. A site's elevational position may dictate water depth or depth in the soil profile to water table. On a time-scale of years, it may affect duration of inundation, and possibly frequency of flooding. On a decades or centuries time-scale, elevation may be related to depth to the permanent water table, as indicated by the level in the soil profile at which continuous gleying occurs. To the extent that massive floods are considered to be the primary agent for disturbance, elevation may influence disturbance characteristics. According to Day *et al.* (1988), elevation affects the length of the growing season, substrate organic content, region of wave and ice scour and region of litter deposition. We selected elevation as a variable for inferential analysis because it has the potential to serve as a surrogate of many other water-related variables.

In wetlands, vegetation is largely a function of water depth (Spence 1982, van der Valk *et al.* 1994). However, to include sites where the water level lies below the soil surface, depth to water table was the second variable chosen for investigation. Because no previous work in the perched basins has tested vegetation distribution along any gradient and water table is the simplest interpretation of the water regime, it may provide a useful starting point. Most perched basins are flooded infrequently, and it would require several years of observation to quantify many of the above variables. However, the level of the water table is easily measured, and data can be collected annually.

2. Data

Species and water table data were from Timoney (1996), and we collected elevation data in 1996. Following Chapter 2, the species and water table data from the 1993 transects were used (Fig. 3-1), and species present in less than 10% of the plots (6 of 600) were eliminated from further analysis. In doing so, three plots became 'empty', and were also eliminated. In addition, three transects (DT12, 18, 30) were excluded because elevation data could not be obtained for them. Thus, the dataset for this statistical analysis included 538 plots along 29 transects.

The primary study variable was presence/absence of species, and was investigated in relation to the primary independent variables of **elevation** and **water table**, both of which were measured on a continuous scale of centimeters. Elevation measurements were specific to each transect because it was impractical to tie the transects together using conventional surveying. As a result, the elevation of each plot along a given transect was determined relative to the plot with the highest elevation. Water table values were positive or negative: positive values for plots where measurements represent depths in the soil profile to the water table, and negative values for plots inundated with a depth of standing water. Zero values indicate that the water table was at the soil surface.

There were concerns that historical water levels and seasonal hydrologic patterns could compromise the quality of the data. By using data collected in 1993, the effect of historical floods on vegetation was reduced. It may take several years for vegetation to adjust to the new hydrologic conditions subsequent to a large-scale flood. However, in 1993 it had been 19 years since the previous large-scale event. Consequently, vegetation had had a long period of time to synchronize with slowly declining water levels. The seasonal pattern of water levels typically exhibits a slow decline throughout the summer. To minimize seasonal effect, water table measurements on all transects were taken within a short time period: three weeks in late-July and early August. This may also have reduced the effects of shorter time-scale fluctuations in water levels due to recent precipitation.

3. Methods

A preliminary analysis showed that there was considerable heterogeneity in species distributions across the perched basins within the PAD. Of the eight most common species, two 'generalist' species were wide-spread (*Carex atherodes* was ubiquitous; *Calamagrostis canadensis* was present on 30 of 34 transects) and were equitably distributed (Figure 3-2). All other species were absent from at least seven transects, and had a low frequency of occurrence on several others. Although *Salix planifolia* was generally widely distributed, its occurrence was conspicuously low near the northeast shore of Lake Claire.

Species heterogeneity had two important implications for further analysis. First, it inhibited drawing conclusions across the PAD on an individual species basis. Second, for each transect the number of plots was too small to describe sufficiently the distribution of most species. Further, overall species coverage in plots was so low that a special analytical tool to deal with such data was sought by redefining the outcome measure from species coverage to a simple binary score representing presence (1) or absence (0).

To yield conclusions across the PAD, this suggested an analysis by individual transect with results combined using meta-analysis. This was undertaken using the following methods, described in four steps.

3.1 Species Grouping

The spatial pattern of species shown in the Detrended Correspondence Analysis (DCA; ter Braak 1992) ordination results from Chapter 2 combined with knowledge of their autecology was used to subjectively group species into seven classes (Fig. 3-3), which were used in subsequent analyses. Other studies have grouped species similarly: Day *et al.* (1988)

assigned species to functional groups based on similarities in morphology, physiology, or role in the community, and Ellison and Bedford (1995) aggregated an unwieldy number of species into a manageable number of functional 'species types'. Similarly, Boutin and Keddy (1993) devised a functional classification of wetland plants.

Figure 3-2 shows a clear delineation among five of the classes: aquatics, emergents, meadow species, disturbed meadow species, and levee species. Two generalist species with widespread occurrence were each treated separately, yielding a total of seven classes. Table 3-1 shows species membership by class, and the scientific names corresponding to species codes in the DCA ordination.

3.2 Logistic Regression

The dependent variable for this portion of the analysis was presence/absence of species classes. Therefore, logistic regression modelling was an appropriate analysis method (Hosmer and Lemeshow, 1989). For each transect, we investigated the functional relationships (positive, negative or quadratic) of the presence or absence of each species class with the explanatory variables of elevation and water table. These were graphically explored initially, and DT07 was eliminated from the analysis because it exhibited no variance for water table (Appendix 1); all plots had water table values in excess of 130cm - the length of the soil auger. For the remaining transects, the number of plots per transect ranged from 8 to 23, and was too low (1) to confirm any definite pattern for all species classes but one, and (2) to be useful in modelling because of violations of the asymptotic distribution assumption. The lack of definite pattern justified pooling of the data across species classes to address the second weakness, i.e. to get a robust estimate of the slope coefficients of elevation and water.

With a pooling approach, there was a potential problem with those classes exhibiting a negative relationship to elevation or water table countering the effects of classes exhibiting a positive relationship, thus potentially reducing the significance of the real effects. To address this possibility, all models initially included interactions between species classes and both water table and elevation. Although the preliminary graphical analysis showed aquatics to exhibit a negative relationship to water and elevation for most transects, there was little general pattern among the other classes when similarly portrayed (Appendix 1). However, these relationships are best described as positive for the highest number of plots. For this reason, the aquatics class was not included in the analysis. Due to the lack of understanding of how the non-aquatic species classes behave, we left all final decisions to statistical testing, incorporating only the plausible assumption that presence/absence of species classes was related to the water level and elevation. Any classes that exhibited either all presence or all absence values were also eliminated prior to this analysis. The possibility of there being a quadratic relationship of species classes to elevation or water table was addressed by initially including quadratic effects in all models.

The dependent variable for the analysis was presence or absence of the species classes. As there was more than one class, dummy variables were created to recognize each observation as referring to a particular species class. Consequently, for an analysis of n classes, n-1 dummy variables were included as secondary independent variables (Hardy 1993). Because logistic regression models investigate relative relationships, a reference class was needed, and the '*Carex atherodes*' class was selected because it was included in all transect models but one; for DT23, '*Calamagrostis canadensis*' was used as the reference category.

Finally, the null hypothesis tested was: presence/absence of species classes is not significantly related to water table or elevation, nor to any differences in species classes. The model form used for the test was: $y = f(\alpha + \beta_1x_1 + \beta_2x_2 + \beta_3x_3 + \beta_4x_4 + \beta_5x_5 + \beta_6x_6 + \beta_7x_7)$, with dummy variables excluded where not required. The 'f ' was the function linking the binary outcome to the relevant influencing factors, and a logistic link function was initially considered. The independent variables were: x_1 = elevation, x_2 = water table, x_3 = emergents, x_4 = *Calamagrostis canadensis*, x_5 = meadow species, x_6 = disturbed meadow species, x_7 = levee species.

The success of the final model run was assessed using the Hosmer-Lemeshow goodness-of-fit test (Table 3-2) (Hosmer and Lemeshow, 1989), and the coefficients of elevation and water table were evaluated for significance using a chi-square test (Table 3-3) (Hosmer and Lemeshow, 1989). In both cases, Type I error was preset to 0.05.

3.3 Cluster Analysis

The logistic regression results for DT06 showed multicollinearity and resulted in extreme beta values (Table 3-3). Consequently, it was eliminated from further analyses. The remaining logistic regression results exhibited some geographic pattern among transects in the significance of elevation and water table. Consequently, the third step used a cluster analysis to classify transects into a pre-selected number of 'strata' for further analysis (Norusis, 1996). A K-means analysis allows the user to pre-specify the number of clusters (Howard, 1991), and the procedure was conducted three times, with the number of strata pre-specified as two, three and four. The variables used for clustering were the slope coefficients for the two independent variables of primary interest: elevation and water table (Table 3-3).

The result for two strata provided the most logical grouping of transects. When plotted geographically, a clear pattern is evident (Fig. 3-4). In general, Stratum 1 (n=10) is composed of transects located in the middle delta (around Lake Mamawi and the NE shore of Lake Claire). Members of Stratum 2 (n=17) tend to be found at the peripheral regions of the PAD complex.

3.4 Meta-analysis

Meta-analysis is the quantitative study of several studies relating to a particular problem (Marriott 1990). The objective of the final portion of the analysis was to combine the results of the coefficients for water table and elevation to obtain meaningful overall conclusions. We used random effects models as a method of meta-analysis to analyze the two strata of transects. The models incorporated the varying sample sizes among transects and the random transect effect (Scheffé 1959). The model used was:

$$Y_{ij} = \mu + \alpha_i + \varepsilon_{ij},$$

where Y_{ij} is the estimated coefficient for water table/elevation, μ is the overall mean effect of elevation/water table and is the variable of primary interest, α_i is the i^{th} transect effect and ε_{ij} is the error of estimating the parameters due to water table and elevation.

For each model, we assumed that the transect effects were random. This assumption is justified because the 29 transects were considered a random sample of a vast number of potential transects. Then we applied general least squares methods to estimate the overall effect (μ) due to water table and elevation.

For each stratum, these values were used to test the null hypothesis that the effect (μ) for all transects in the stratum equals zero. Again, significance levels of 0.05 were considered. The program used for meta-analysis calculations is in Appendix 2.

3.5 Detrended Correspondence Analysis

The DCA methods were described in Chapter 2. Here, the 'sites' ordination, which has not yet been presented, was of primary interest (Figure 3-5). To ease interpretation, individual transects were then portrayed separately (Figures 3-6a to 3-6e).

4. Results

4.1 Logistic Regression Results

Interaction effects were significant in only four cases out of 29 (DT03, 13, 15 and 24), and because they added little additional explanation overall, they were removed from all models for obtaining parsimony.

Quadratic effects were found to be significant in only two cases: DT10, where the p-value for water^2 was 0.0413, and DT13, where the p-value for water^2 was 0.0161. However, in both cases the odds ratios were close to 1 (0.9996 and 1.0005 respectively), indicating no substantial quadratic relationship between species classes and water^2. Thus, we did not pursue the quadratic effects further.

The plot prediction rates were generally high and averaged 77.8% for all transects (Table 3-2). The Hosmer-Lemeshow statistic showed that the final models were satisfactory in all but two of 29 cases. Although they varied in significance from 0.0037 (DT05) to 0.88

(DT27), only two models significantly diverged between observed and expected values at $p < 0.05$ (DT05 and DT19, Table 3-2).

The slope coefficients for elevation and water and their corresponding p-values are summarized in Table 3-3. In logistic regression models, each slope coefficient represents a 'log odds ratio', or the logarithm of the probability of presence over the probability of absence per unit change in the independent variable. For elevation and water, it quantifies their relationship to the odds of presence/absence, adjusting for the differences among the species groups. Elevation exhibited a significant relationship to the distribution of species classes for four transects; water table exhibited a significant relationship for five transects.

4.3 Meta-analysis Results

Neither elevation nor water table were significantly related to the distribution of vegetation when examined over the large geographic areas represented by the two strata (Table 3-4).

5. Discussion

5.1 Logistic Regression

The plot prediction rates are high for all models and the goodness-of-fit results indicate that only two of the individual models are not useful for successfully predicting presence or absence of these species groups: DT05 and DT19 (Table 3-2). For the remaining transects, the range of model significance and the variation among variables of significance illustrates the difference in character among them. This makes it difficult to draw PAD-wide conclusions regarding the influence of these variables on the distribution of vegetation in the perched basins. As a result, the models are not useful beyond the basin in which the transect is situated.

In considering general patterns among transects, however, two results were noteworthy. Elevation was significant in four transects, and water table in five. As such, both variables exhibited surprisingly weak overall relationships with the distribution of vegetation.

5.2 Meta-analysis

Given the arrangement of species along a wet-to-dry trend that is evident in Fig. 3-2, it is surprising that neither elevation nor water table was found to be significant for the two strata of transects. However, the results are not surprising considering the general low significance of both elevation and water table for the models of individual transects. In turn, these can be attributed to two general factors.

The first factor relates to two shortcomings in the design of the study and their effect on the results. The perched basins characteristically have slight elevational changes occurring over large distances, and it is questionable whether 8-23 plots per transect are sufficient to understand species distributions. For example, DT27 exhibited the largest elevational difference among plots, with 209 cm of elevational change manifested over a 700m distance, but included only 16 plots. Because of the low number of plots, transects could not be analyzed by species, and a grouping scheme was required. The result was a loss of information at the first stage of the analysis that reduced the power of all subsequent analyses. Although the grouping of species may be appropriate when analyzing basins of different species compositions, all transects should have been designed to allow analysis by individual species.

These results would have provided more information at the first stage of the analysis, and may have affected the results for both the cluster analysis and the meta-analysis.

The low significance of elevation was especially surprising. However, the elevation data suffered a second deficiency in that it was impossible to properly register the elevations of each transect to a common benchmark. The only option was using the elevation of the plot of highest or lowest elevation as a baseline, and adjusting the values for the remaining plots relative to it. Consequently, for each transect the plot of highest elevation was given a baseline value of '0'. However, the baseline plots differed with respect to vegetation composition. For example, the baseline plot for DT01 contained species characteristic of a wet meadow (and even included an aquatic), but for DT10 contained primarily levee species. The differential positions of transects along a PAD-wide elevational gradient could not be reconciled, and this further contributed to the negative result for elevation.

The second factor that may explain the negative results is the possibility that both variables exert less influence than conventionally believed. The level of the water table changes over space and time, and a one-time measurement may be highly variable, and an over-simplified interpretation of the water regime. The elevational gradient of individual basins may be too weak to segregate species into their realized niches. If either or both of these are the case, then other variables likely are of importance.

The difference among transects in the significance of both variables combined with the heterogeneity of species distributions among basins suggests ecological complexity. This may indicate that the influence that variables exert on the distribution of species may vary from basin to basin.

5.3 Discussion of Ordination Results

The DCA ordination results from Chapter 2 can be used to help identify which processes may be the primary determinants of vegetation pattern. Figure 3-5 shows the distribution of all 600 plots in relation to the first two axes of variation. The majority are situated in a diagonal triangle from lower left to upper right, corresponding to the wet-to-dry trend among species. While plots from some individual transects also followed this pattern, many did not. We explore below possible causal factors of the PAD-wide heterogeneity among transects.

5.3.1 Transects Following the General Trend

The transects that follow the general pattern are DT04, 05, 07, 10, 22, 26, 27, 29, 32 (Fig. 3-6a). Their plots traversed much of the wet-to-dry gradient, and thus they are expected to show the strongest relationship between vegetation and both elevation and water table. However, the logistic regressions showed that the only relationships of significance were between species groups and water table on DT10 and DT22 (Table 3.3).

Although these transects exhibit a similar general pattern, closer examination reveals considerable heterogeneity. All transects present levee plots at the upper right of the ordination plot, but differ with respect to the placement of the remaining plots. The location of the transects may provide some insight. DT22 is in the Birch Delta; DT26 and 27 are on the southeast shore of Lake Claire; DT04 is adjacent to Mamawi Creek; DT05, 10, and 25 are adjacent to the Quatres-Fourches River; DT29 is adjacent to the Rocher River; DT07 is in an isolated basin in the northern part of the PAD; and DT32 is in the Athabasca Delta (Fig. 3-1). It is likely that the important influences on plant distribution vary among these basins.

The location of DT26 and 27 on the shore of Lake Claire may subject them to a different disturbance regime. They are located far from the origins of overbank flooding, and may experience lake-related disturbances (e.g. wind driven seiches, wave action, and ice push). Bayrock (1972) shows these two transects are located in the region of highest wave action in the PAD.

Several of the other basins are adjacent to high-energy rivers (DT04, 07, 10, 22, 29, 32; Fig. 3-1), and DT05 and 25 are adjacent to medium-energy rivers. Their location can subject them to periodic large-scale disturbances as floodwaters deposit seeds and large amount of silt. This, combined with the weakness of the elevational gradient, may prevent species from fulfilling their realized niches along the gradient. The most obvious mechanisms for this are the pre-emption of resources by the species that first establishes following disturbance, and its ensuing ability to persist. A prerequisite for it being displaced by a competitively superior species is that the latter must be close enough for interaction. However, the establishment by colonizers of large monospecific areas may reduce interspecific interaction. In the event that displacement can occur, the time it might take for a weak elevational gradient to segregate species into their realized niches would be considerable. In the meantime, the species present may not accurately reflect the environmental conditions.

Rather than being a simple function of environmental conditions, the presence of a species at a particular site may be dictated by its proximity to the site following disturbance, by the timing of the release of its propagules, or by its composition in the seed bank. These possibilities have been noted by others: Dirschl *et al.* (1974) describes emerging silt flats as rapidly colonized by germinating seed present within the silt and distributed by wind; PADPG (1973) describes new willow and meadow communities as well-established three years subsequent to the exposure of mudflats. If any of these factors play an important role, the influence of elevation and water table would be diminished.

5.3.2 Middle Delta Transects

Eight transects had a narrow spread of plots across the ordination axes indicating that the majority of plots had similar compositions, primarily dominated by meadow species (Fig. 3-6b). For five of these (DT08, 09, 13, 16, 28), the plots were located as a poorly organized group near the centre of the diagram; for two (DT11, 15) the plots are similarly located but there is a vague trend along the wet-to-dry gradient; and for DT24 the grouping is tight and linear.

Given the general lack of trend, it is surprising that one of the transect regressions revealed that both variables were significant (DT16), and two others showed elevation to be significant (DT09, 11) (Table 3.3). However, the similarity among plots coupled with the locations of the transects may provide an explanation.

Except for DT13 and DT28, these transects are situated in basins in the middle region of the PAD and are adjacent to Lake Claire or Mamawi. During large-scale floods, water from the Peace or Athabasca Rivers first flows through the large lakes, losing energy and depositing sediment. Upon recharging the adjacent basins, less silt is introduced and thus declining water levels following recharge do not expose mineral soil. Therefore, there is a reduced likelihood of both the mortality of pre-established individuals and the introduction of new species. Because species are more able to persist through floods, they may be more able to arrange themselves according to long-term hydrological conditions. This may result in the elevational gradient better reflecting the distribution of species.

5.3.3 Transects in Active Areas

Four transects follow the wet-to-dry gradient, but have no plots at the extreme dry end (Fig. 3-6c). Two of these are located in the Athabasca Delta (DT21, 31), one is in the Birch Delta (DT23) and one is adjacent to the Rocher River (DT14). These locations are similar in that they are all subject to overbank river flooding. Except for DT14, they are situated in areas of active deltaic processes. In addition, the location of DT21 possibly makes it susceptible to the effects of wind-driven seiches from Lake Athabasca. Strong easterly winds have been observed to raise water levels at the western end of Lake Athabasca by over a meter (PADPG 1973). For these reasons, these transects may endure higher flood frequencies such that high levee species do not persist.

With frequent inundations species may not come into equilibrium with water conditions. This has been noted by others: Jean and Bouchard (1993) assert that changes in the hydrological characteristics of the basins and changes in vegetation may occur on different time scales. If vegetation is responding to dynamic water-related variables, it may constantly be lagging. This asynchronicity may inhibit the detection of a statistically significant relationship.

5.3.4 Bison Disturbance Transects

The transects exhibiting the most obvious deviation from the primary trend are DT17, 19, 20 (Fig. 3-6d). Most plots are in the lower right of the figure and indicate transect-wide dominance by the disturbed meadow species of Fig. 2-1.

These transects are located in a region of high bison activity (Allison 1973), where it is likely that ongoing animal disturbance has had an important influence on the vegetation composition, thus overriding the effects of elevation and water table.

5.3.5 Recently Flooded Transects

DT06, and to a lesser extent, DT01 show plots to be clustered at the wet end of the gradient (Fig. 3-6e). These transects, along with DT02 and DT03 were almost completely flooded when sampled. Trends were complicated by the fact that floating aquatics were present in nearly every plot, and co-occurred with the species existing prior to flooding, primarily meadow and levee species.

For these transects the vegetation composition was a product of pre-flood and post-flood hydrological conditions. Likely not enough time had elapsed to allow the majority of species to synchronize with the water-related variables.

6. Conclusion

Previous descriptive studies showed that plant communities are related to a water gradient in the perched basins of the PAD. Although this is supported by the descriptive results of Chapter 2, neither elevation nor water table were found to be statistically significant using these data.

Although these negative results may be due in part to shortcomings in the study design, the remarkable differences in character of the perched basins may also be a contribution. The distribution of species across basins is extremely heterogeneous, as is the influence of elevation and water table on vegetation distribution from the logistic regression results. It is evident that the vegetation ecology in the perched basins is still poorly understood.

It is important that further research recognize the heterogeneity of species distributions in the perched basins, and the impact that large and small-scale disturbances may have on their distribution. Several other variables may be influential, and should be considered regionally.

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Table 3-1. Seven classes of species, including species codes and scientific names, Peace-Athabasca Delta, 1993. All species were present in at least 10% of the plots (6 of 597 total). Due to high frequency of occurrence and widespread distribution, *Carex atherodes* and *Calamagrostis canadensis* each comprise separate classes.

Aquatics

Species Code	Scientific Name
acor cal	*Acorus calamus*
utri vul	*Utricularia vulgaris*
cera dem	*Ceratophyllum demersum*
lenm tri	*Lemna trisulca*
lemn min	*Lemna minor*
utri min	*Utricularia minor*
ment arv	*Mentha arvensis*

Meadow Species

Species Code	Scientific Name
scol fes	*Scolochloa festucaceae*
care aqu	*Carex aquatilis*
care ros	*Carex rostrata*
epil cil	*Epilobium ciliatum*
gali trf	*Galium trifidum*
geum ale	*Geum aleppicum*
equi flu	*Equisetum fluviatile*
aste pun	*Aster puniceus*
stac pal	*Stachys palustris*
rori pal	*Rorippa palustris*
geum mac	*Geum macrophyllum*
rume mar	*Rumex maritimus*
urti dio	*Urtica dioica*

Disturbed Meadow Species

Species Code	Scientific Name
vice ame	*Vicea americana*
poa pal	*Poa palustris*
anem can	*Anemone canadensis*
agro rep	*Agropyron repens*
epil ang	*Epilobium angustifolium*
achi sib	*Achillea sibirica*
cala str	*Calamagrostis stricta*
pote nor	*Potentilla norvegica*
sonc arv	*Sonchus arvensis*
poa int	*Poa interior*
pote ans	*Potentilla anserina*
tara off	*Taraxacum officinale*
hord jub	*Hordeum jubatum*
ranu cym	*Ranunculus cymbalaria*
agro sca	*Agrostis scabra*
beck syz	*Beckmannia syzigachne*
cirs arv	*Cirsium arvense*
plan maj	*Plantago major*

Levee species

Species Code	Scientific Name
sali pla	*Salix planifolia*
sali lut	*Salix lutea*
sali exi	*Salix exigua*
sali dis	*Salix discolor*
pice gla	*Picea glauca*
sali beb	*Salix bebbiana*
orth sec	*Orthilia secunda*
alnu inc	*Alnus incana*
corn sto	*Cornus stolonifera*
equi arv	*Equisetum arvense*
rosa aci	*Rosa acicularis*
rubu ida	*Rubus idaeus*
rubu pub	*Rubus pubescens*
scut gal	*Scutellaria galericulata*

Emergents

Species Code	Scientific Name
typhlat	*Typha latifolia*
phra com	*Phragmites communis*
ranu scl	*Ranunculus sceleratus*
scir val	*Scirpus validus*
spar eur	*Sparganium eurycarpum*

Carex atherodes

Species Code	Scientific Name
care ath	*Carex atherodes*

Calamagrostis canadensis

Species Code	Scientific Name
cala can	*Calamagrostis canadensis*

Table 3-2. Logistic regression model results for 28 transects, Peace-Athabasca Delta, 1993. Percent of plots predicted is from Chi-sq. results; Goodness-of-fit is from Hosmer-Lemeshow significance test; models showing significance at 0.05 are shaded. The dependent variable was pres/absence of species groups; the independent variables were elevation, water table, and dummy variables representing species classes. For complete results, see Appendix 4.

Transect	% of plots predicted	Chi-sq. stat.	Chi-square Goodness-of-fit
DT01	81.9	14.1	0.0804
DT02	79.17	11.7	0.1671
DT03	83.53	6.7	0.4646
DT04	88.24	7.9	0.4399
DT05	62.5	21.1	0.0037
DT06	85.71	8.6	0.3793
DT08	89.47	11.7	0.1667
DT09	86.25	4.4	0.8145
DT10	73.33	9.4	0.3060
DT11	83.53	3.9	0.7896
DT13	78	5.1	0.7444
DT14	77.78	3.9	0.7887
DT15	82.11	7.0	0.4260
DT16	71.25	8.8	0.3625
DT17	61.25	10.9	0.2086
DT19	73.81	17.6	0.0241
DT20	89.58	7.5	0.4881
DT21	72.92	9.3	0.2348
DT22	73.81	10.9	0.2059
DT23	86.67	7.3	0.2004
DT24	73.33	7.5	0.4854
DT25	66.67	8.0	0.4384
DT26	70.31	8.7	0.3697
DT27	81.43	3.8	0.8784
DT28	76.25	9.4	0.3129
DT29	78.95	4.7	0.7871
DT31	78.95	15.1	0.0575
DT32	84.21	11.5	0.1194

Table 3-3. **Logistic regression results for 28 transects showing slope coefficients and p-values for elevation and water table. Those significant at 0.05 are shaded.**

Transect	Beta for Elev.	p value	Beta for Water	p value
DT01	0.085	0.193	-0.038	0.606
DT02	0.145	0.088	-0.077	0.174
DT03	0.062	0.049	-0.006	0.823
DT04	0.100	0.148	-0.018	0.730
DT05	0.082	0.281	-0.035	0.248
DT06	8.210	0.853	-8.379	0.850
DT08	0.143	0.052	-0.041	0.188
DT09	0.117	0.037	-0.009	0.352
DT10	-0.011	0.389	0.070	0.010
DT11	0.044	0.076	0.001	0.899
DT13	0.018	0.358	-0.057	0.018
DT14	-0.031	0.453	0.001	0.943
DT15	0.020	0.250	0.002	0.791
DT16	0.105	0.000	-0.029	0.016
DT17	-0.011	0.613	0.010	0.149
DT19	-0.009	0.737	0.002	0.873
DT20	0.124	0.071	-0.010	0.606
DT21	0.026	0.265	0.011	0.604
DT22	-0.020	0.181	0.026	0.030
DT23	-0.071	0.491	0.007	0.913
DT24	0.173	0.008	0.017	0.546
DT25	0.062	0.071	-0.030	0.107
DT26	0.013	0.130	-0.003	0.650
DT27	0.015	0.279	-0.009	0.503
DT28	-0.015	0.369	0.015	0.189
DT29	0.038	0.134	-0.035	0.082
DT31	-0.041	0.354	0.182	0.019
DT32	0.018	0.403	-0.020	0.405

Table 3-4. Meta-analysis hypothesis test results for two strata of transects in the Peace-Athabasca Delta. For Stratum 1, n=12; for Stratum 2, n=15.

Stratum 1

	beta	s.e	Confidence Interval		Reject Null Hypothesis?
			2.50%	97.50%	
elevation	0.079	0.041	0.159	-0.001	no
water table	-0.019	0.024	0.028	-0.066	no

Stratum 2

	beta	s.e	Confidence Interval		Reject Null Hypothesis?
			2.50%	97.50%	
elevation	0.004	0.030	0.063	-0.054	no
water table	0.005	0.047	0.097	-0.088	no

Figure 3-1. Map of the Peace-Athabasca Delta showing locations of 29 vegetation transects established in 1993, modified from PADTS 1996.

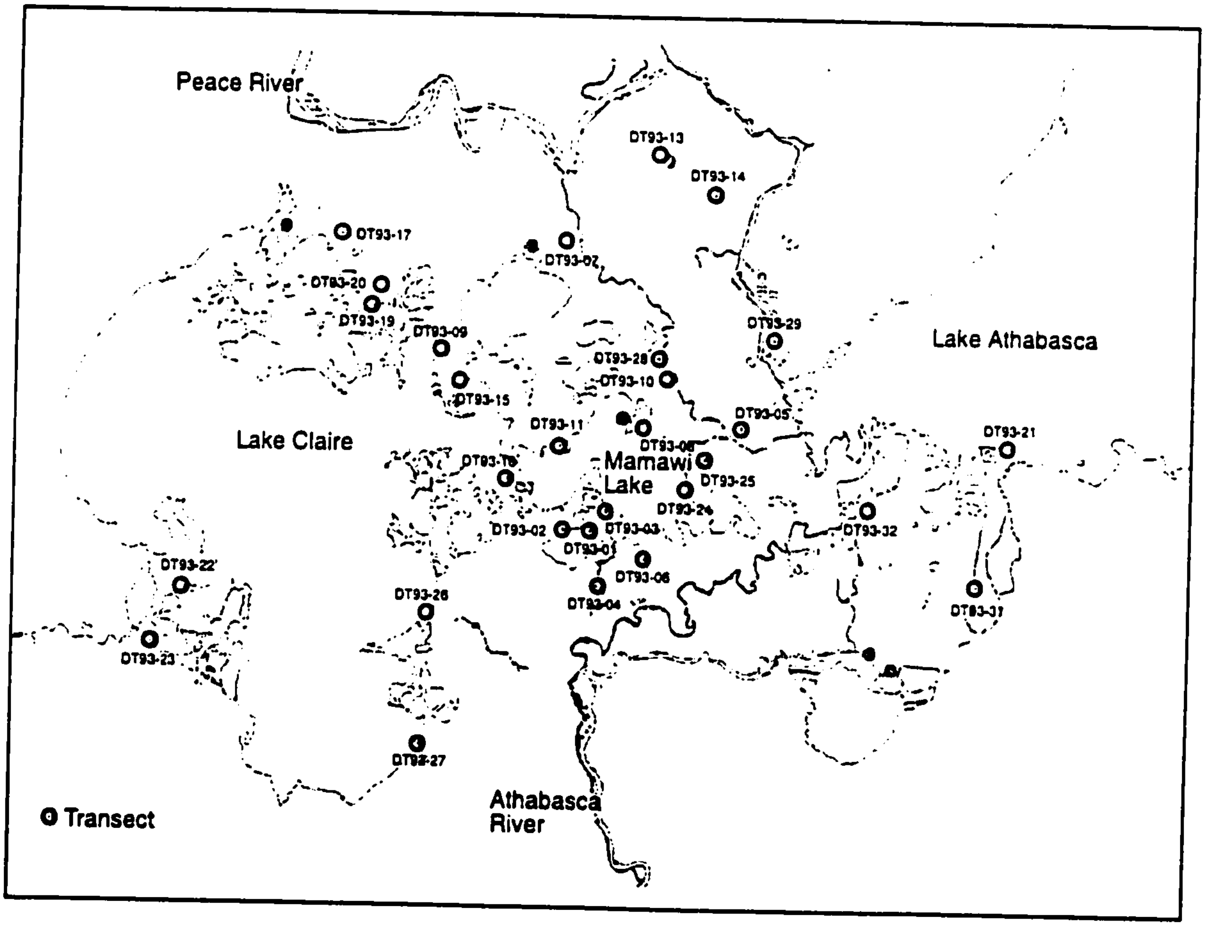
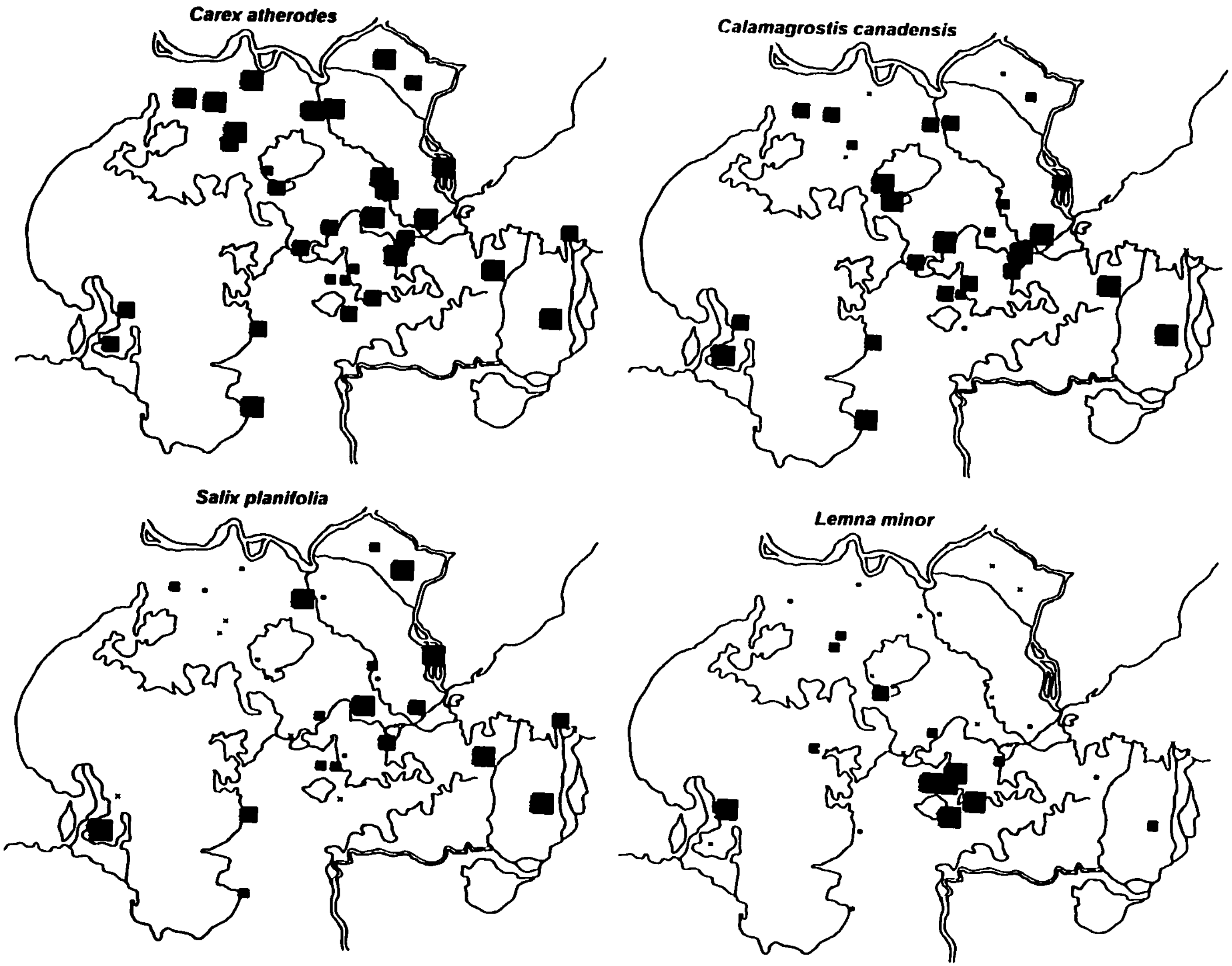


Figure 3-2. Spatial depiction of percent occurrence of the eight commonest species in the Peace-Athabasca Delta. The size of the square corresponds to percent occurrence in transect plots. In ascending size they are: 1-9%, 10-24%, 25-49%, 50-100%; x denotes presence in 0% of plots. **(2 pages)**



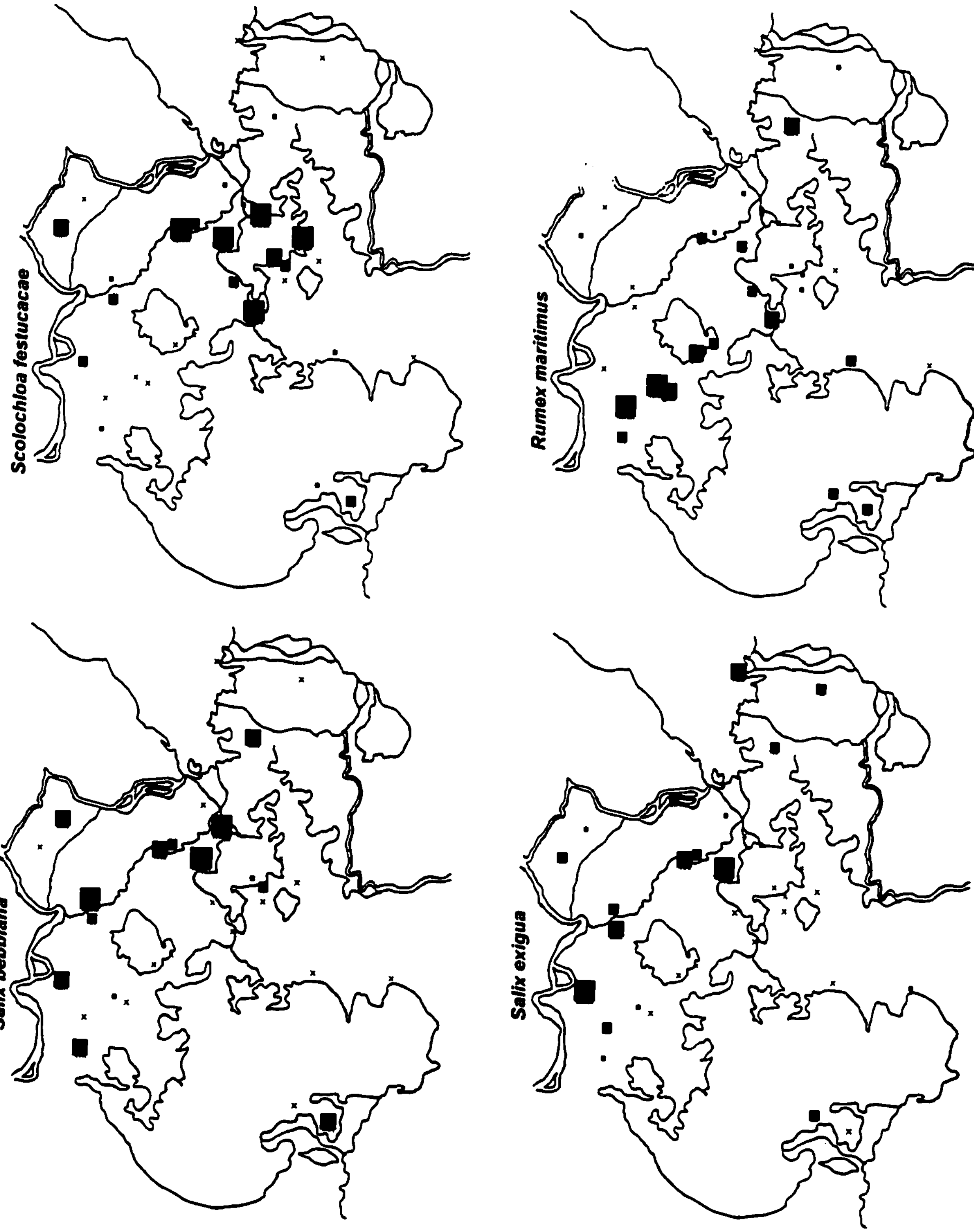
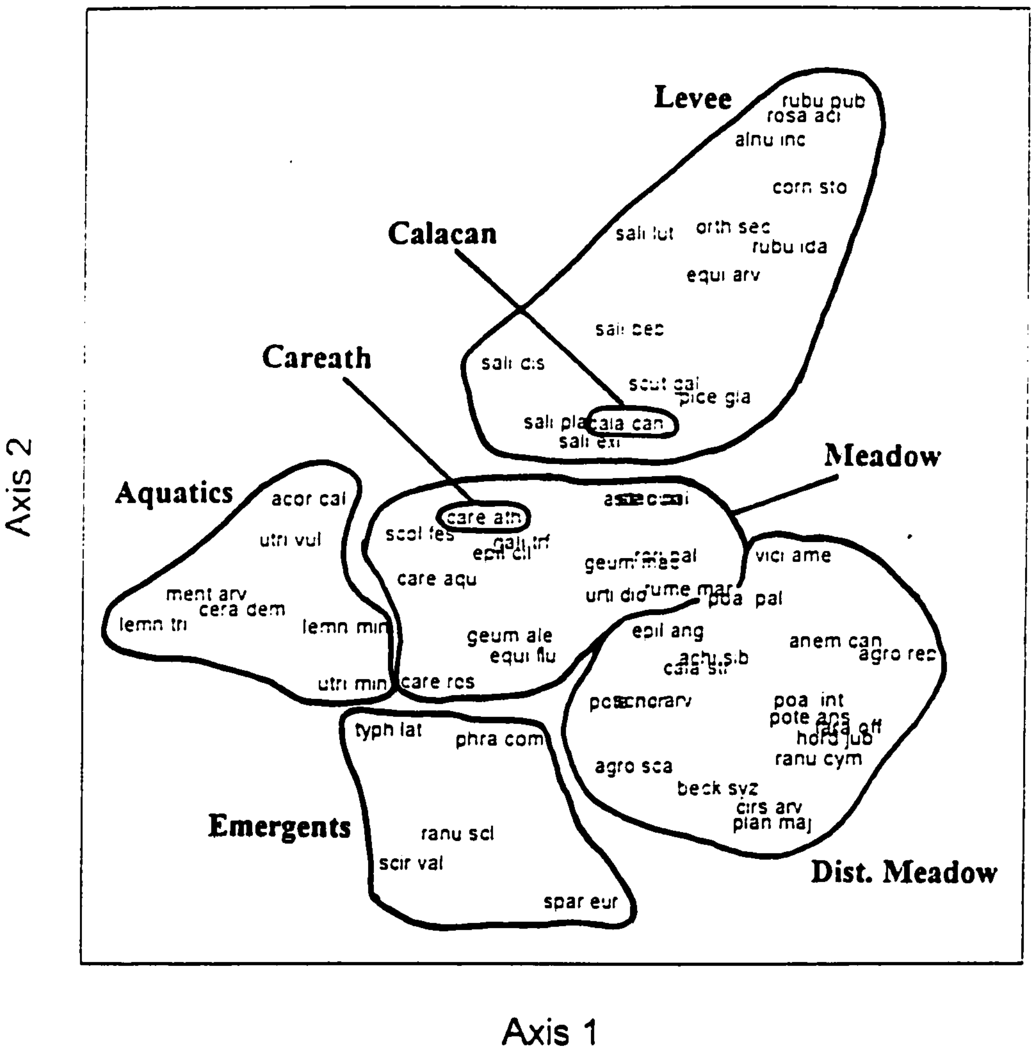

Scolochloa festucacae
Rumex maritimus
Salix bebbiana
Salix exigua

Figure 3-3. Detrended Correspondence Analysis ordination of 59 species showing seven species classes, Peace-Athabasca Delta, 1993. The classes Careath and Calacan are each composed of only one species: *Carex atherodes* and *Calamagrostis canadensis*.



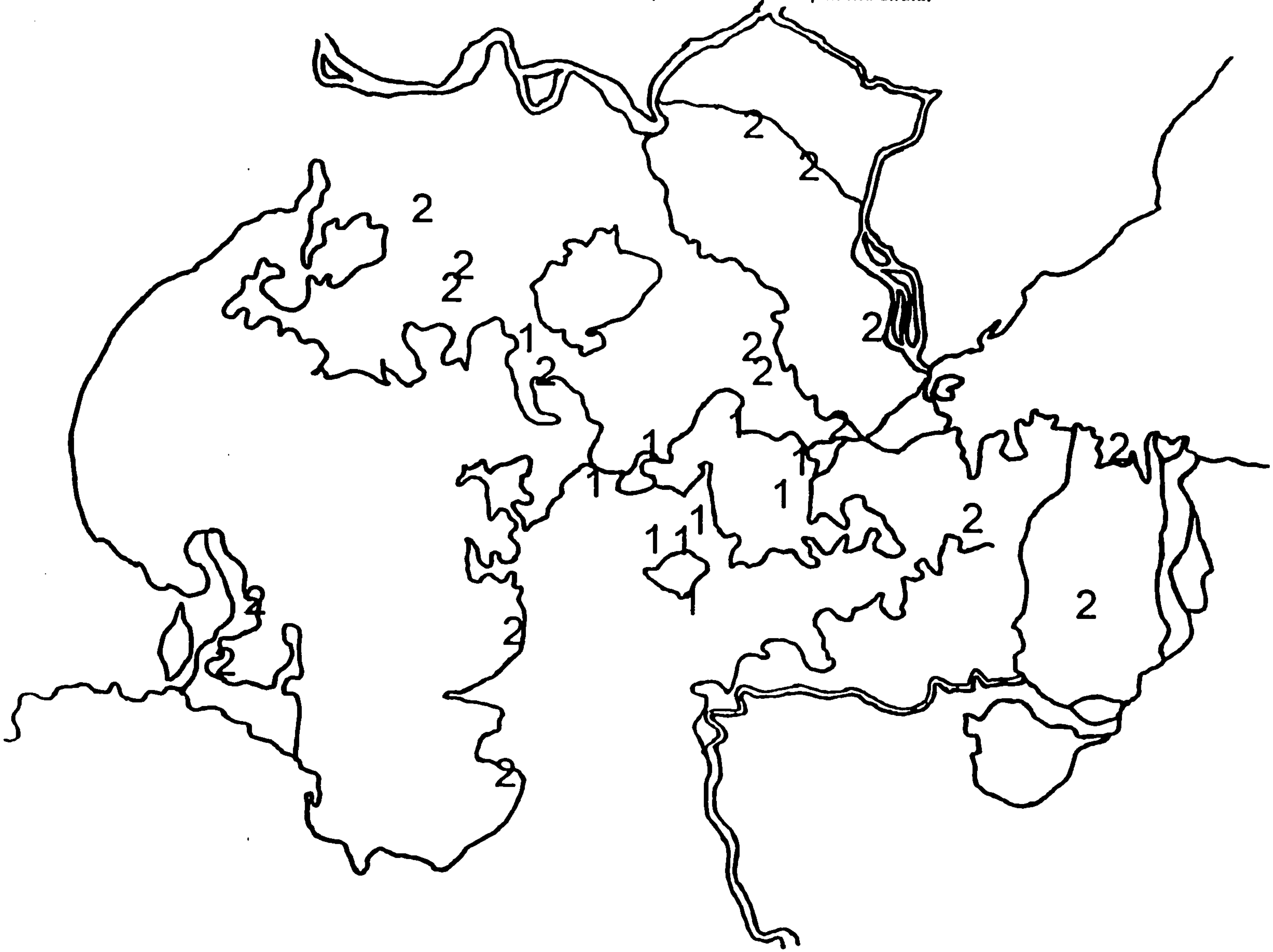


Figure 3-4. Results of cluster analysis of 27 Peace-Athabasca Delta transects. Analysis was conducted using logistic regression slope coefficients for elevation and water table. Numbers represent membership in two strata.

Figure 3-5. Detrended Correspondence Analysis ordination of 597 plots, from 29 transects in the Peace-Athabasca Delta, 1993.

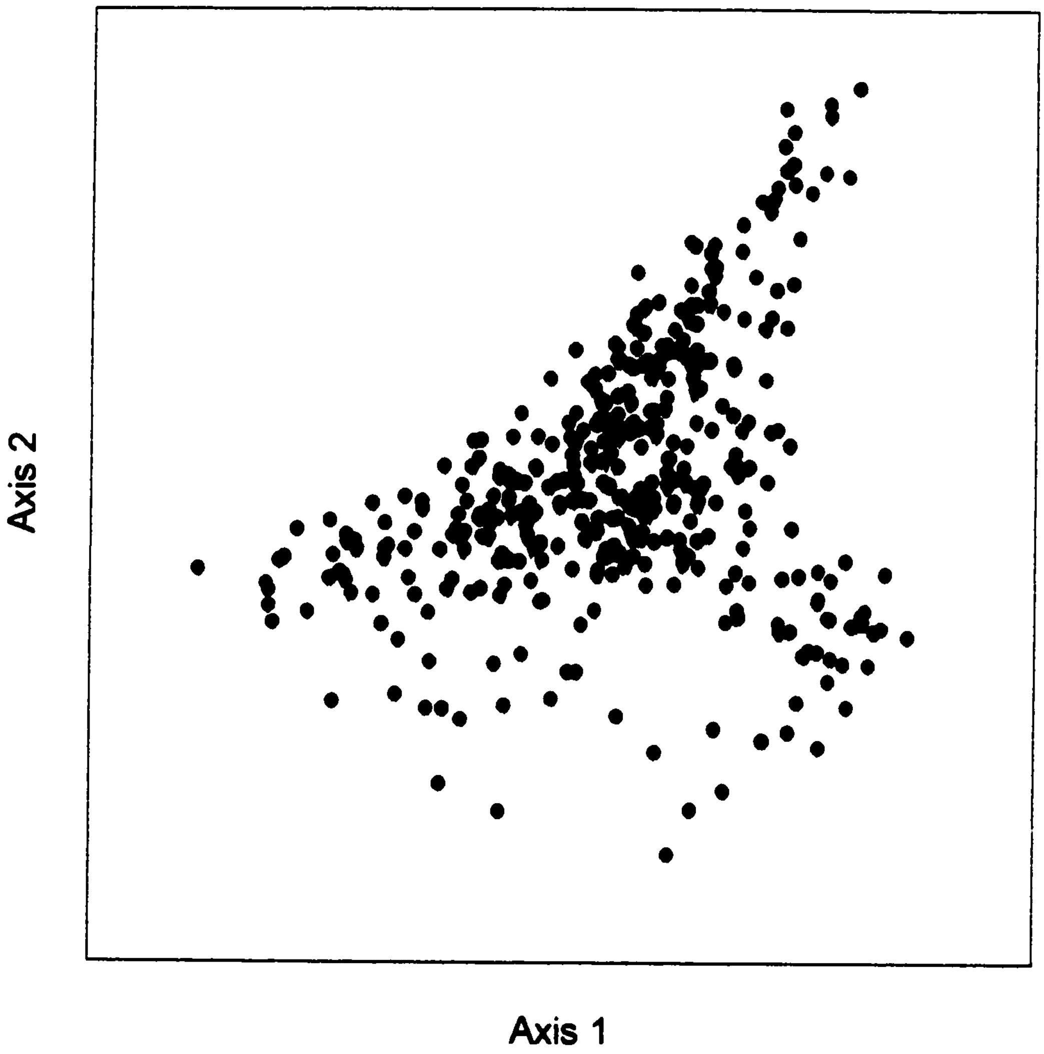
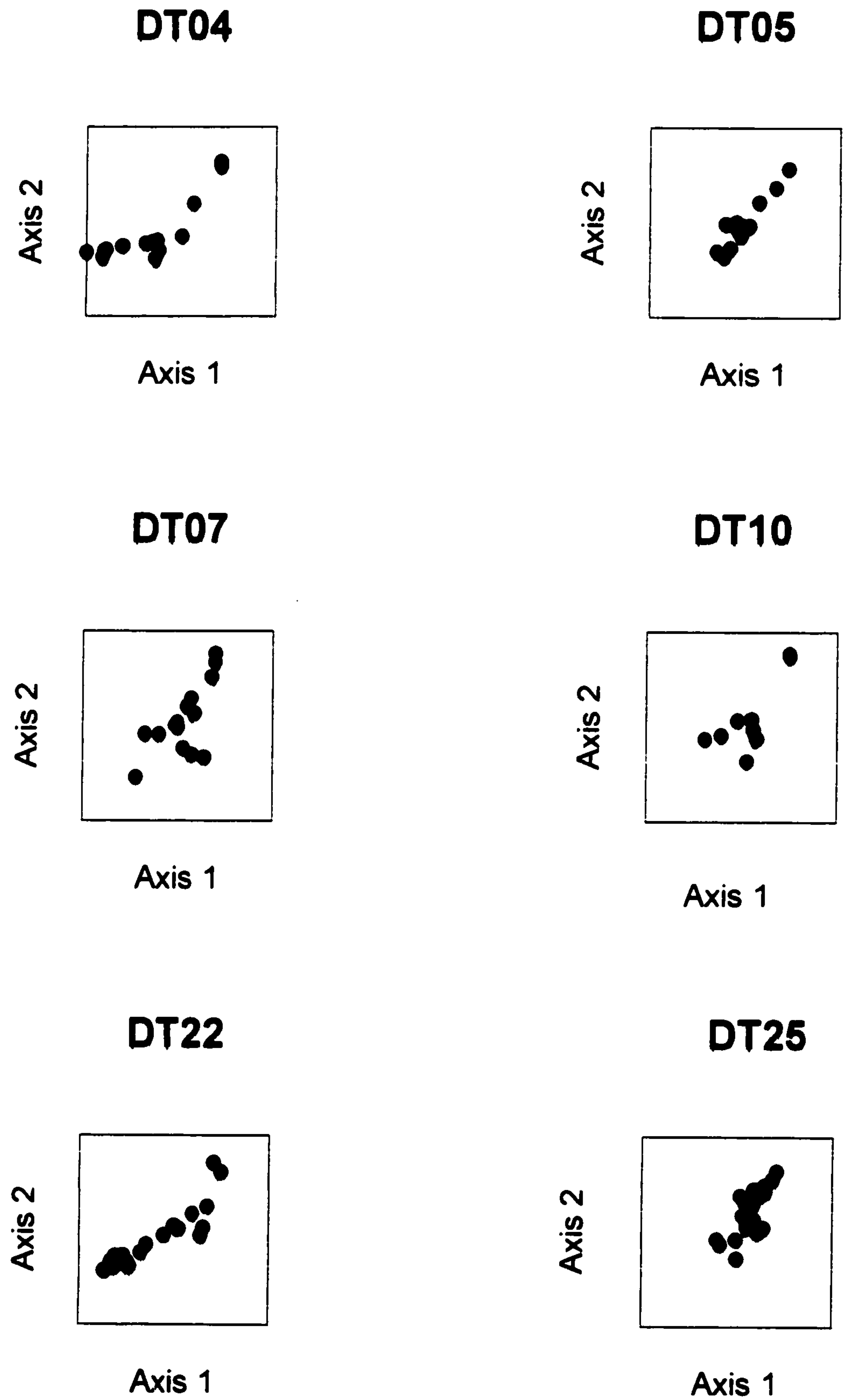
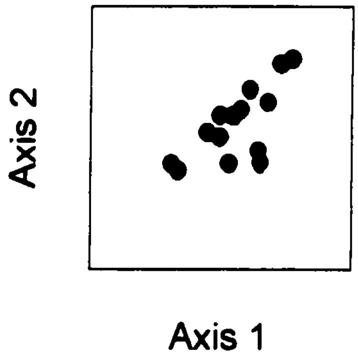


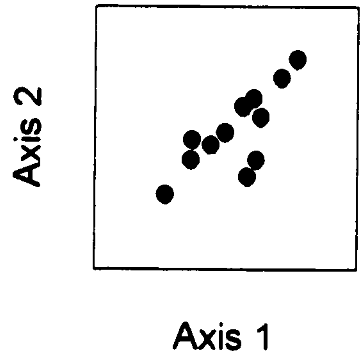
Figure 3-6a. Plot ordinations of 10 Peace-Athabasca Delta transects following the wet-to-dry trend (2 pages).



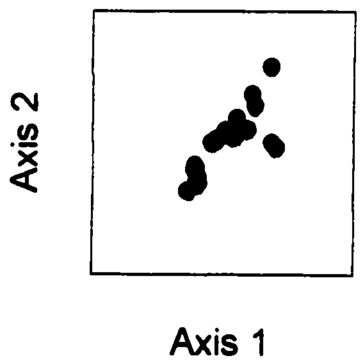
DT26



DT27



DT29



DT32

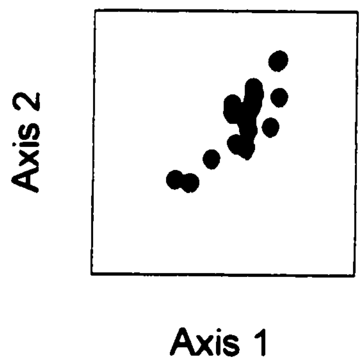
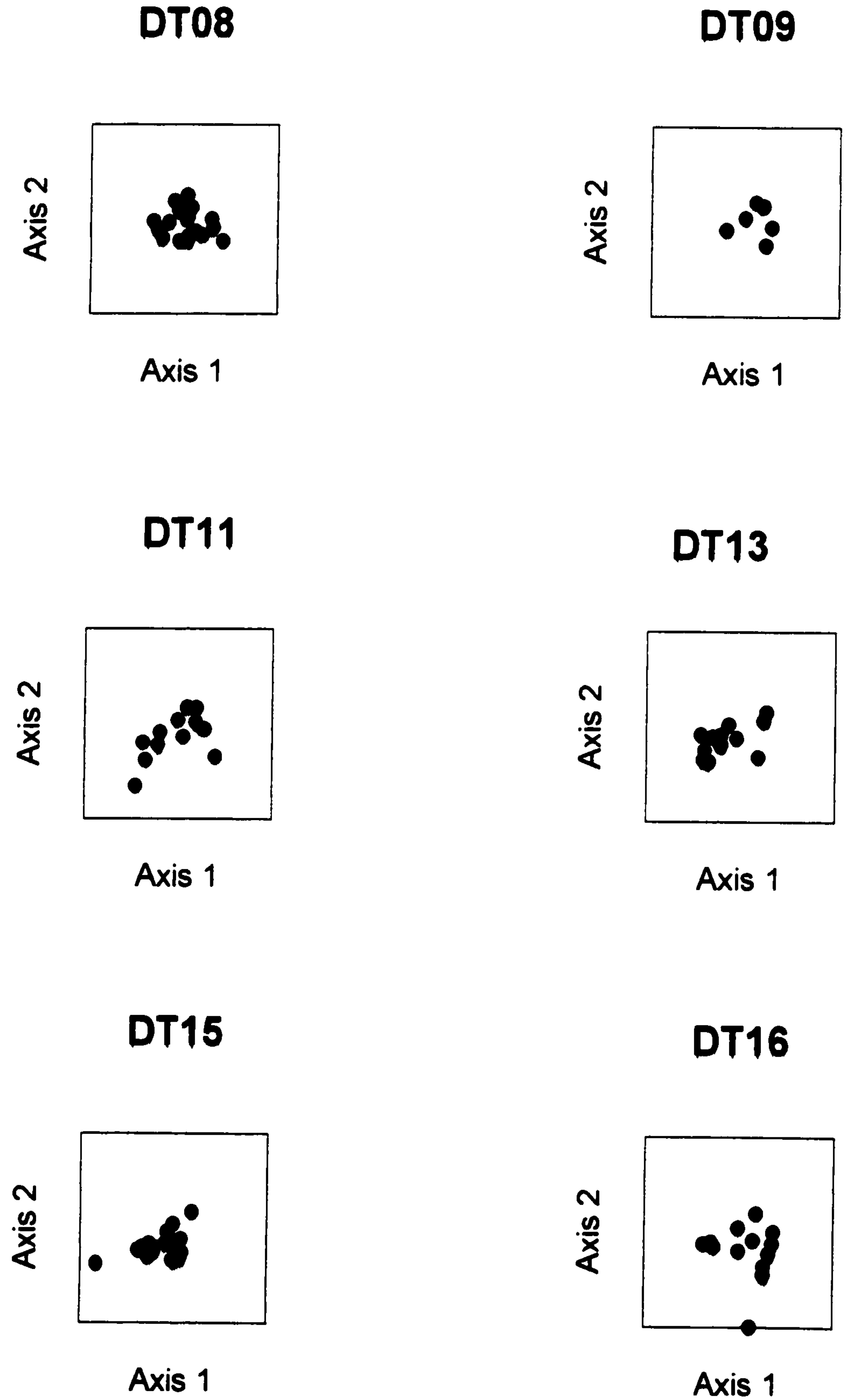


Figure 3-6b. Plot ordinations for 8 Peace-Athabasca Delta transects (2 pages). All but DT13 and 28 are in the middle delta area.



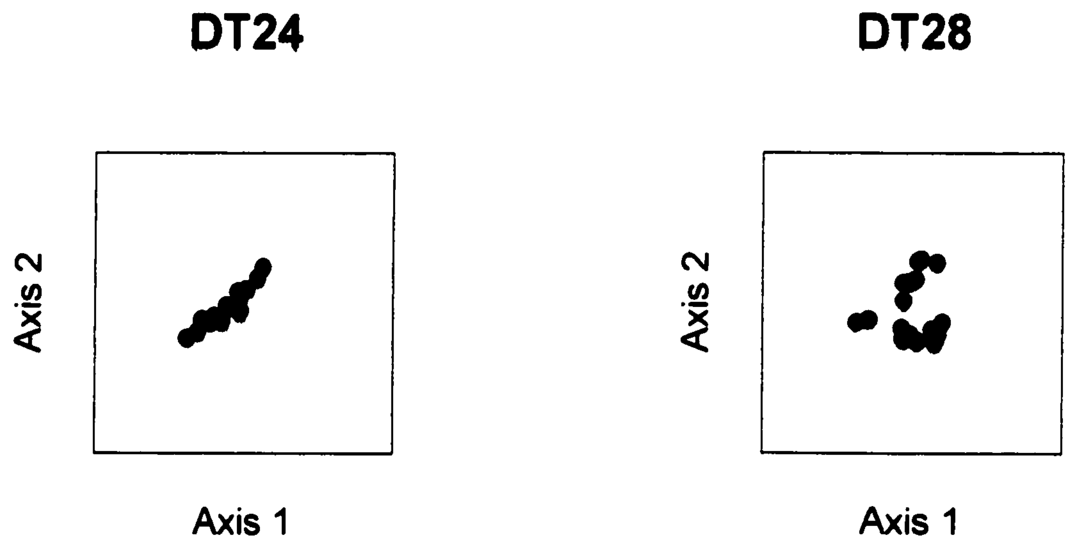

DT24
Axis 2
Axis 1
DT28
Axis 2
Axis 1

Figure 3-6c. Plot ordinations of 4 Peace-Athabasca Delta transects; DT21, 23 and 31 are in active areas.

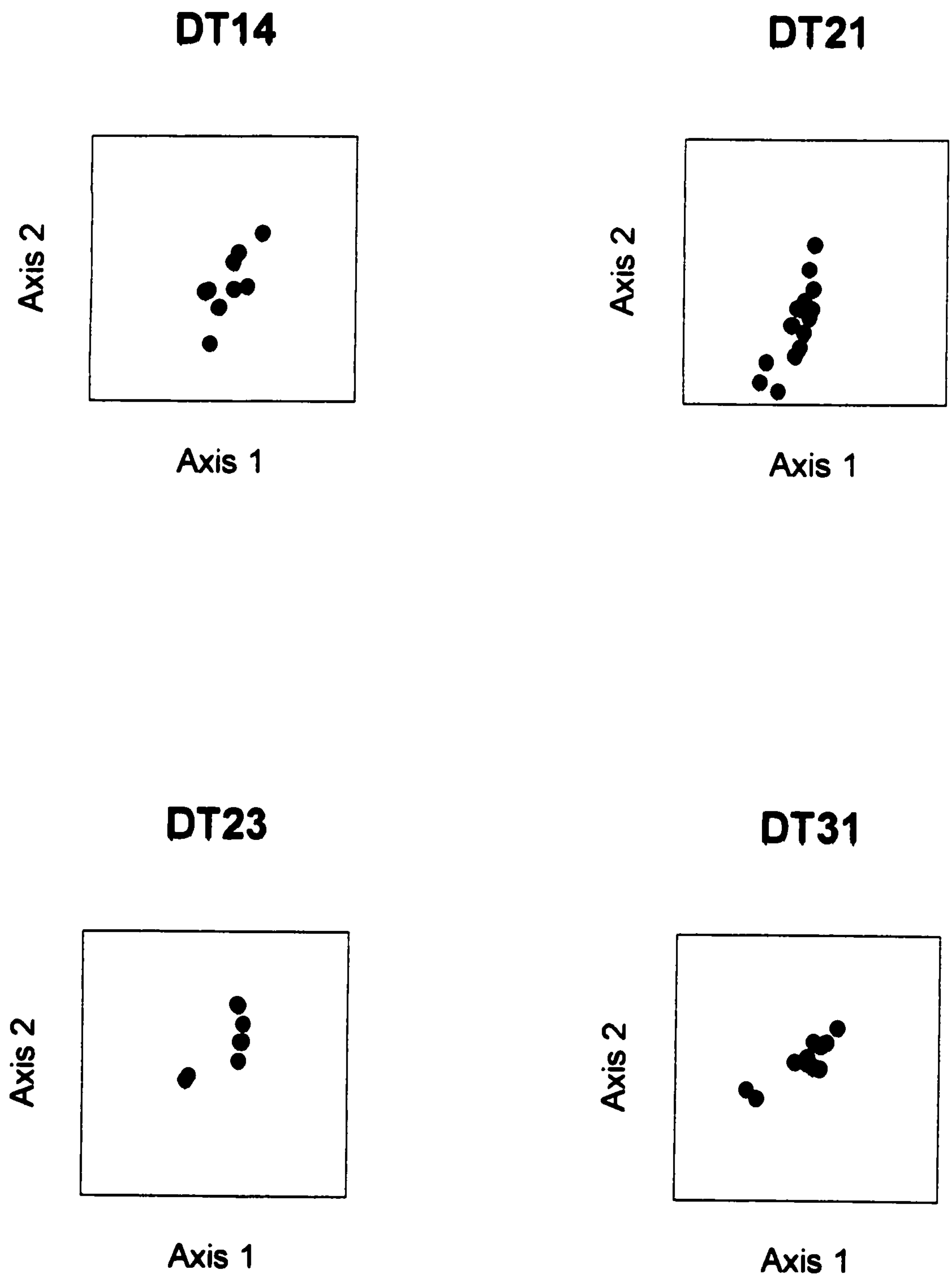


Figure 3-6d. Plot ordinations of 3 Peace-Athabasca Delta transects disturbed by bison activity.

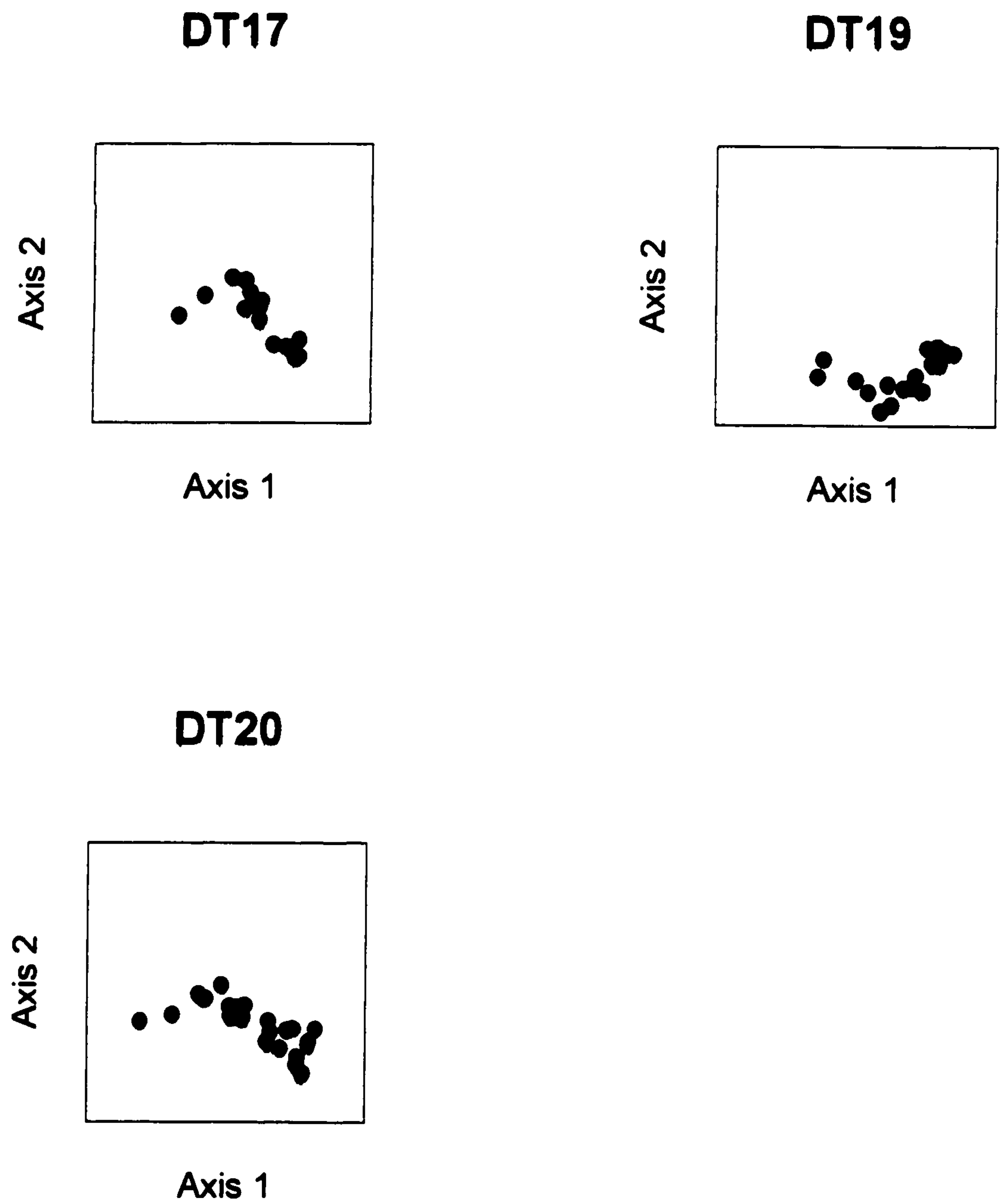
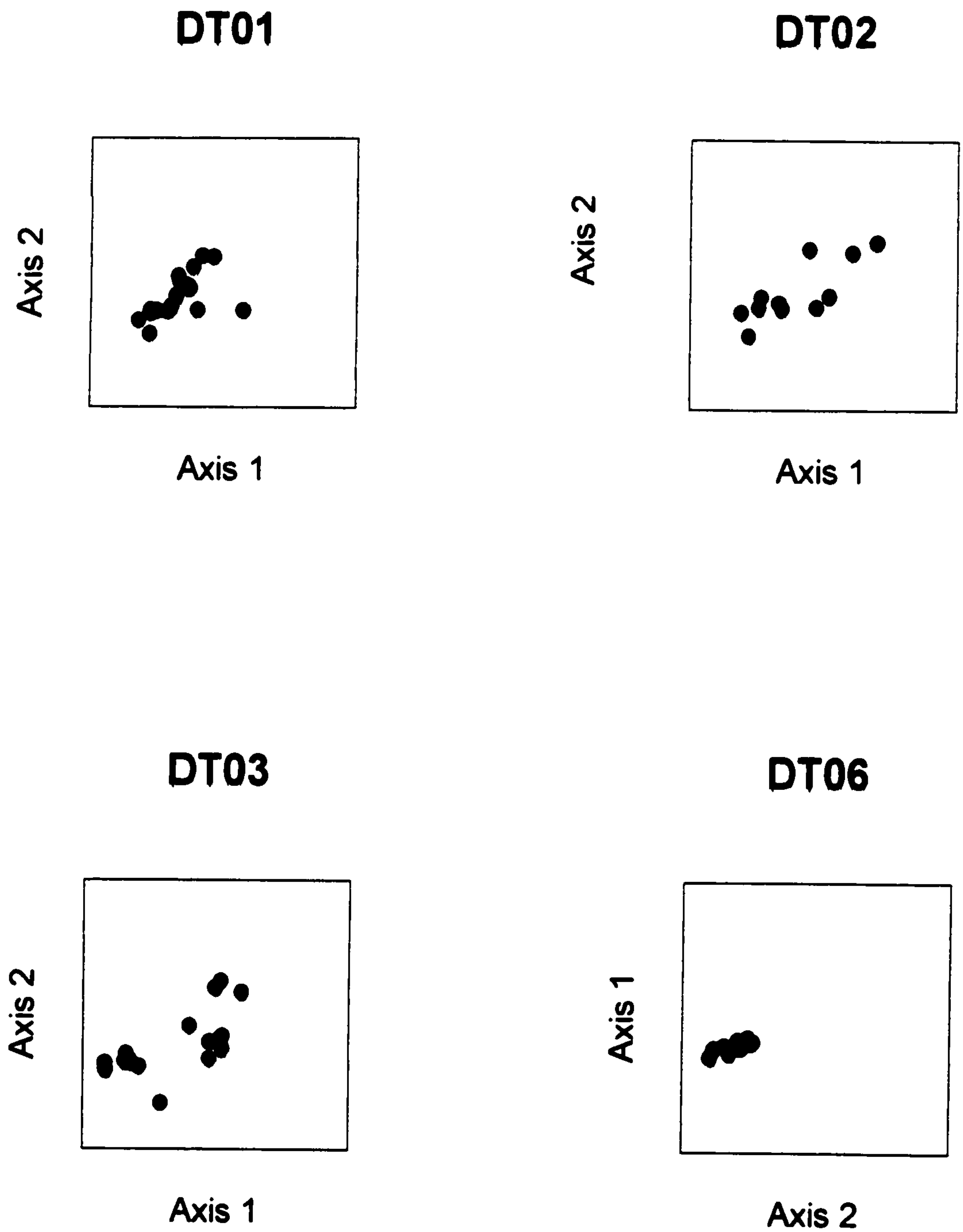


Figure 3-6e. Plot ordinations of 4 Peace-Athabasca Delta transects that have been recently flooded.



Chapter 4

GENERAL CONCLUSIONS AND FURTHER RESEARCH

1. Introduction

The vegetation ecology of the perched basins of the PAD is complex and remains poorly understood. While the descriptive gradient analyses (Chapter 2) showed a wet-to-dry gradient underlying species composition in the perched basins, the two inferential gradient analyses (Chapter 3) did not show elevation or water table to be significantly related to the distribution of species groups in the majority of perched basins, nor across large areas of the PAD comprising multiple basins. However, some basins in the central portion of the PAD did yield significant results: three basins had a significant relationship with elevation; four had a significant relationship with water table; and one had a significant relationship with both.

The general negative results were surprising, and can be attributed to (1) an inappropriate sampling design which may have impeded the detection of a significant relationship, if it exists, (2) patterns of heterogeneity among basins which may have inhibited my ability to draw conclusions across the PAD, (3) the dynamic nature of plant communities such that they are rarely in equilibrium with environmental conditions, or (4) a combination of the three.

This Chapter discusses these problems, provides options for management that may alleviate them, and recommends directions for future research.

2. Addressing Shortcomings of the Study

2.1 Sampling Design

For two reasons, the transects were unable to represent adequately distribution ranges of species classes along either the elevational of water table gradient. First, the shallow nature of the basins meant that only a small breadth of the elevational and water table gradients was captured by individual basins. Although many transects included both the dry extreme of the distribution of the aquatic species class and the wet extreme of the meadow and levee species classes, they rarely encompassed both extremes for either class. Several transects were unable to capture either extreme for many of the terrestrial classes, and in a small number of cases, transects were unable to represent either extreme for the aquatic class. Although the inherent shallowness of the basins restricts what can be learned of the distribution limits of species classes, an investigation by individual species may have provided more information. However, this was not practical given the transect sampling design.

The second reason was the small number of plots established in each basin. For most of the species classes represented along a given transect, either the number of plots where they were absent or the number where they were present was low. This was problematic in that a small number of outliers could have had a dramatic impact on the analysis results. The low sample size inhibited gaining a clear understanding of the distribution of species classes, and may have compromised the results of the logistic regressions.

Both of these concerns may be alleviated by establishing more plots to increase the sample size per basin. Although the narrow breadth of the basin gradients would remain a problem, a sufficiently large sample size would allow analysis by individual species. A sample size of at least sixty plots is recommended for a logistic regression analysis, and this would require the establishment of at least two additional transects per basin.

2.2 Elevation

Another important shortcoming of the study design was that transects were situated too far apart to allow elevational data for each transect to be properly registered to a baseline.

A benchmark is needed to identify where individual transects exist with respect to the elevational gradient across the PAD. There are logistical difficulties in tying the elevation data for each transect to a common baseline, especially considering the inaccessibility and remote location of many transects and the slight topographic differences that likely exist among them. However, many basins could be tied together by establishing several elevational benchmarks along the major water routes.

2.3 Patterns of Heterogeneity

The general lack of significance of elevation and water table combined with the heterogeneity in species distributions suggest that. other environmental variables are important, and shift in importance from region to region within the PAD.

The disturbance regime likely has a major impact on the distributions of species, but it is complex and remains poorly understood. The most evident role of disturbance is in the northeast portion of the PAD where small-scale disturbances by bison have given rise to plant communities that differ fundamentally from other regions of the PAD. The effect of large-scale disturbances is less clear. However, overland flooding may be an especially important process in basins near the origin of a flood. The energy of the water filling a basin affects the amount of sediment deposited, and thus the degree of disturbance.

In other areas of the PAD, the water regime may have an important but complex and varied relationship to vegetation. Because the vegetation of recently flooded areas may reflect past hydrological conditions, a time component is likely important, especially where floods occur regularly but subject the vegetation to a low degree of disturbance. Wind-driven seiches and wave action may be influential where there is a considerable fetch.

Biotic factors may be important under special circumstances. On recently exposed silt flats, the composition of the seedbank, the proximity of species, and the timing of the release of their propagules may dictate which species establish.

The main impediment to investigating these processes on a regional scale is the small number of plots per transect. Although several of the basins that are currently represented by transects can be grouped with others, there still may be a danger of under-sampling. Again, the option that best addresses this problem is the establishment of more plots.

2.4 Circularity among the Data

Another concern is circularity among the data. Species data were used to define species groups, which then were used as the dependent variable for the logistic regression analyses. More transects would have eliminated this problem by allowing some to be used for defining species groups, and others for hypothesis testing.

3. Management Alternatives

3.1 Short-term Alternatives

Although the study suffered some deficiencies, the results provide some direction for work to be undertaken during the coming field seasons.

The collection of vegetation data should continue, especially considering the recent large-scale flooding. These data would be essential to understanding how the distribution of vegetation changes over time, and under conditions of flooding and subsequent drying.

It is important that the collection of water table data continues annually to allow longer-term water variables to be defined for future analyses. To deal with possible asynchronicity between water levels and vegetation, Timoney (1996) recommends a hydroperiod index that integrates water depth and the duration of inundation.

More plots need to be established before the vegetation ecology of the perched basins can be sufficiently understood. To maintain consistency, they should be placed using the sampling design of current transects. However, to increase the sample size per basin, transects should be situated in basins where there currently is a transect. They should also have a common elevational baseline.

3.2 Long-term Alternatives

With respect to other research in the PAD, a flood history study using sediment coring techniques would be informative. Results may clarify the disturbance effects of flooding, as indicated by the thickness of layers of deposited silt. Pollen and seeds trapped in the sediment layers may identify which species were available for colonization subsequent to flooding, and may be useful markers for identifying the extent of large-scale flood events. Historical vegetation patterns may also be revealed in the intervening organic layers. Together, this information may provide a clearer regional understanding of large-scale disturbance characteristics, and the influence they have on the distribution of vegetation.

An elevation map with high spatial and topographical resolution would be helpful for a better understanding of the flood regime. It could be useful in identifying which basins would be successively impacted by rising flood waters, as well as the possible extent of both historical and future floods, and their point of origin.

4. Conclusion

In general, elevation and water table were not significantly related to the presence/absence of vegetation classes in individual perched basins, nor across large areas of the PAD comprising multiple basins. Given the shortcomings in the sampling design and the likelihood that disturbance, environmental, and biotic processes affect the distribution of vegetation in the perched basins, further research is strongly recommended. The influences of these processes likely varies in importance among regions across the PAD, and can vary temporally. Future research should identify the regional role of variables before a sufficient delta-wide understanding can be gained.

References Cited

Timoney, K., 1996. Peace-Athabasca Delta Technical Studies - Vegetation Monitoring Study: Final Report. Wood Buffalo National Park, Fort Smith, N.W.T., 66 pp.

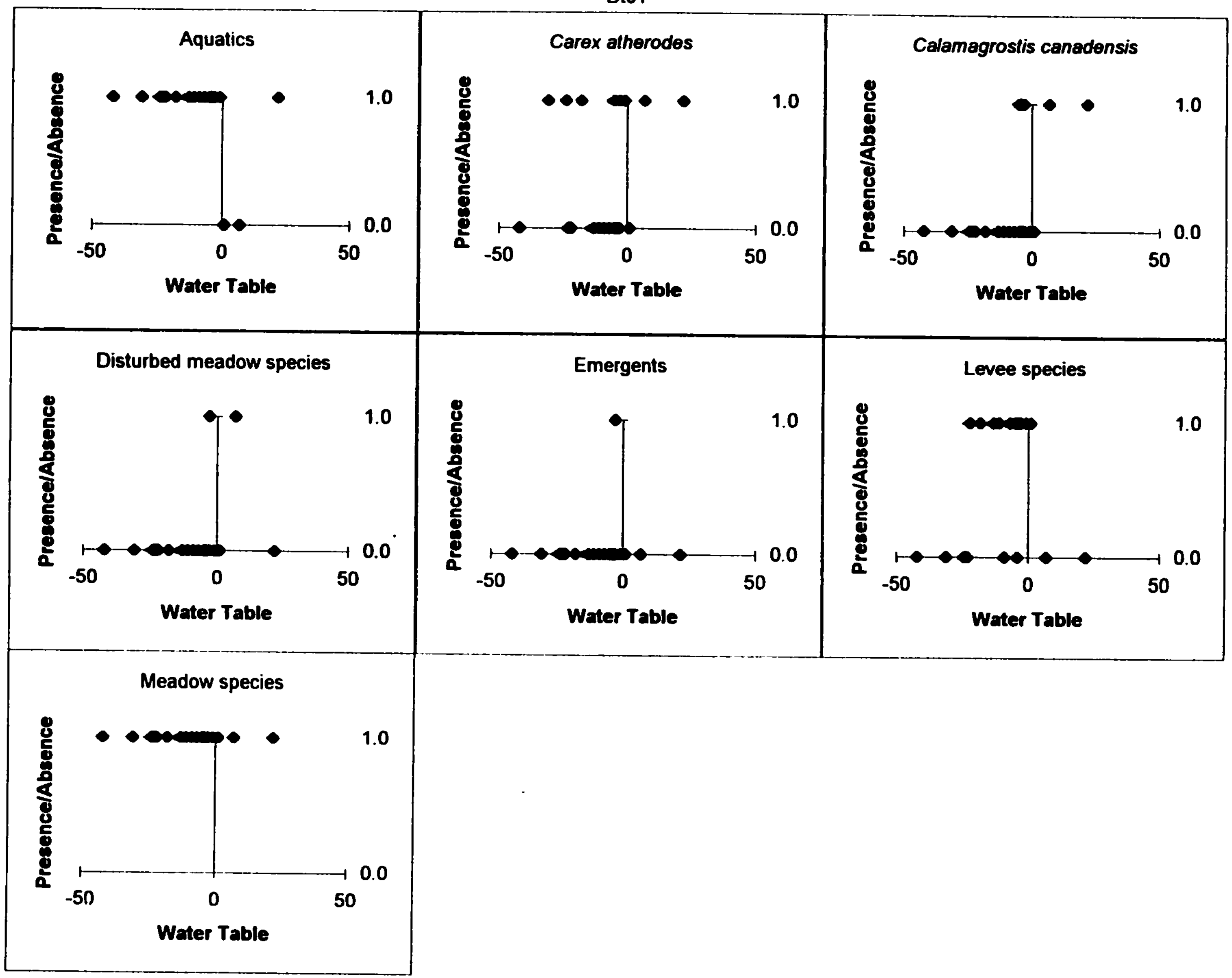
Appendices

Appendix 1. Plots for each transect showing presence/absence of seven species classes along gradients of water table and elevation.

Appendix 2. SAS Program used for meta-analysis.

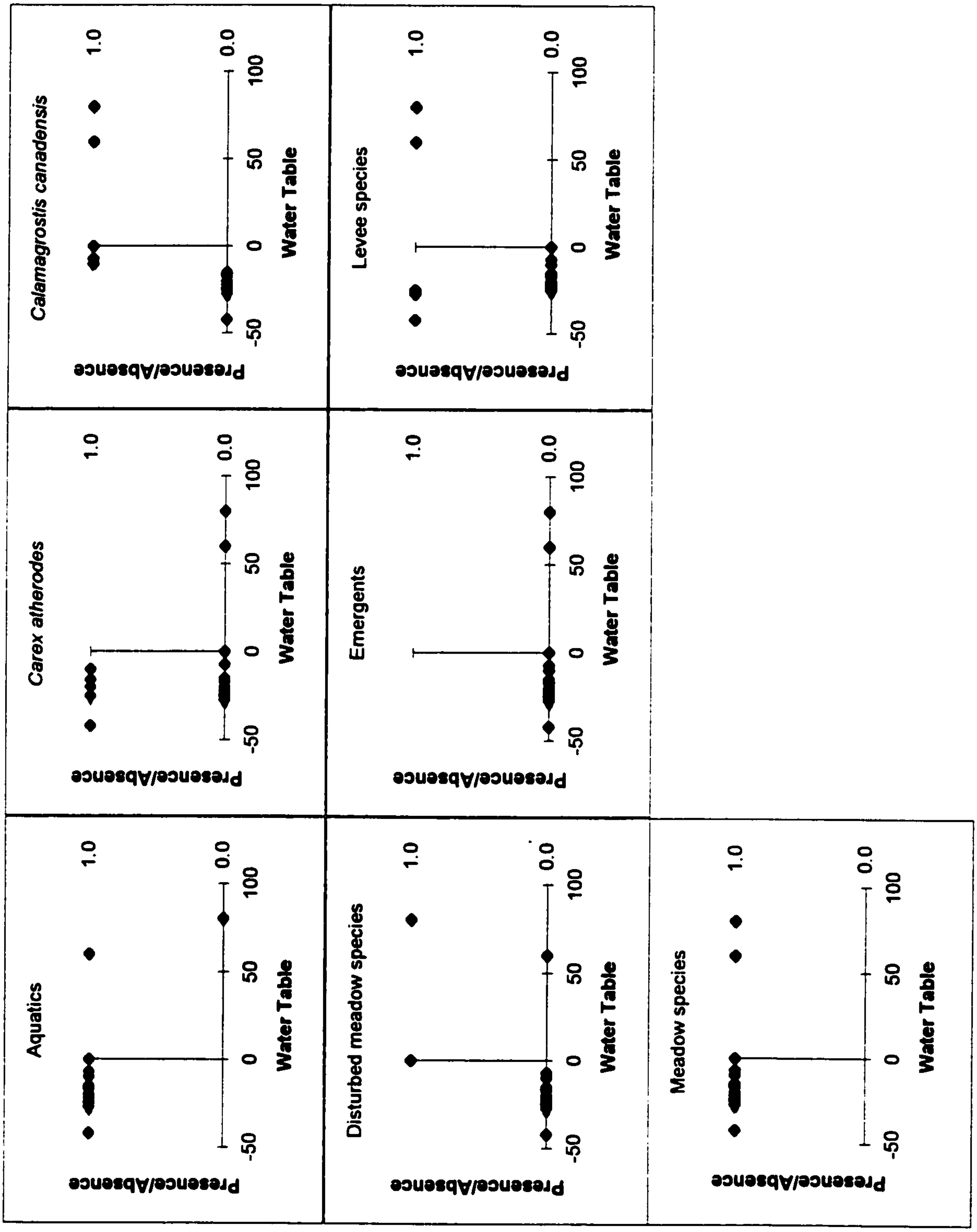
Appendix 1. Plots for each transect showing presence/absence of seven species classes on gradients of water table and elevation.

Dt01

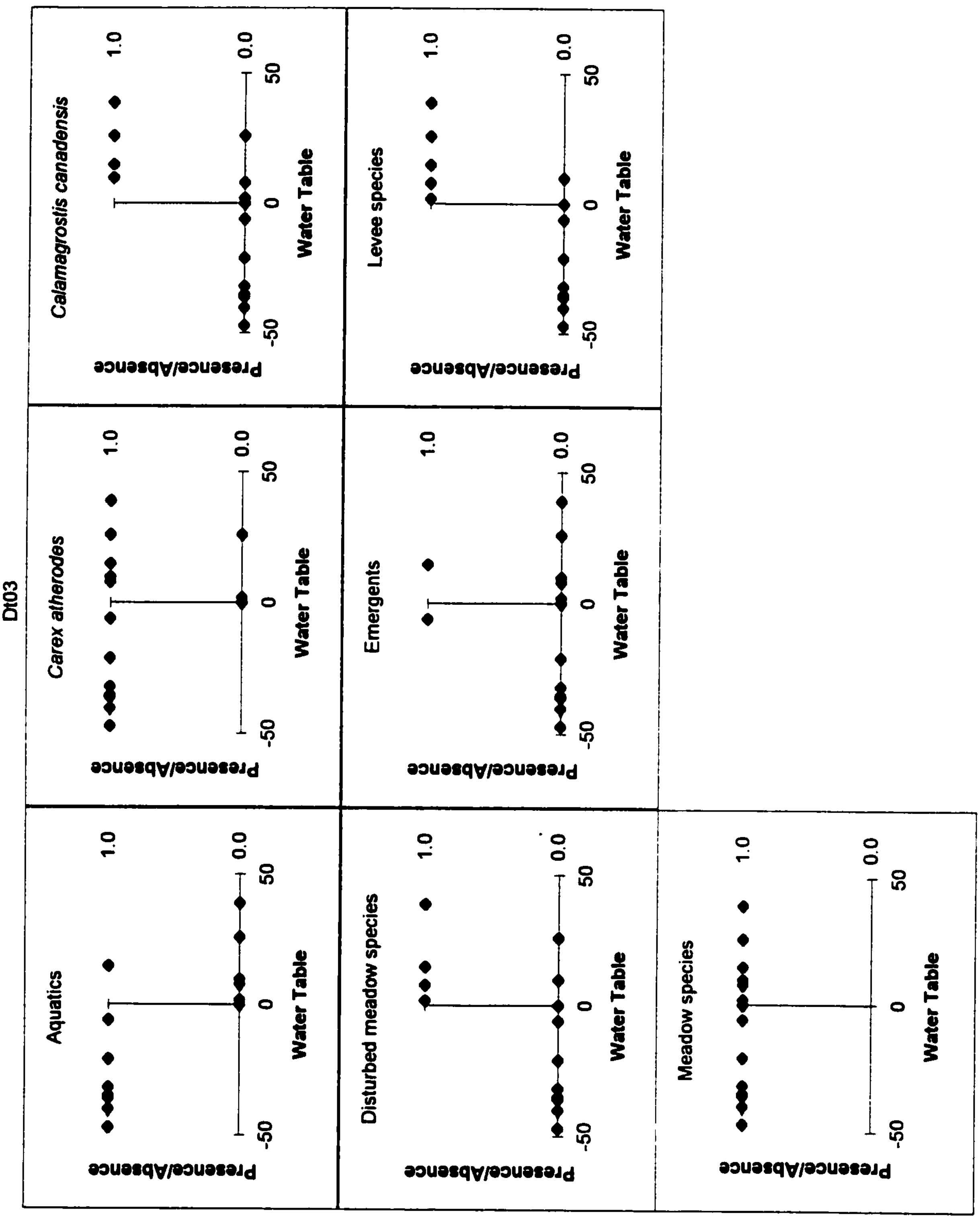


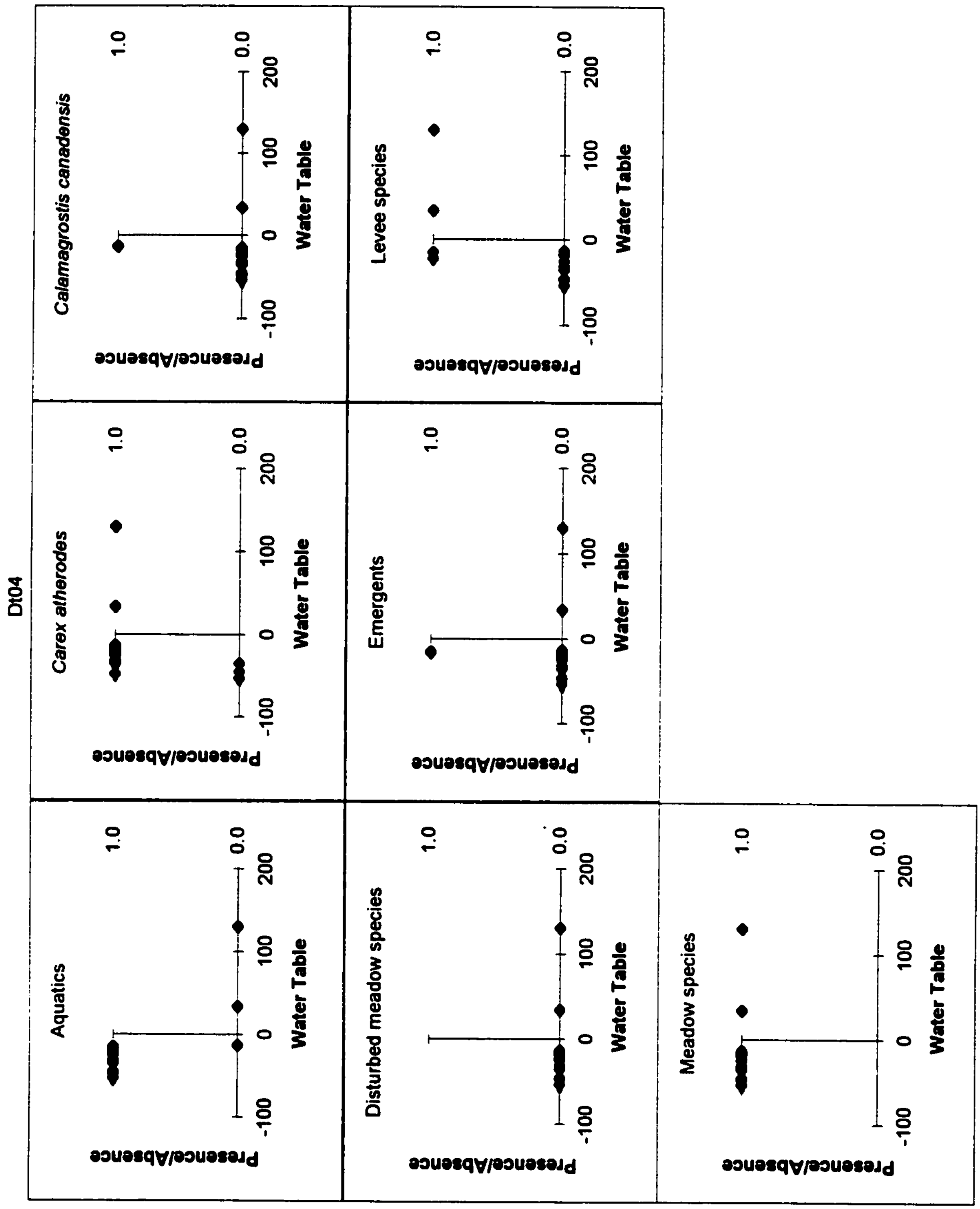
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50

Dt02

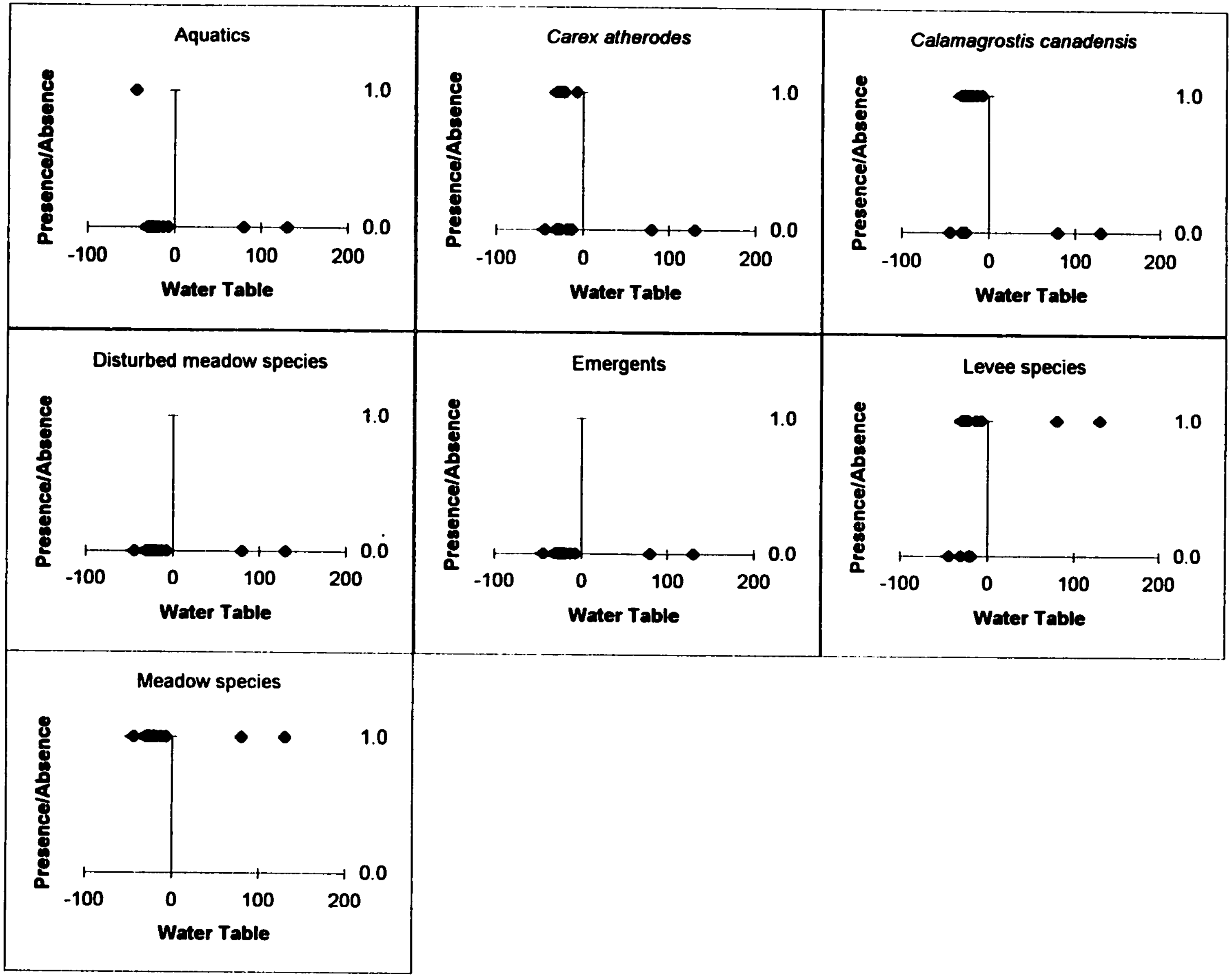


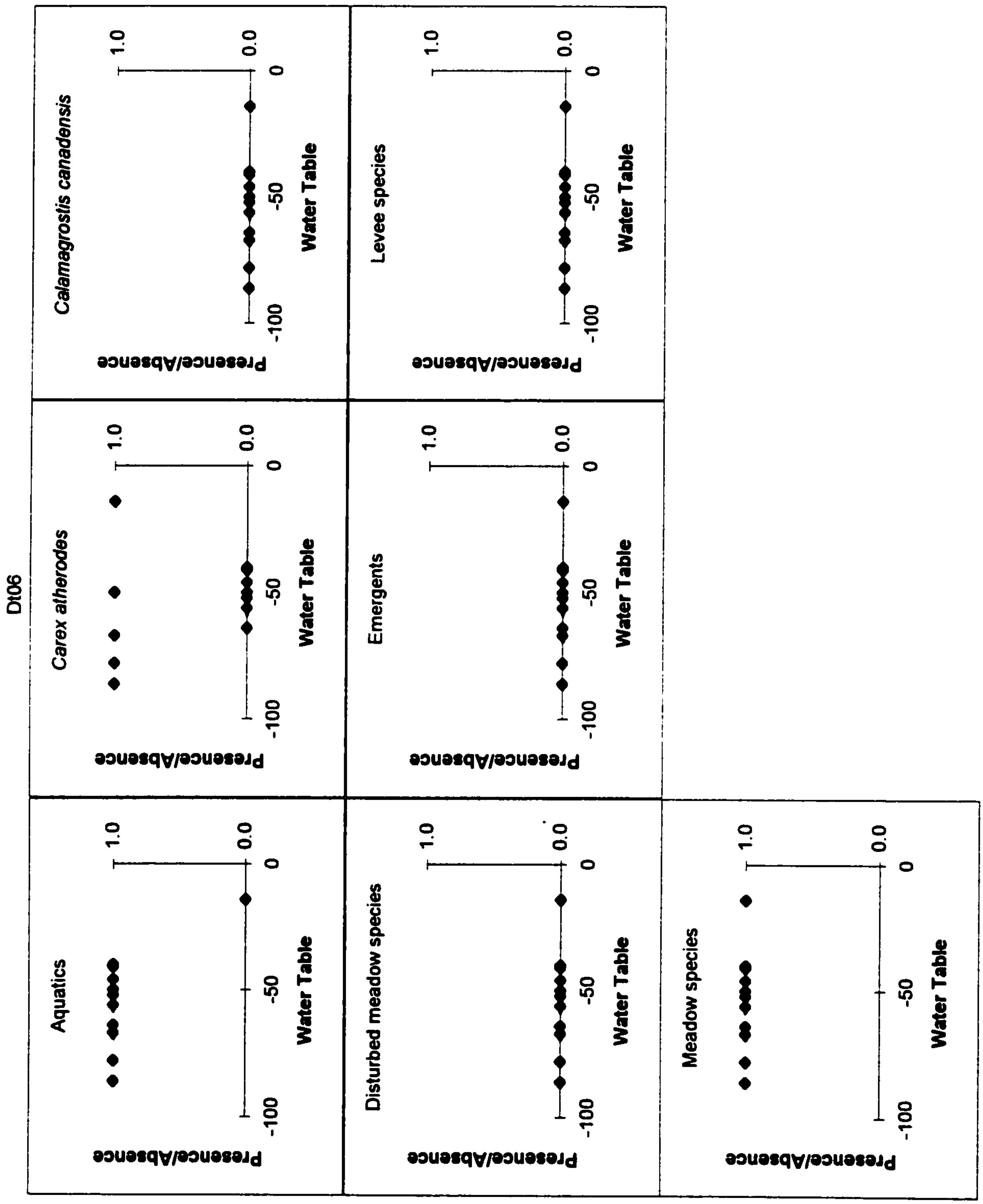
Calamagrostis canadensis
Levee species
Carex atherodes
Emergents
Aquatics
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50
100


Dt03
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50


Dt04
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-100
0
100
200

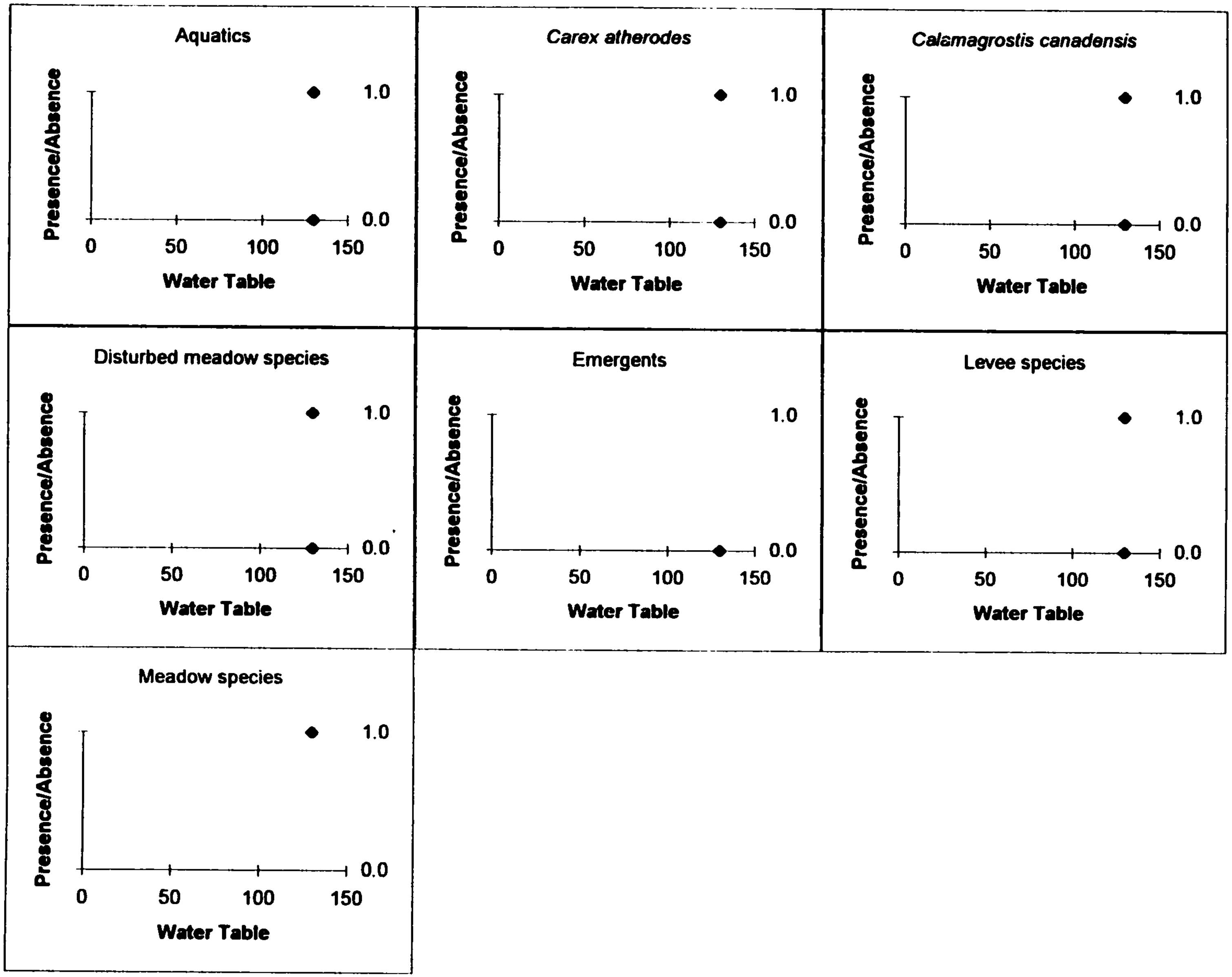
Dt05


Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-100
0
100
200

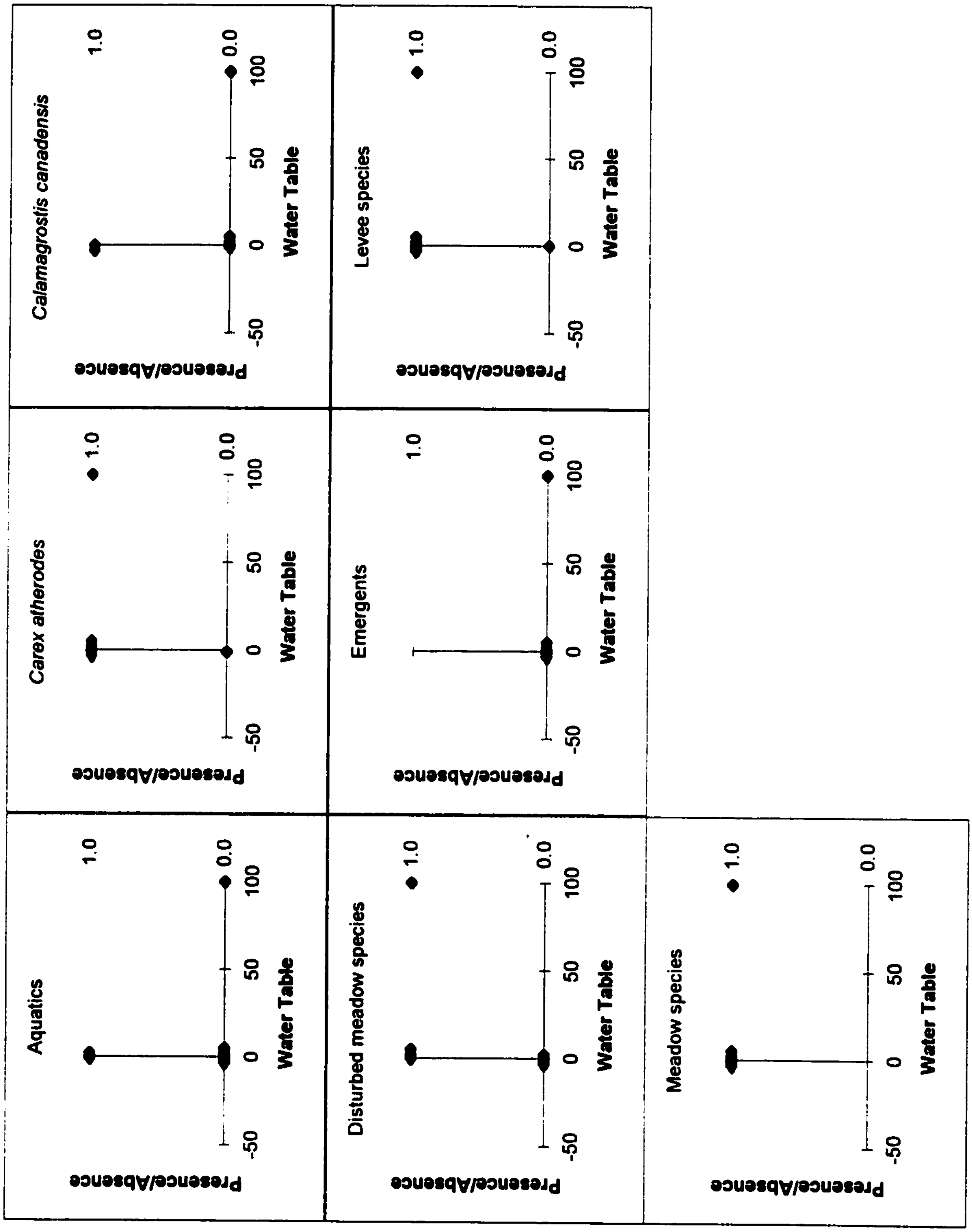


Dt06
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
1.0
0.0
0
-50
-100

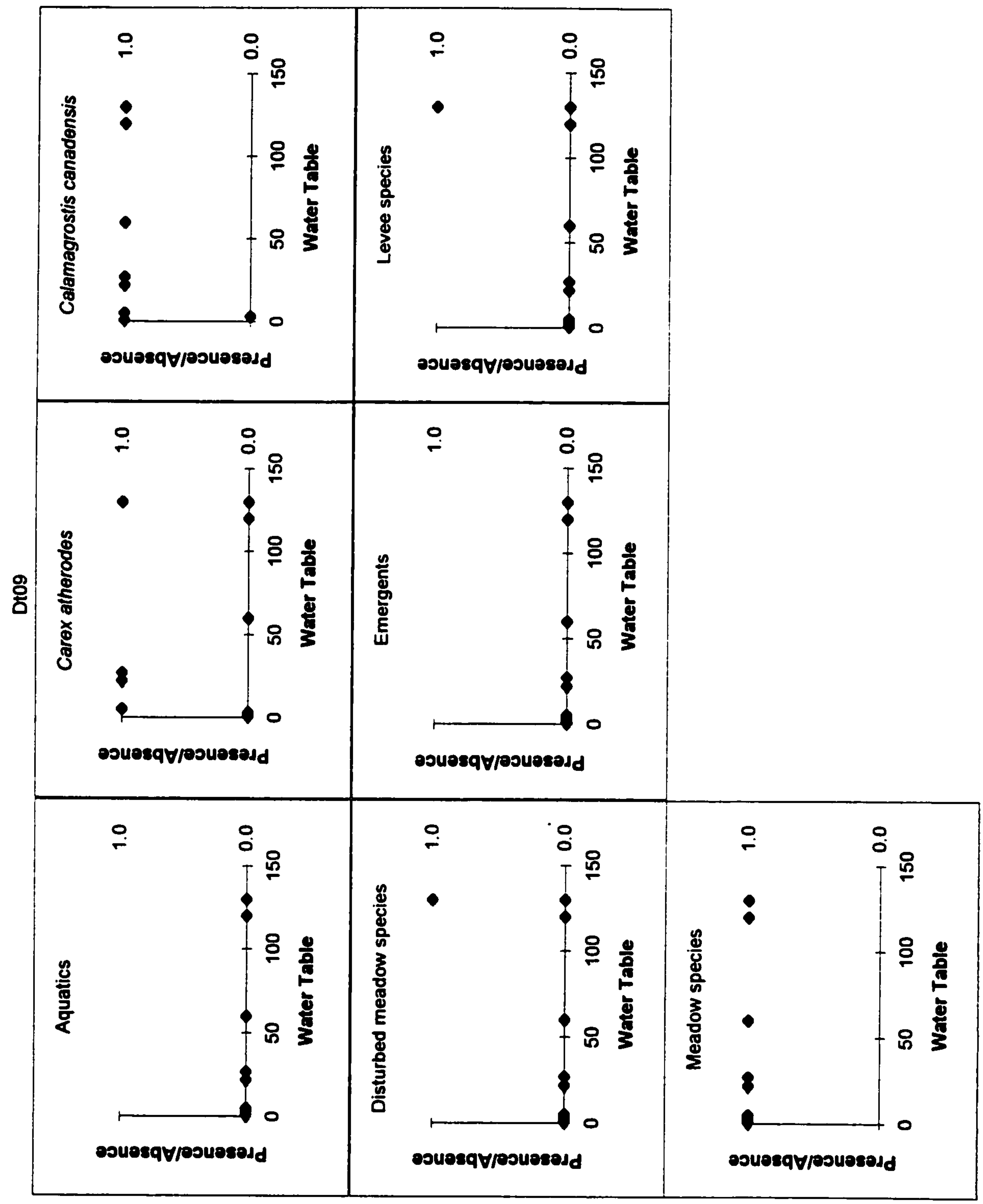
Dt07



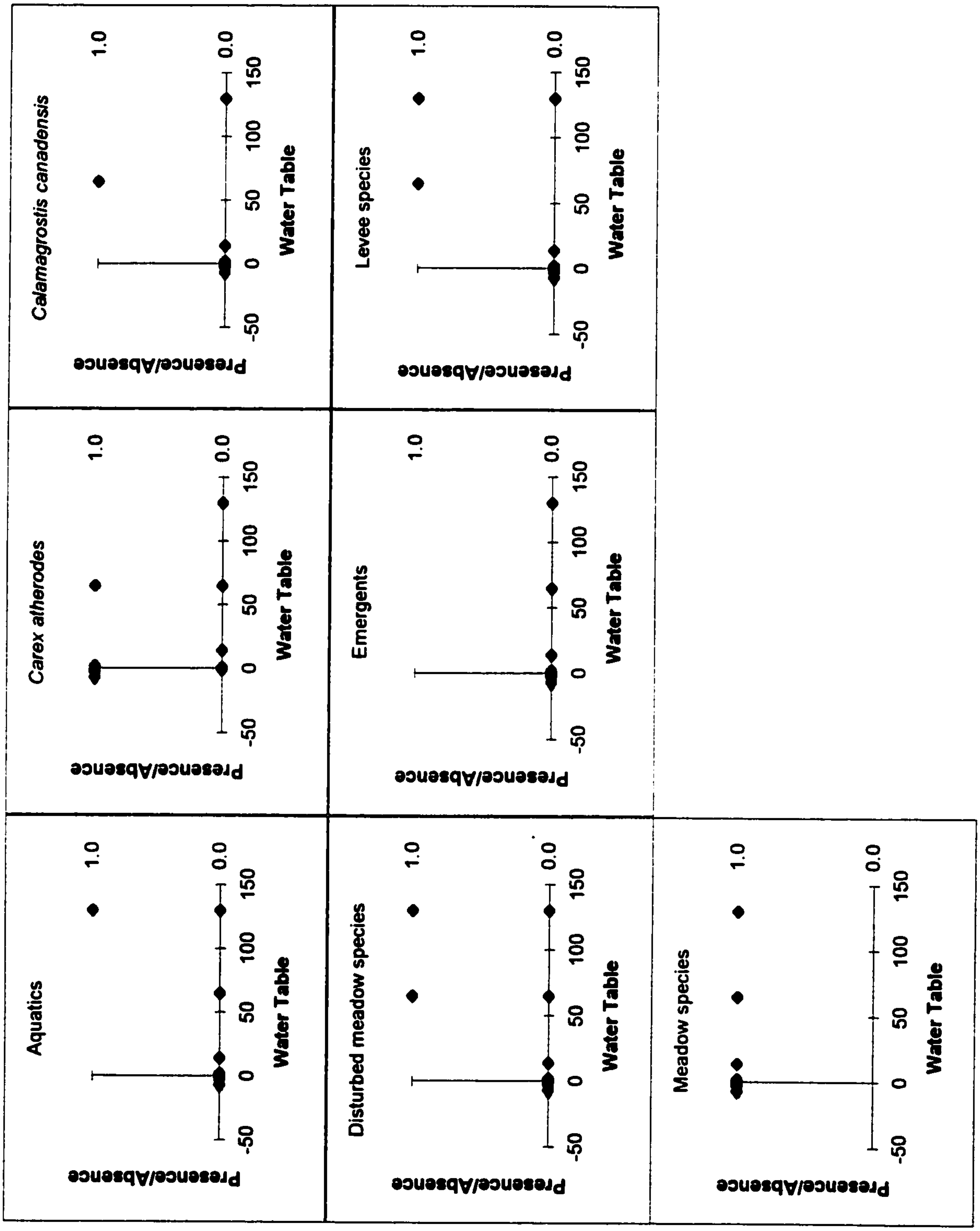
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
0
50
100
150
0.0
1.0

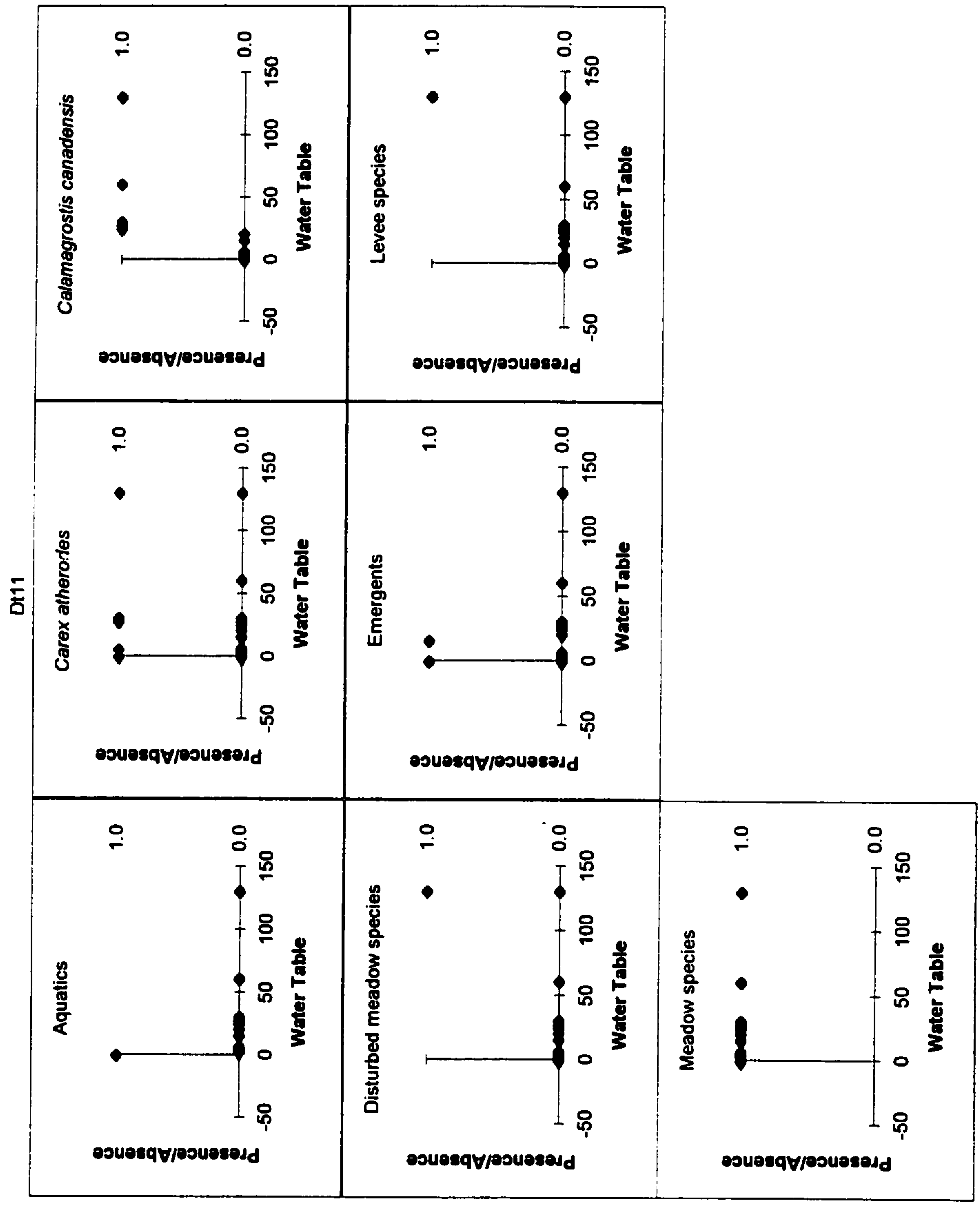


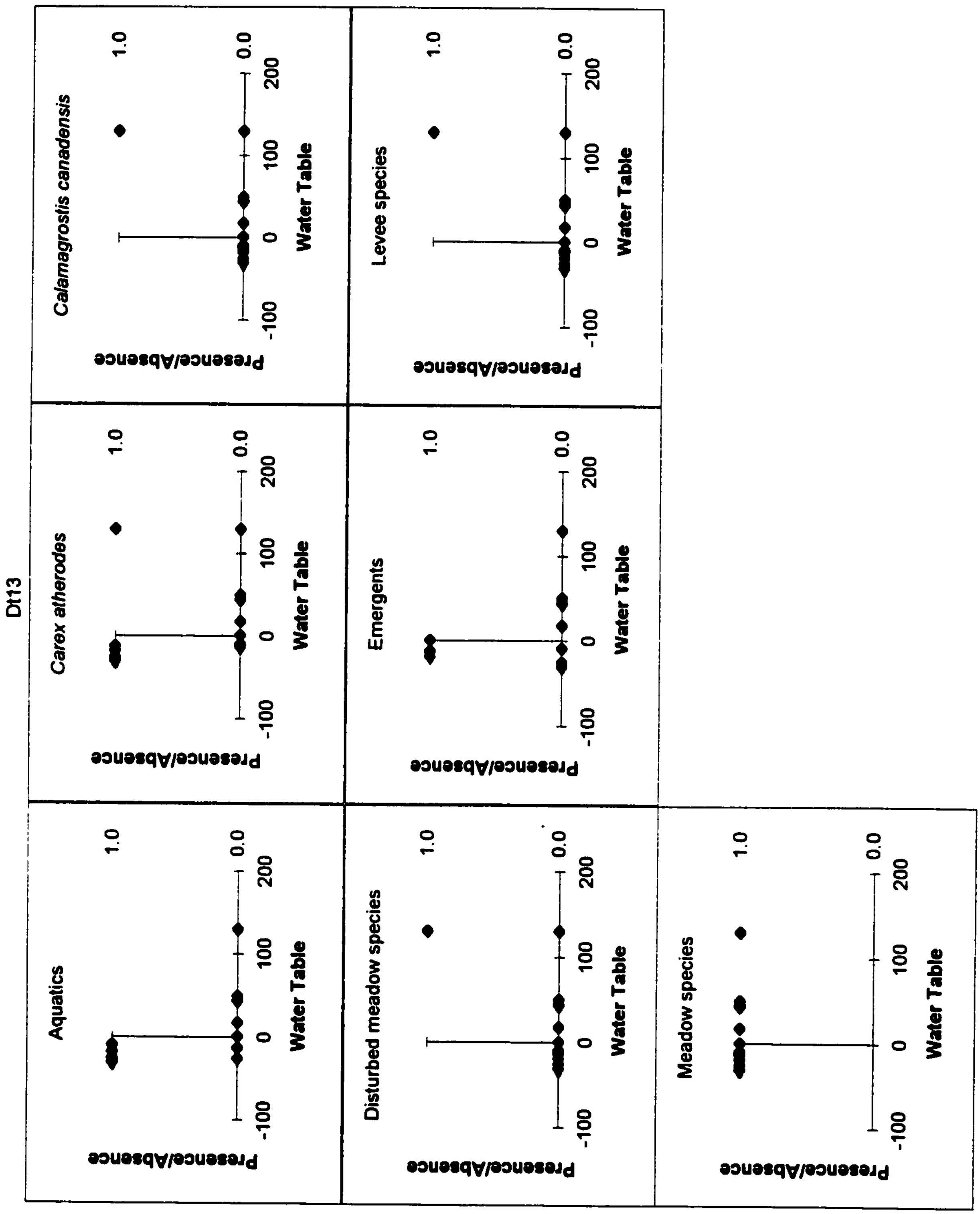
Dt08
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
-50
0
50
100
0.0
1.0


Dt09
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
0
50
100
150
0.0
1.0

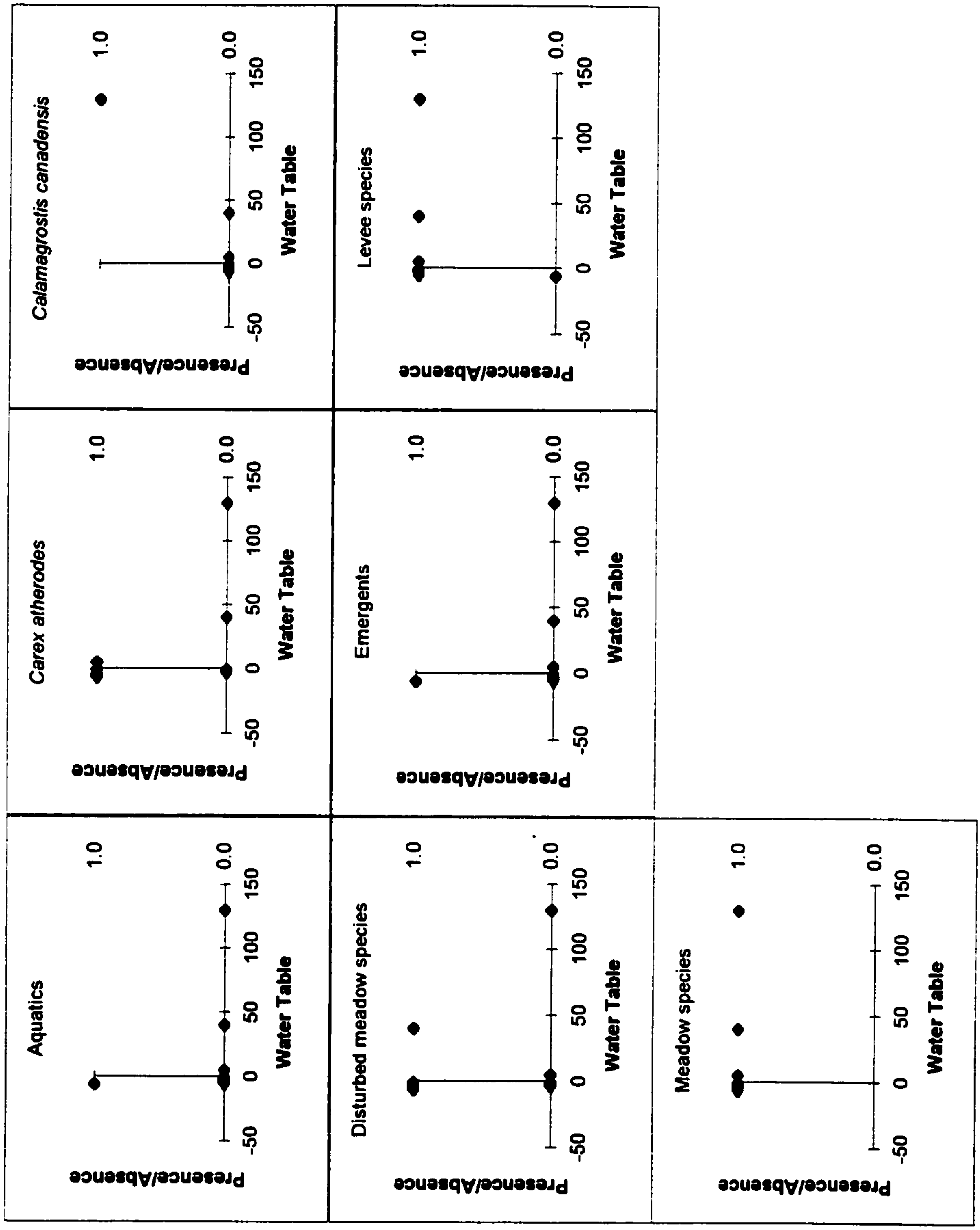
Dt10

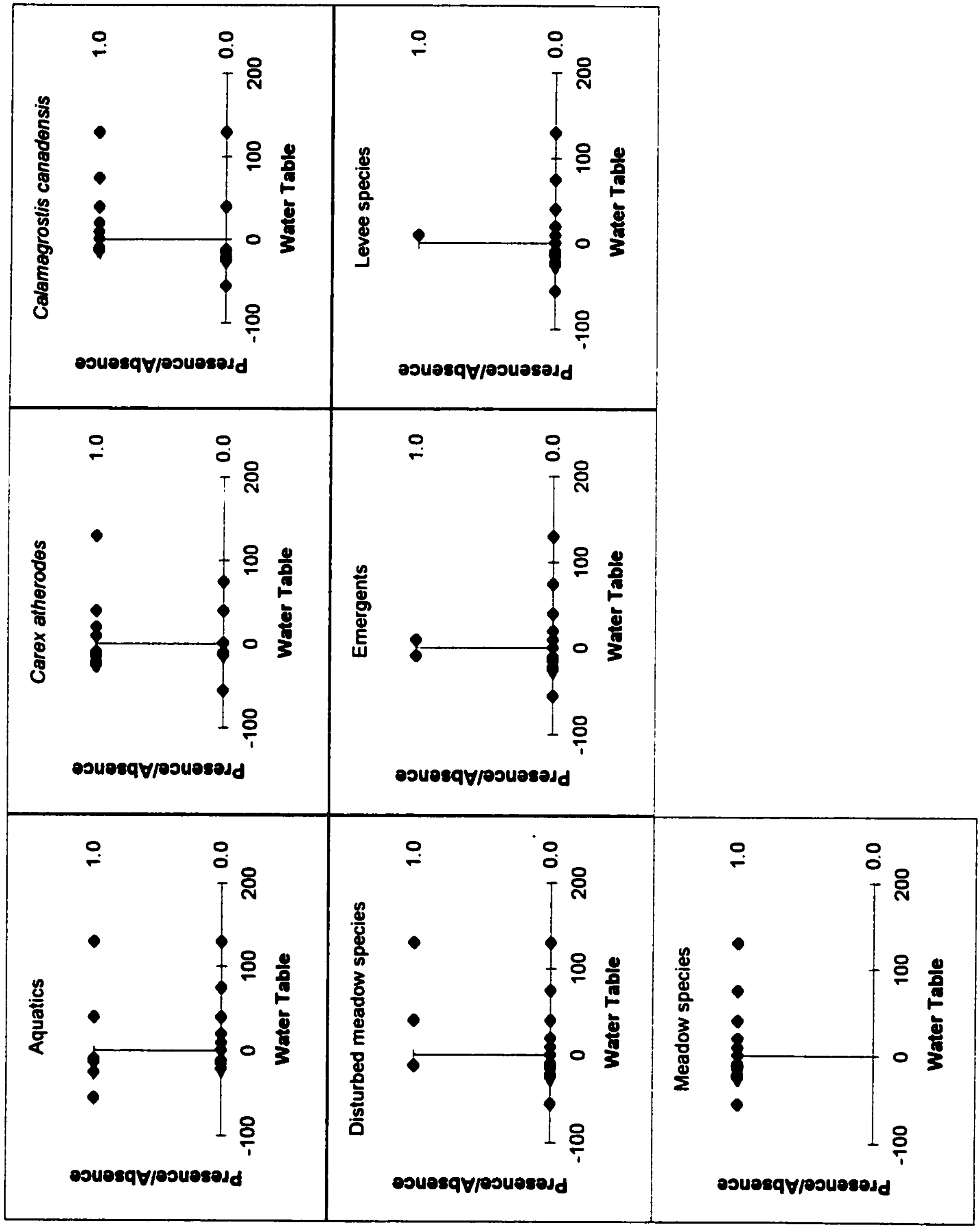

Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
-50
0
50
100
150
0.0
1.0


Dt11
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50
100
150


Dt13
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-100
0
100
200

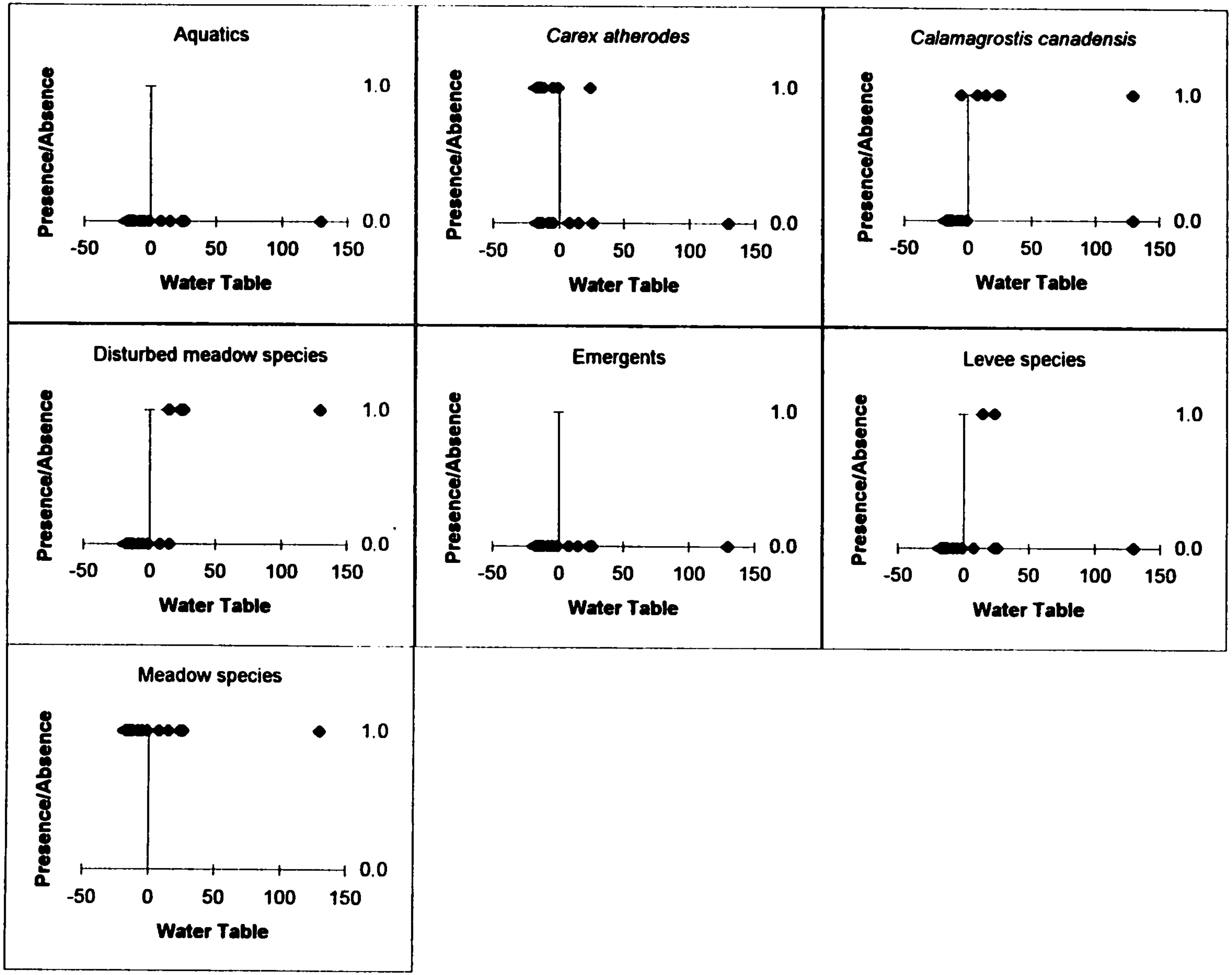
Dt14


Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50
100
150

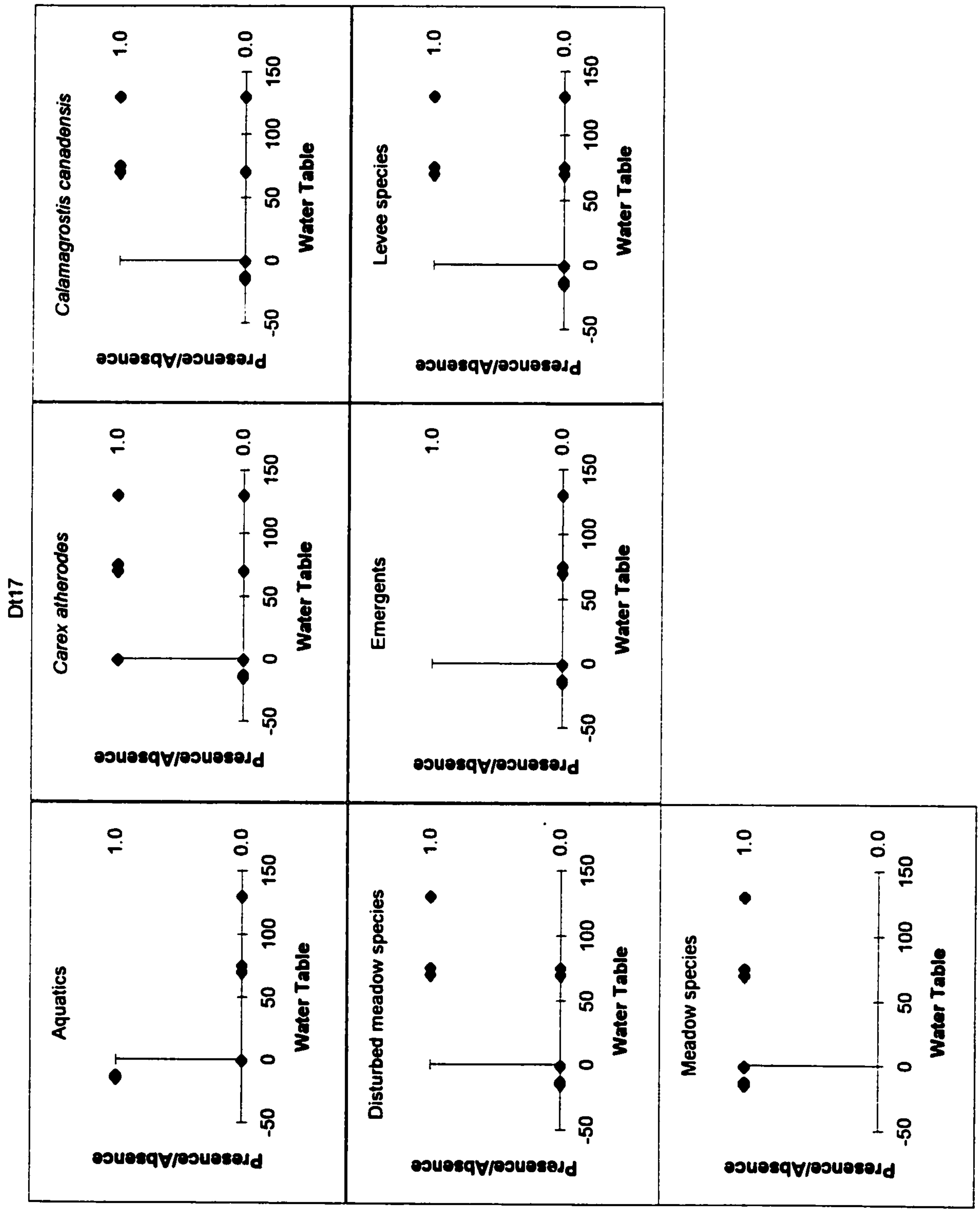


Dt15
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
1.0
0.0
Water Table
-100
0
100
200

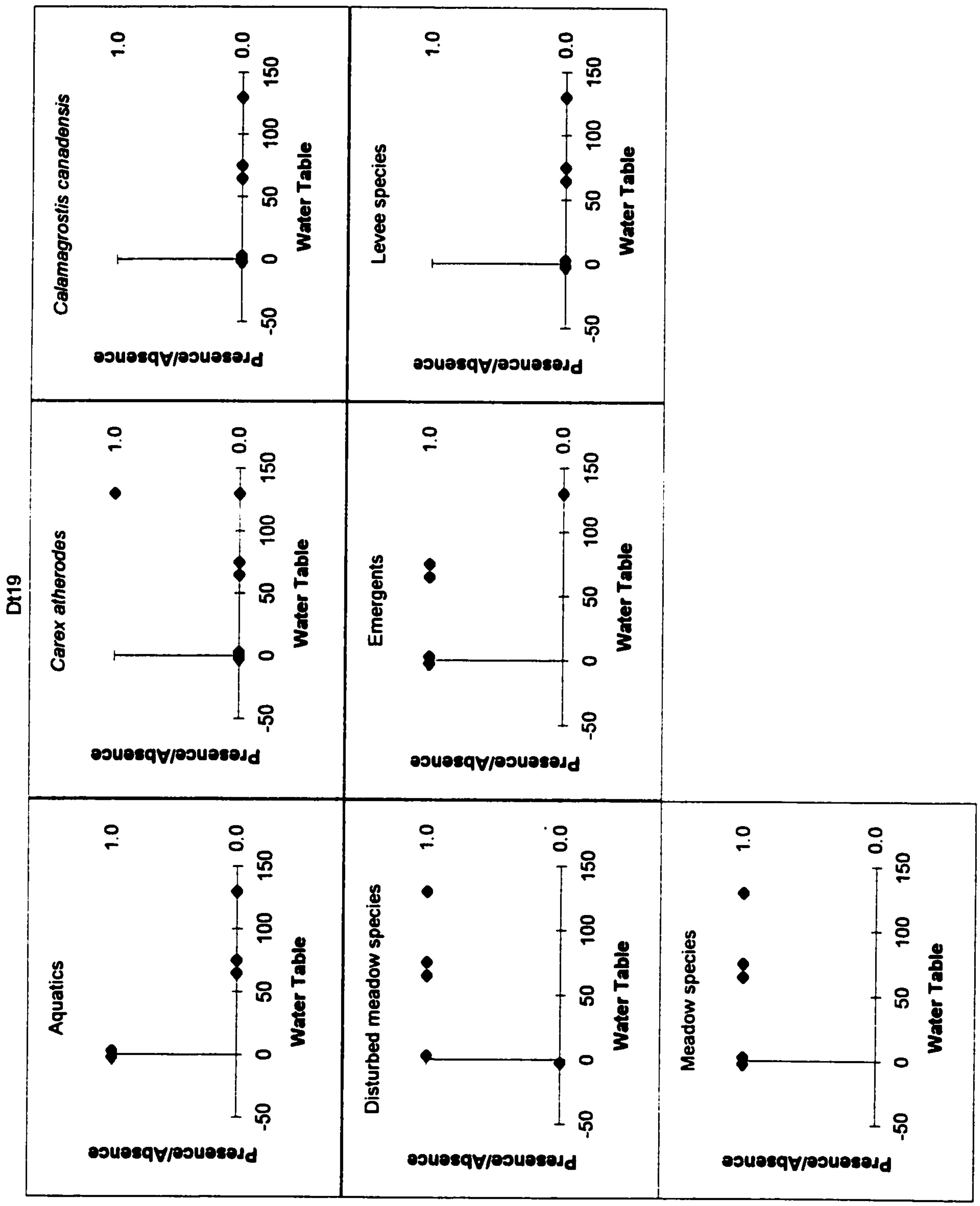
Dt16



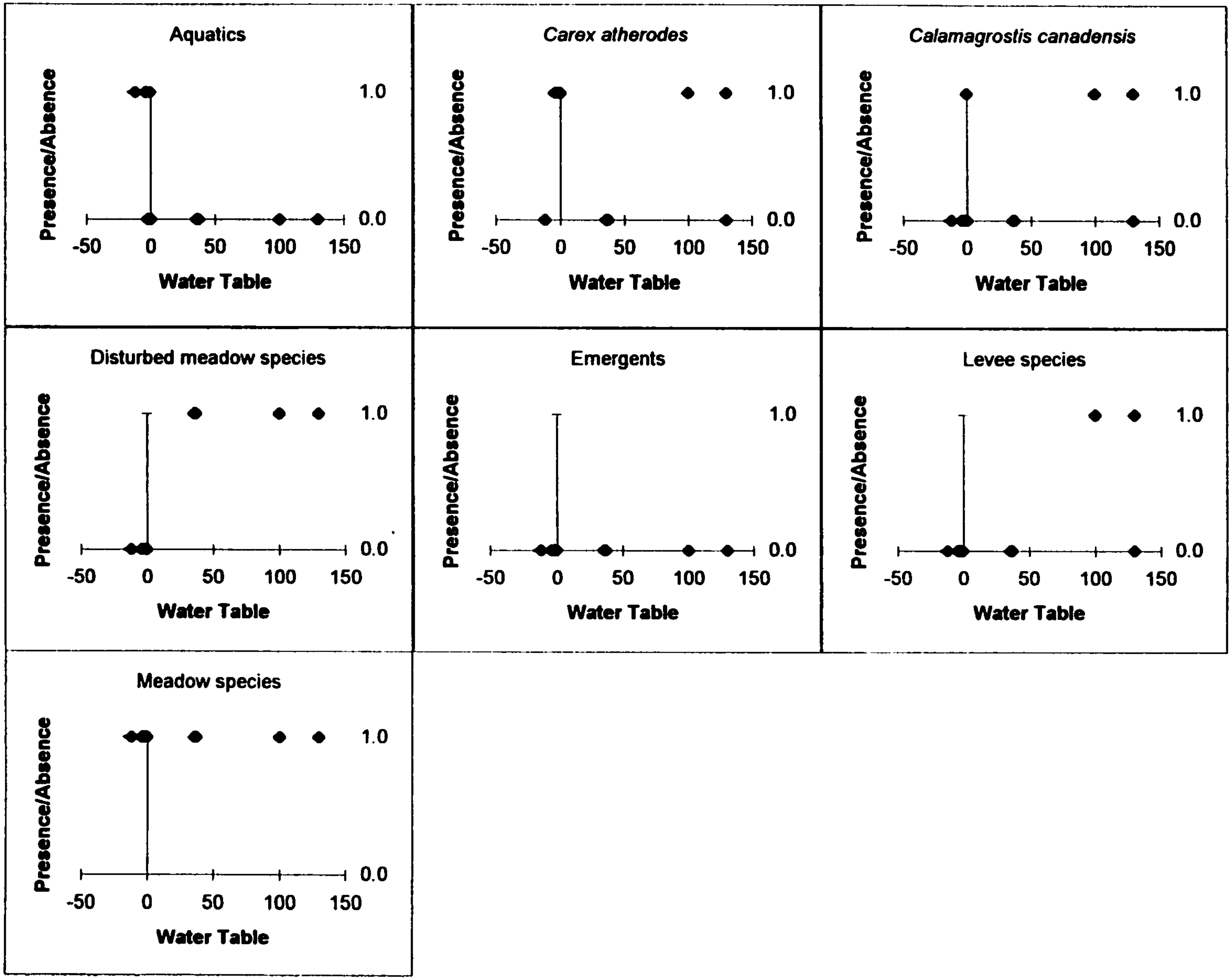
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50
100
150



Dt17
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50
100
150

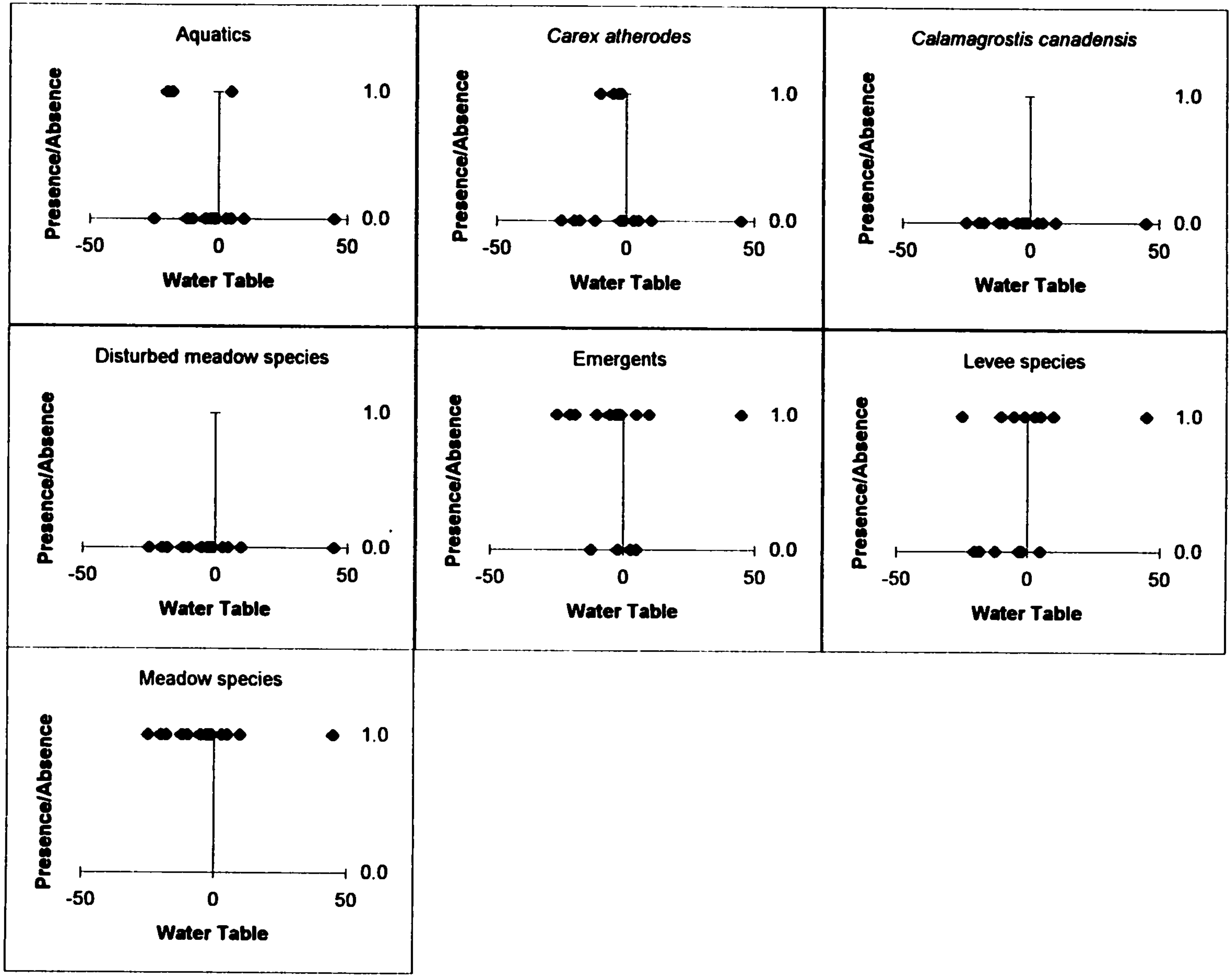

Dt19
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50
100
150

Dt20

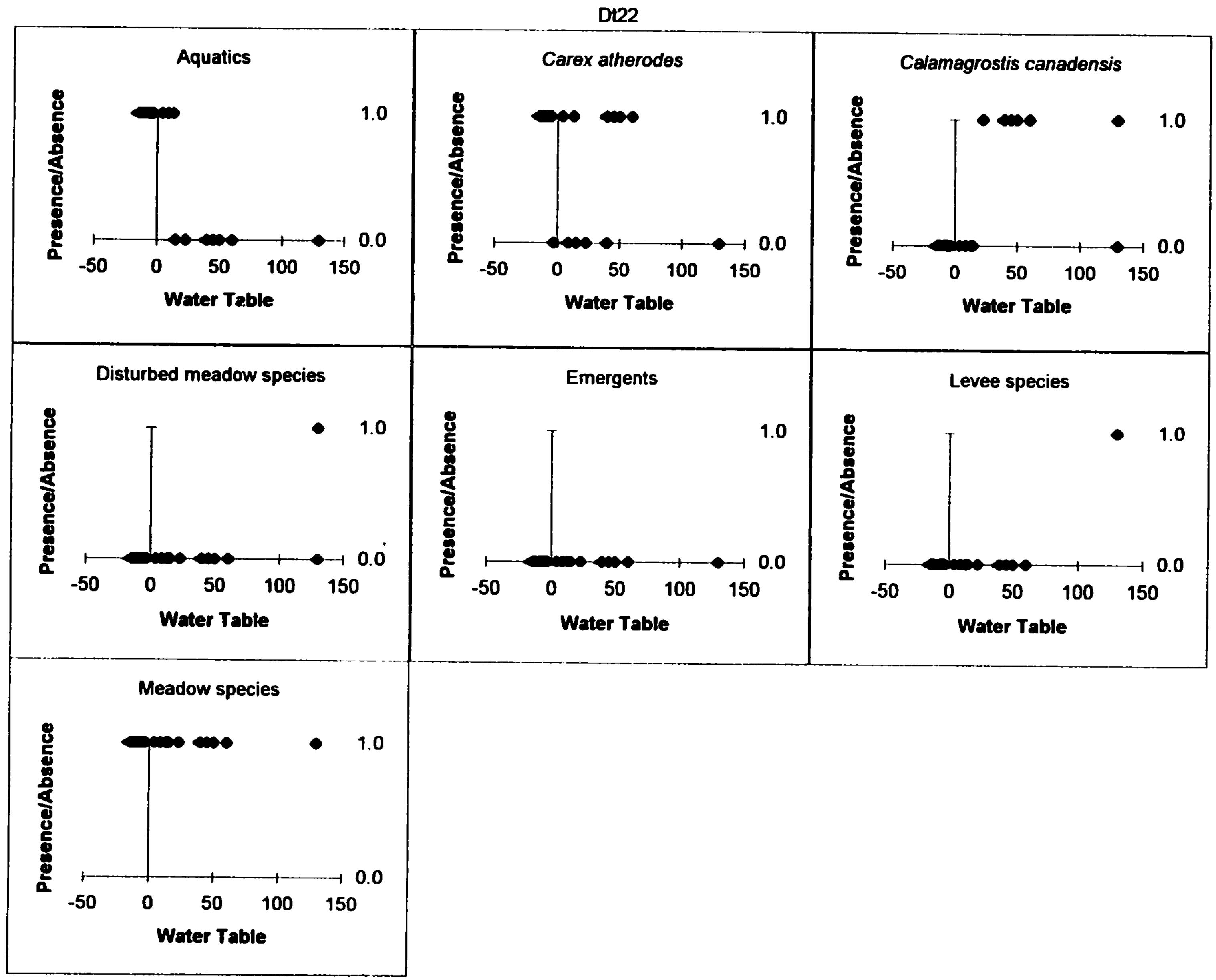


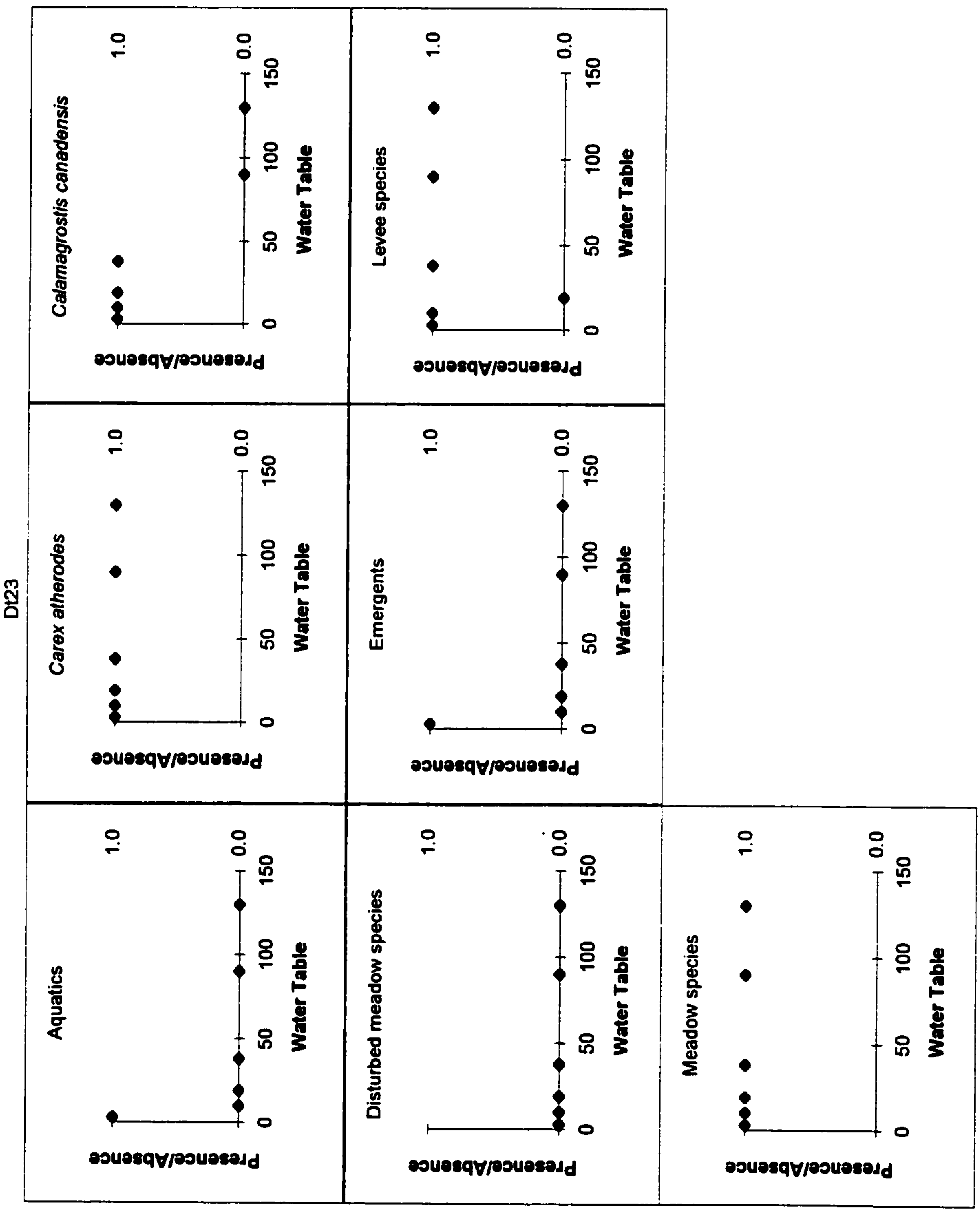
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50
100
150

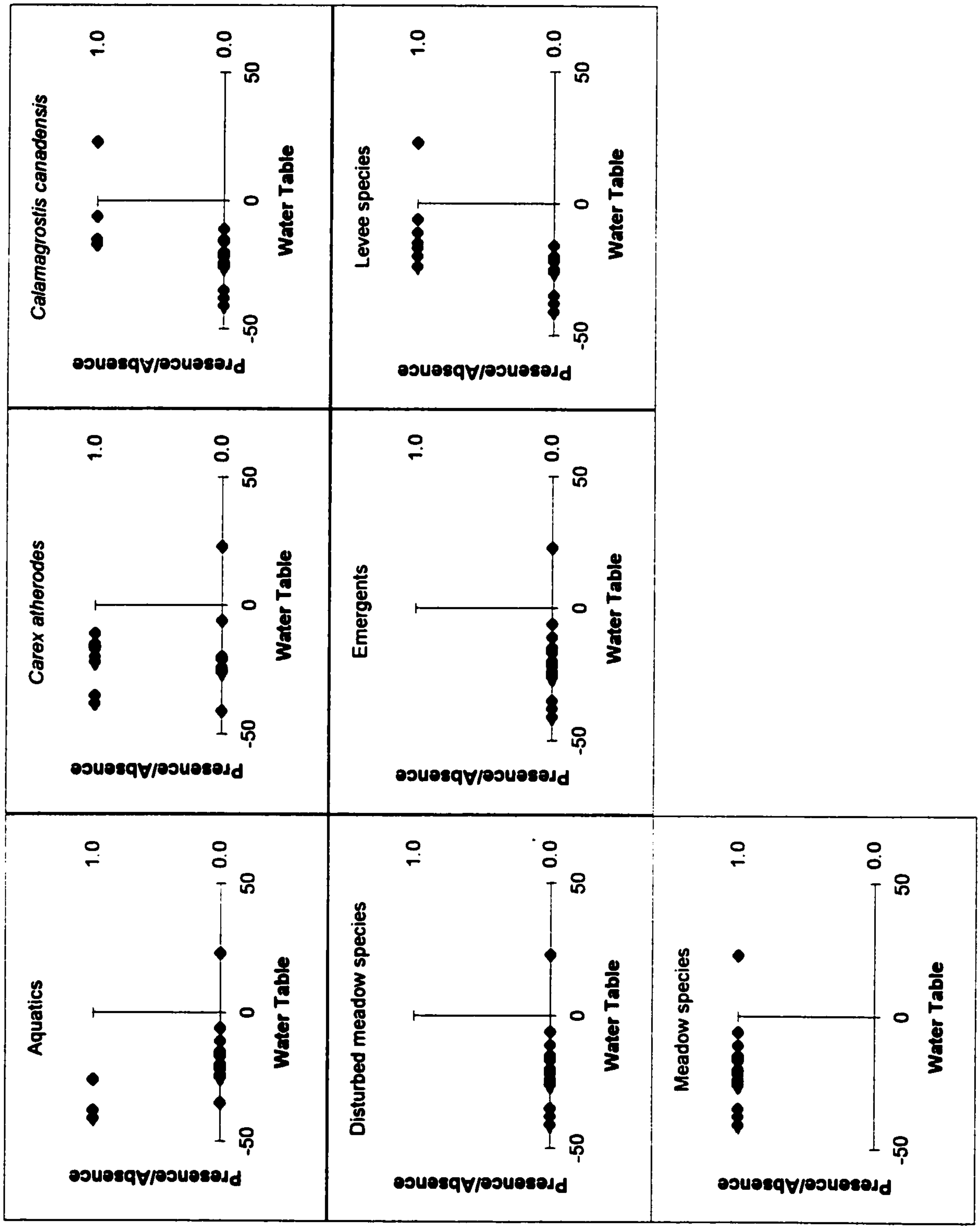
Dt21



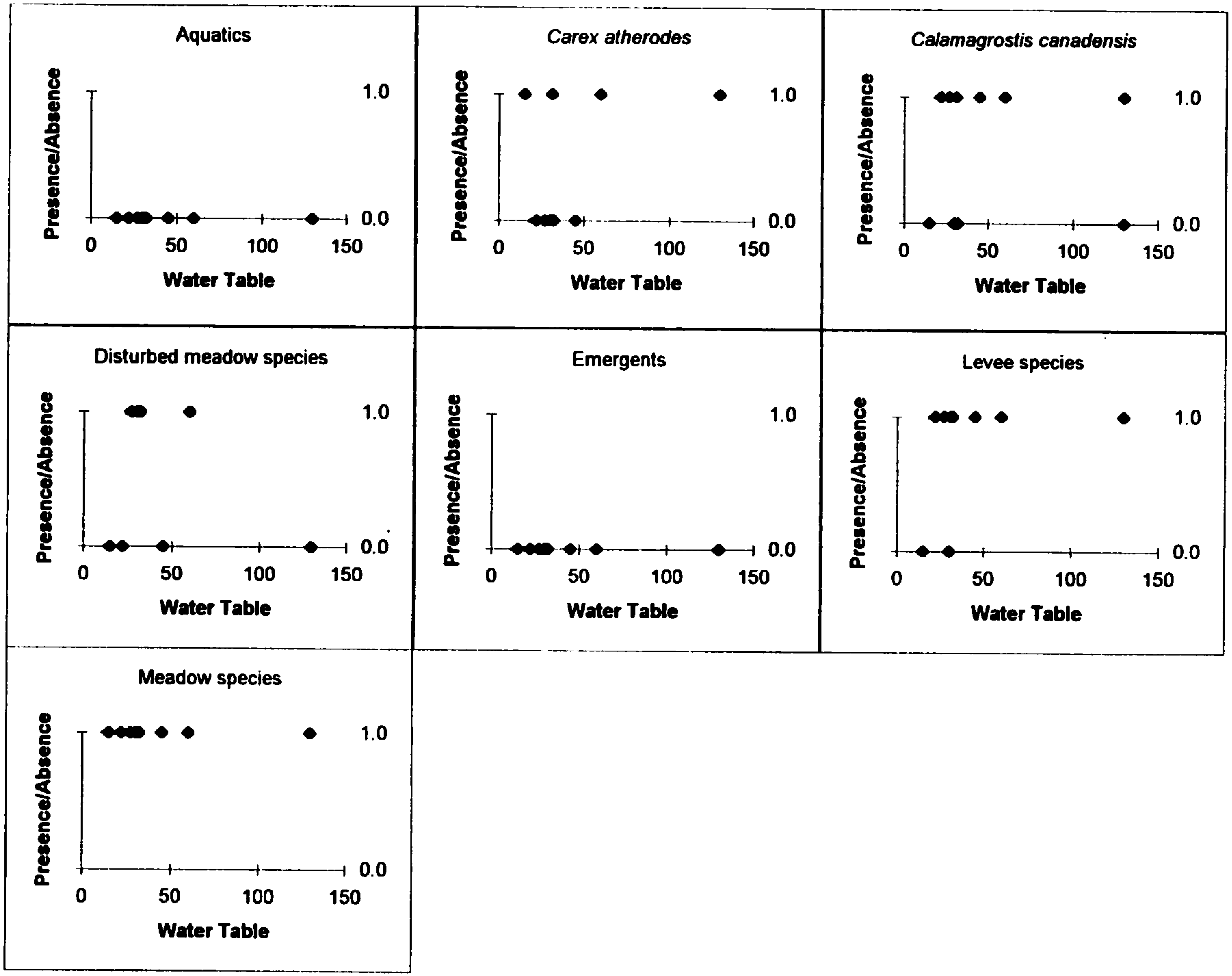
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50


Dt22
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50
100
150

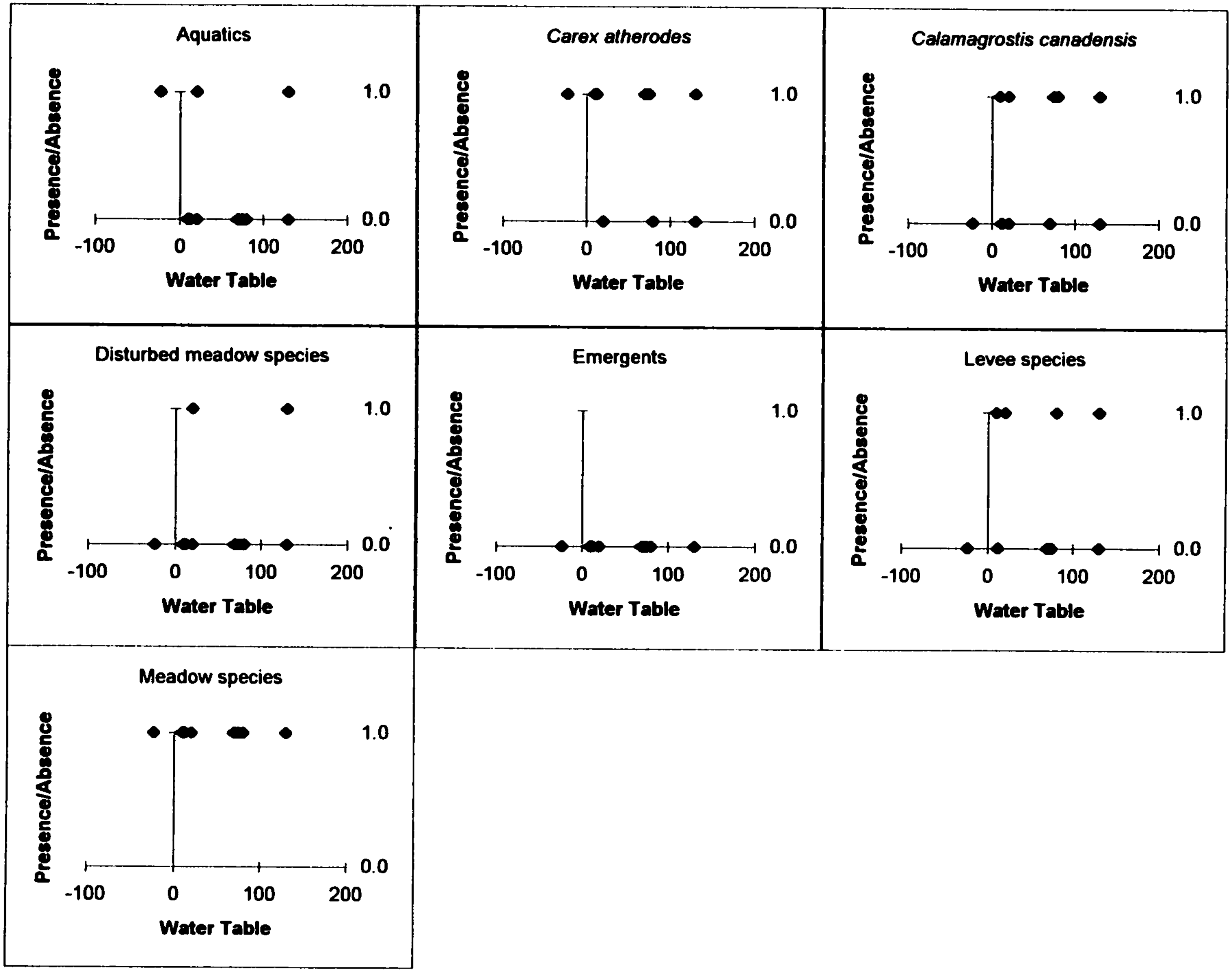

Dt23
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
1.0
0.0
0
50
100
150


Dt24
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-50
0
50

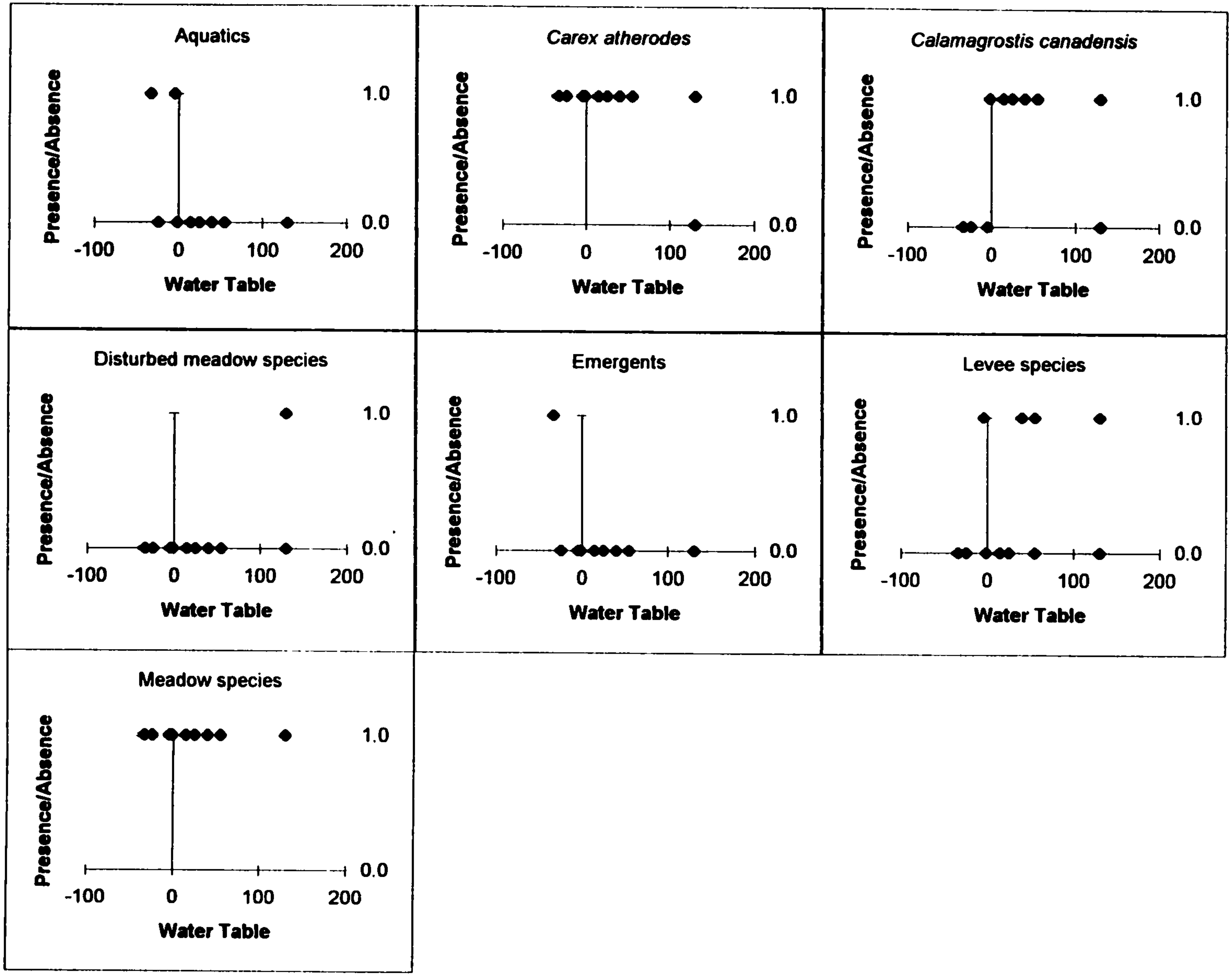
Dt25

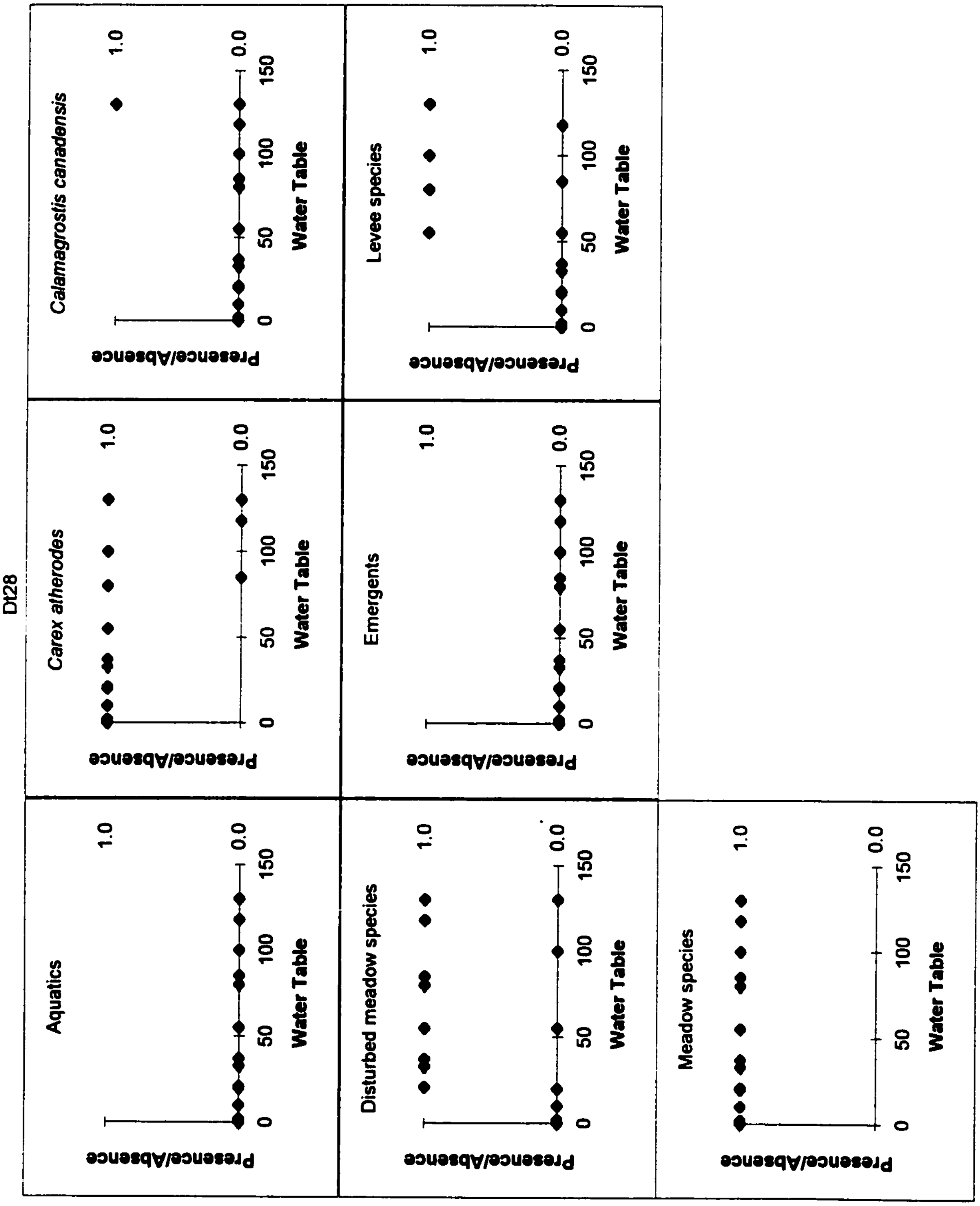

Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
0
50
100
150
0.0
1.0

Dt26

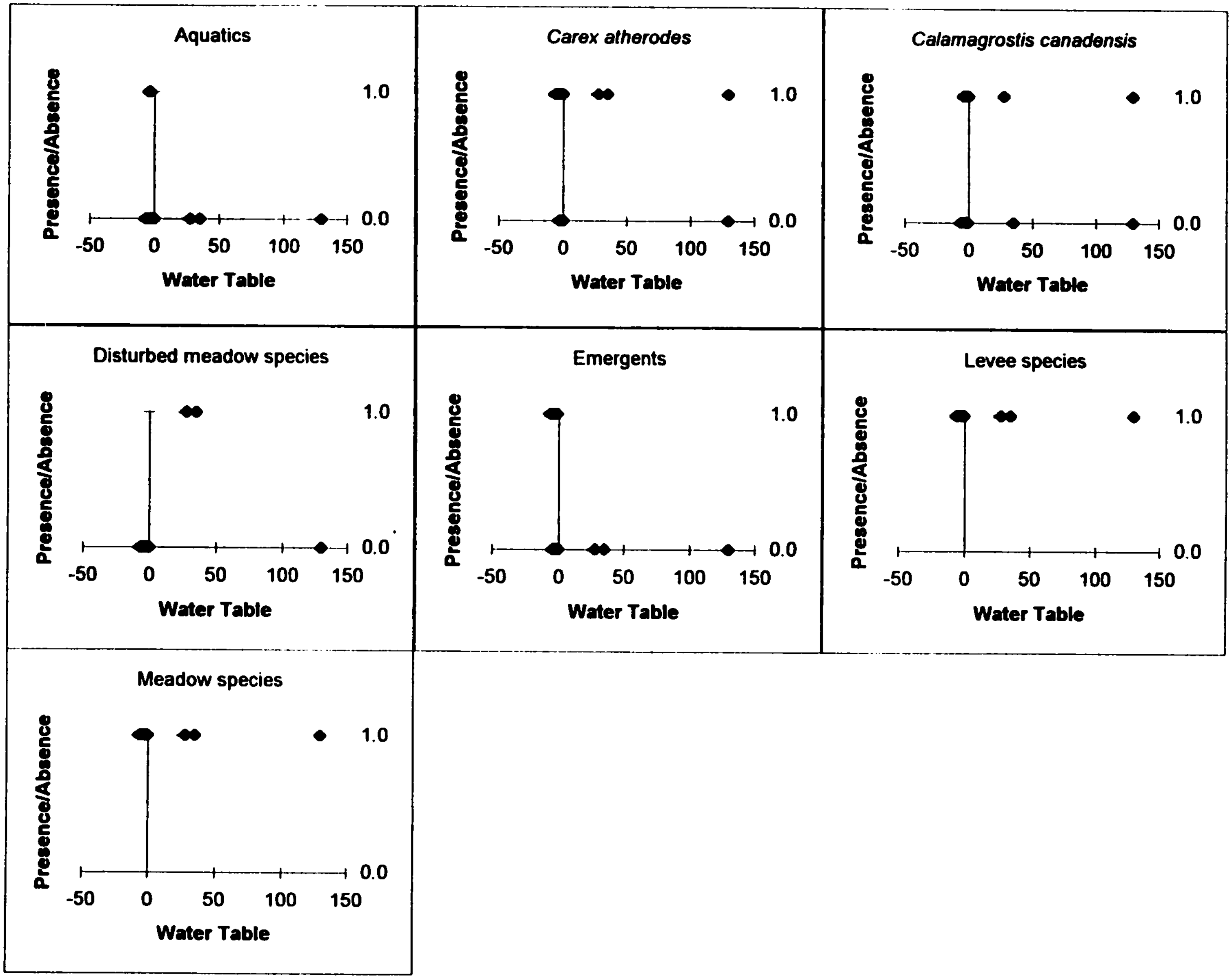

Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
-100
0
100
200
0.0
1.0

Dt27

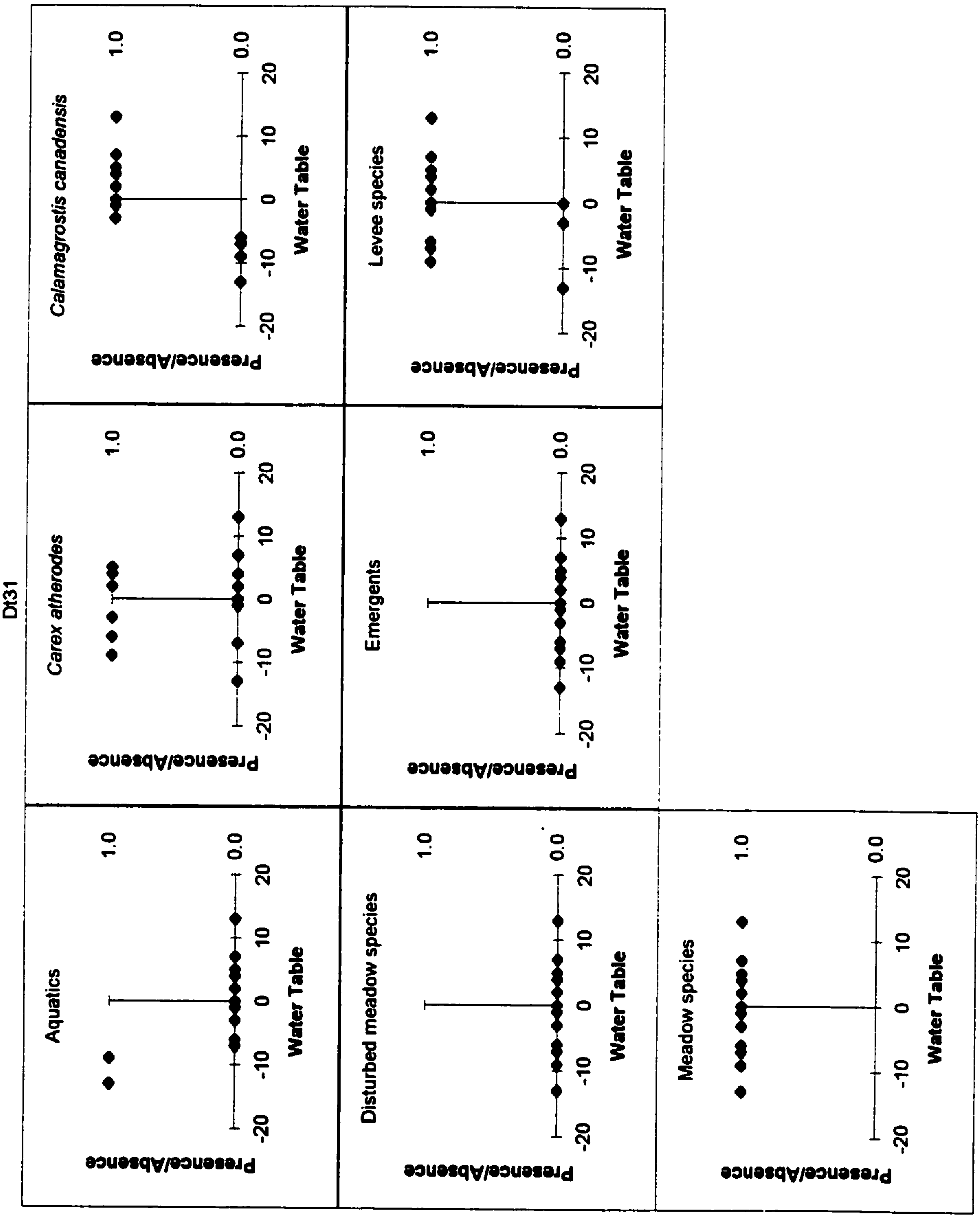

Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-100
0
100
200


Dt28
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Water Table
0
50
100
150
0.0
1.0

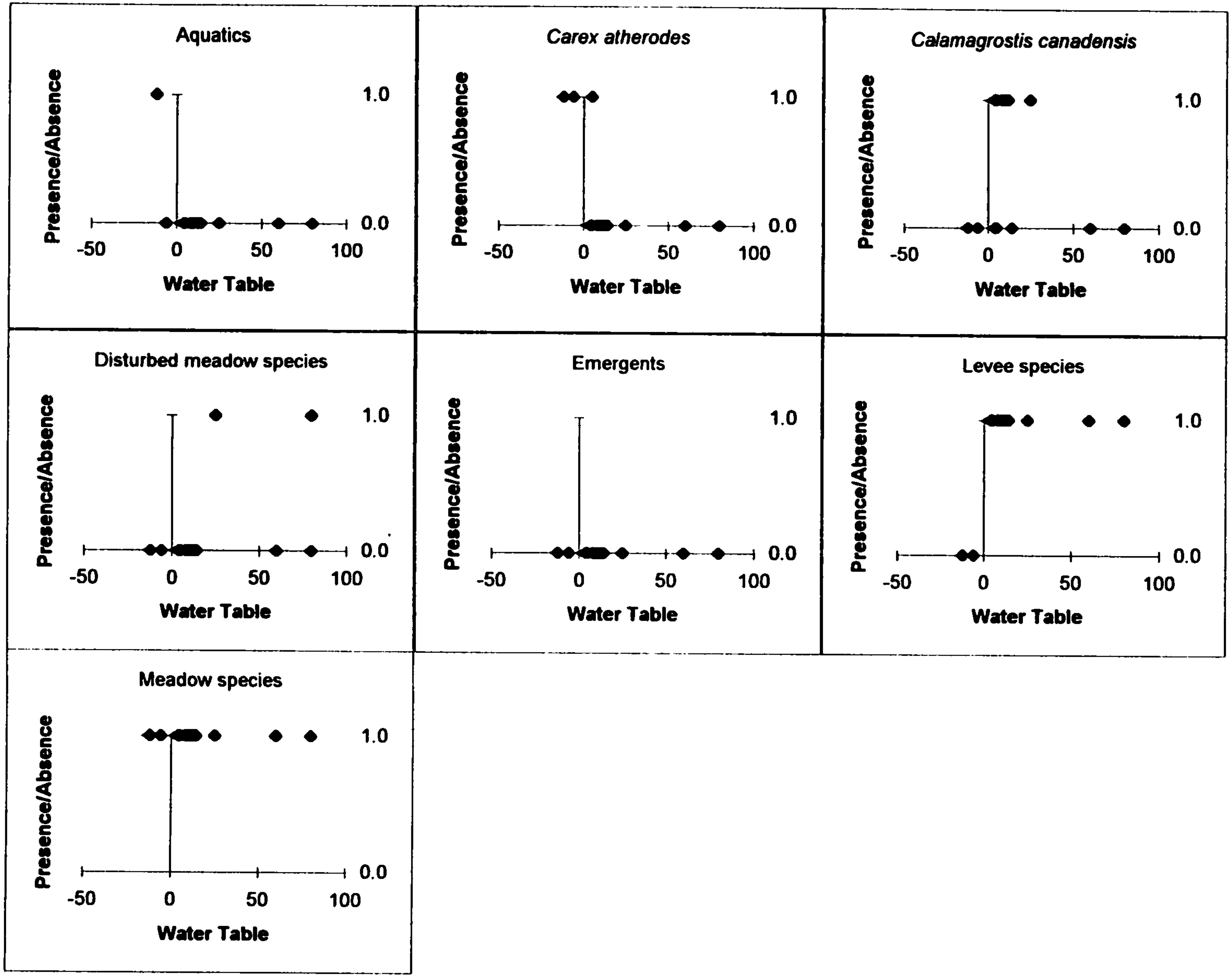
Dt29

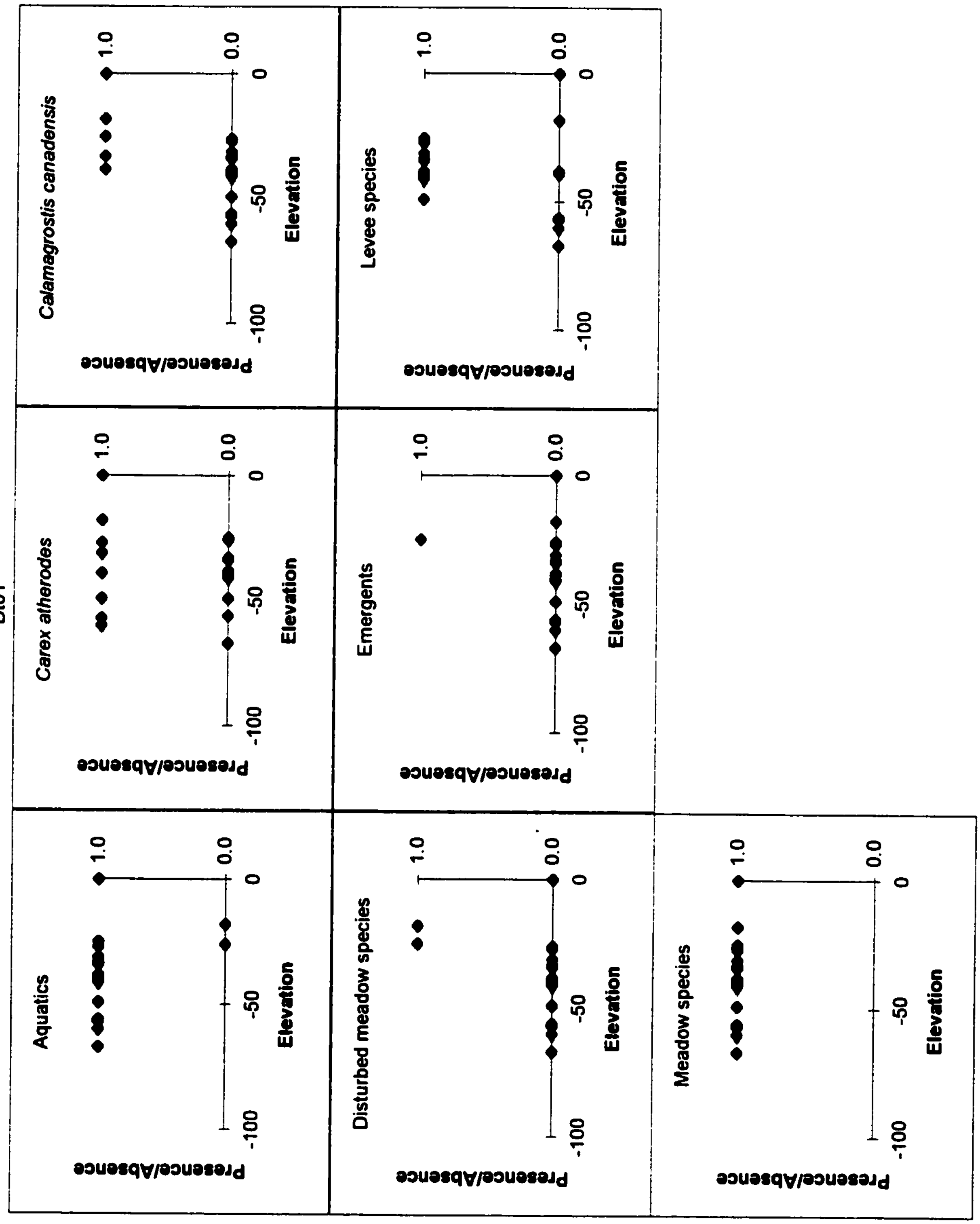


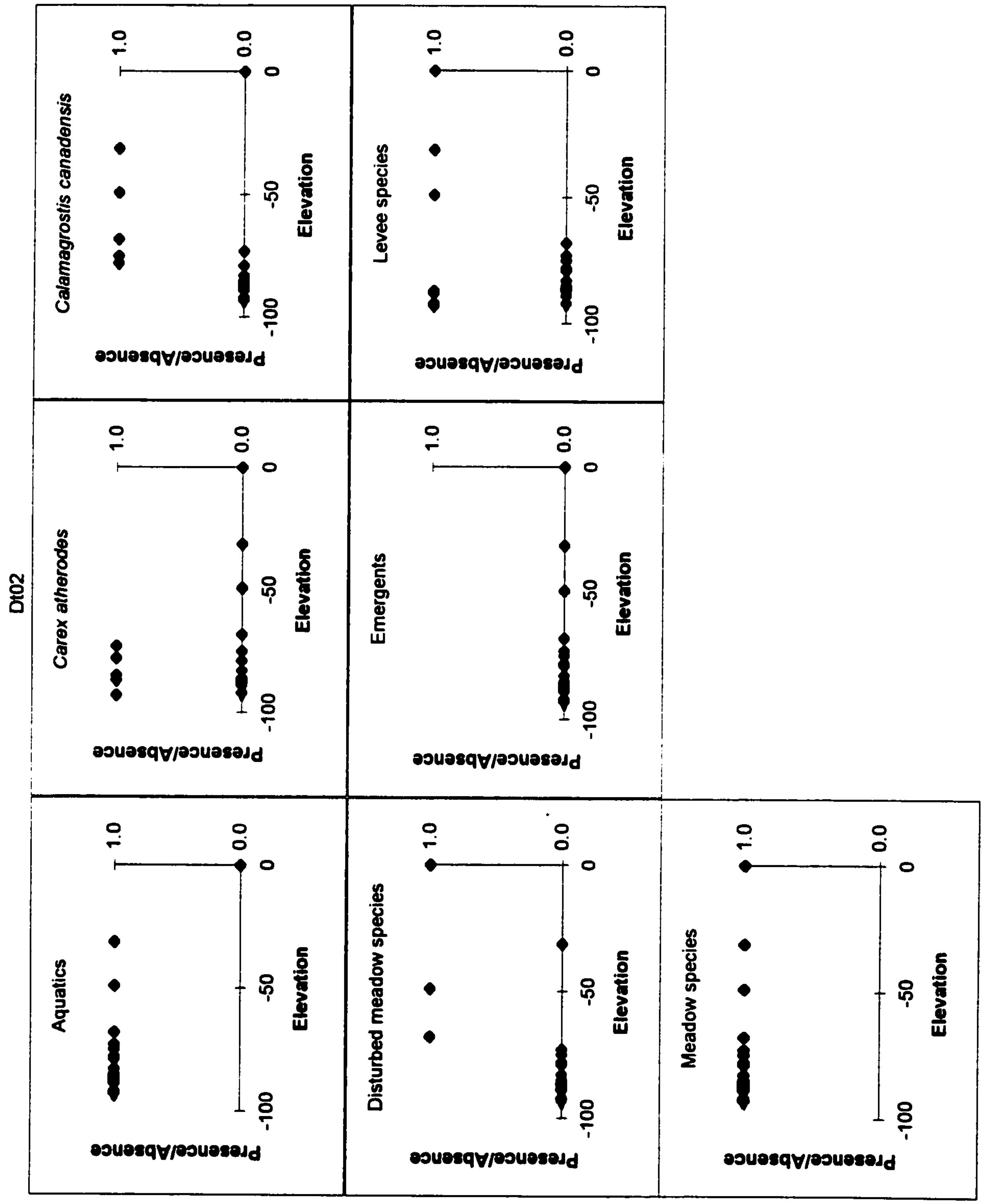
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
1.0
0.0
-50
0
50
100
150
Water Table


Dt31
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Water Table
1.0
0.0
-20
-10
0
10
20

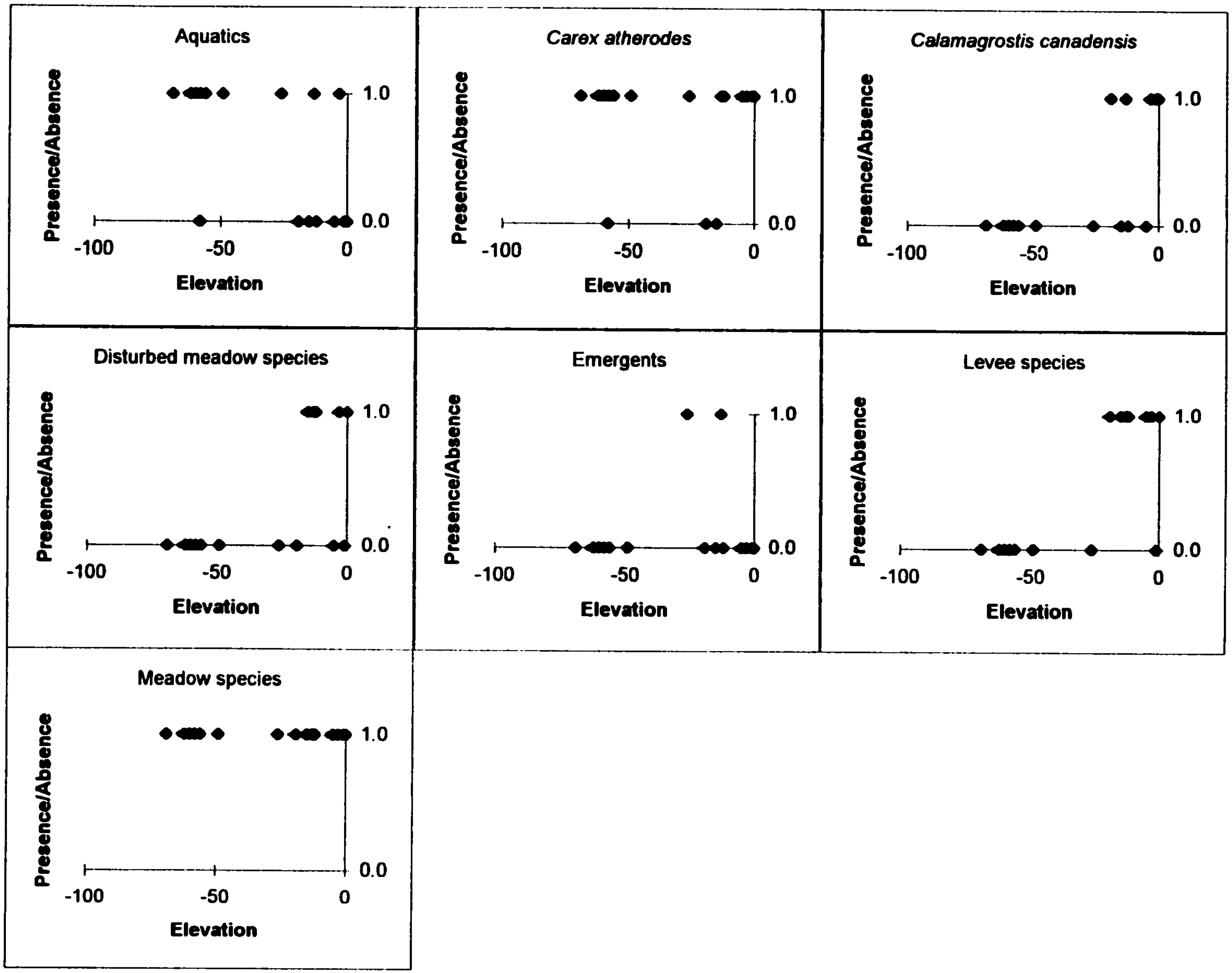
Dt32

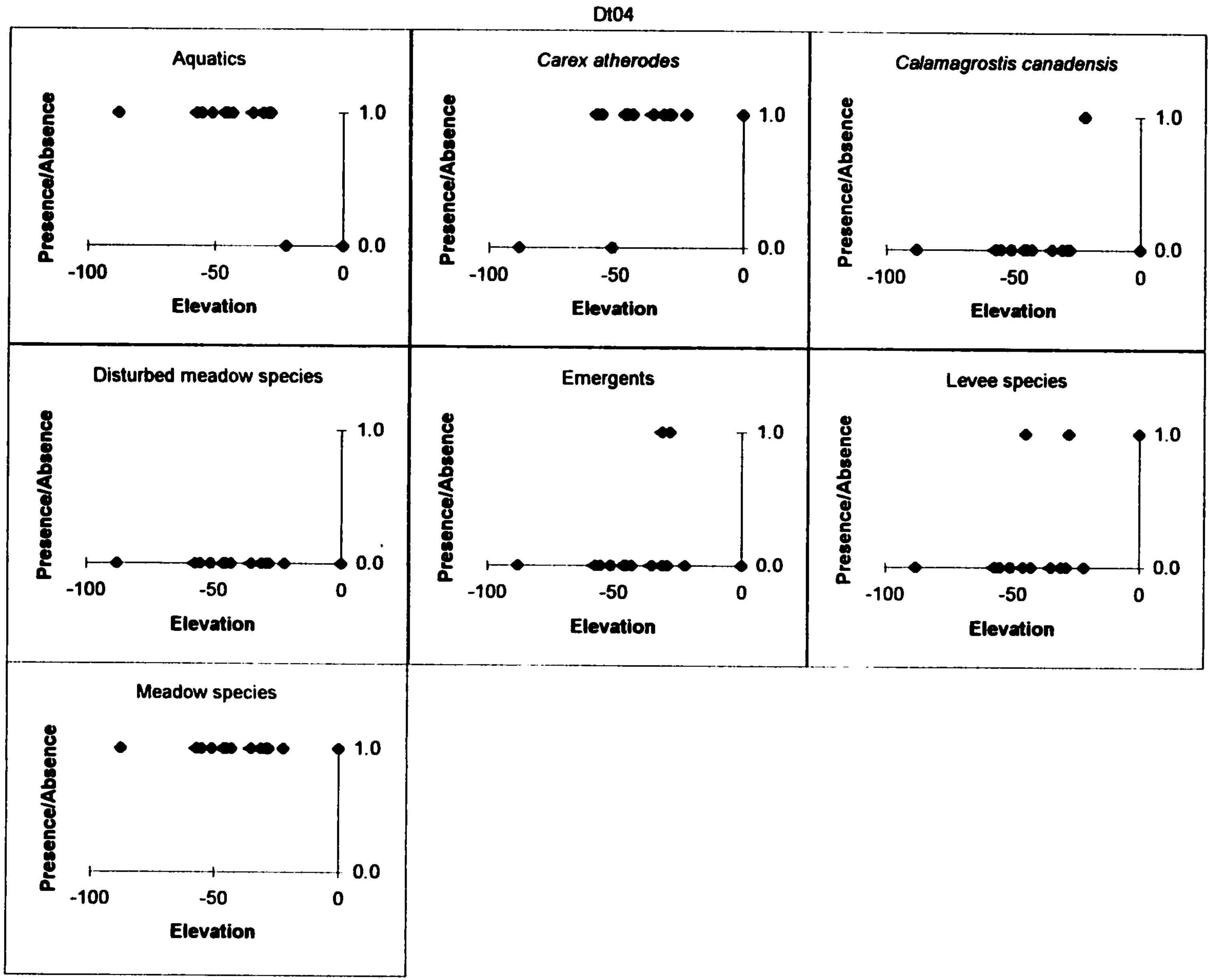

Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
1.0
0.0
-50
0
50
100
Water Table


Dt01
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
1.0
0.0
Elevation
-100
-50
0

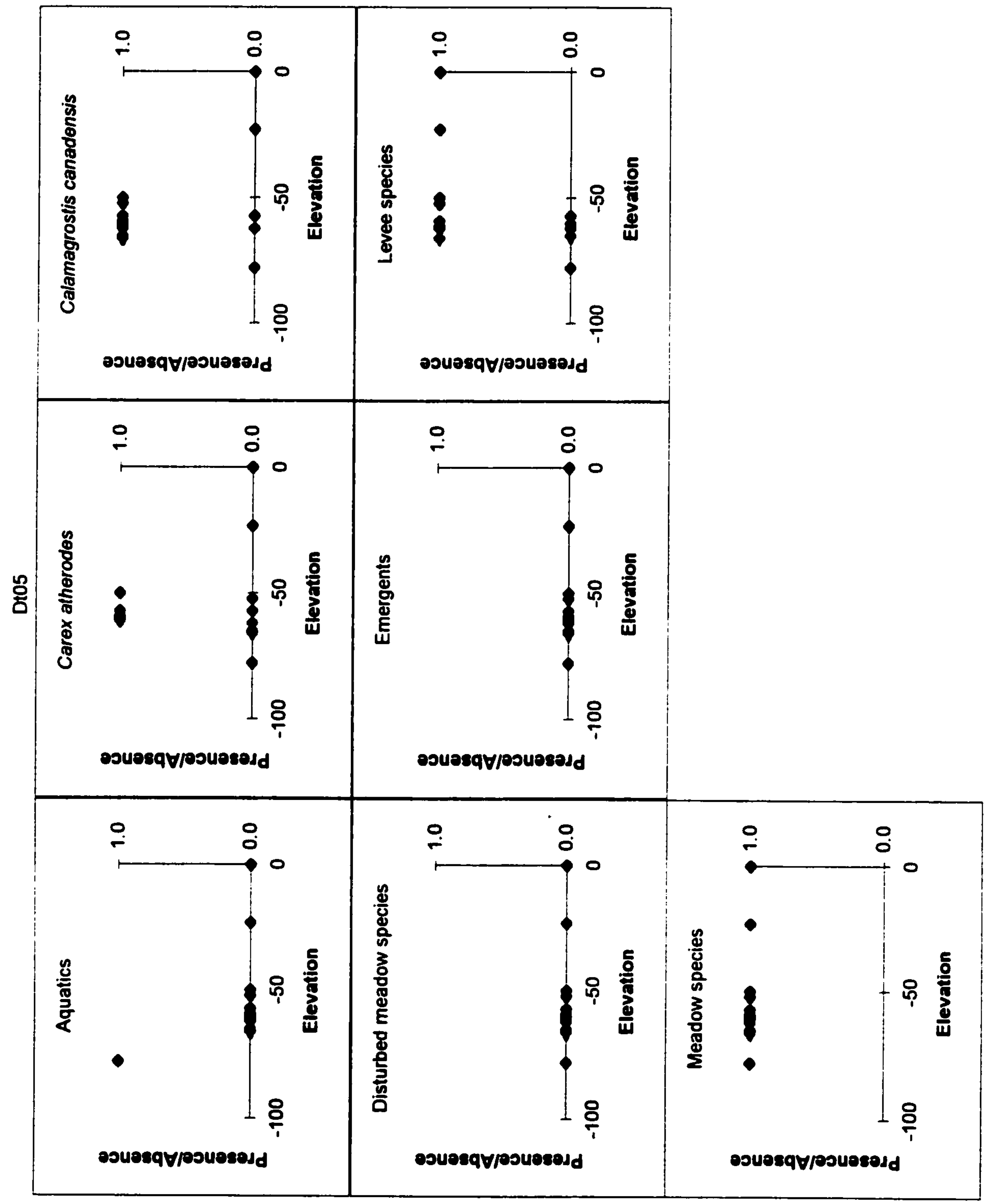

Dt02
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
0
-50
-100

Dt03

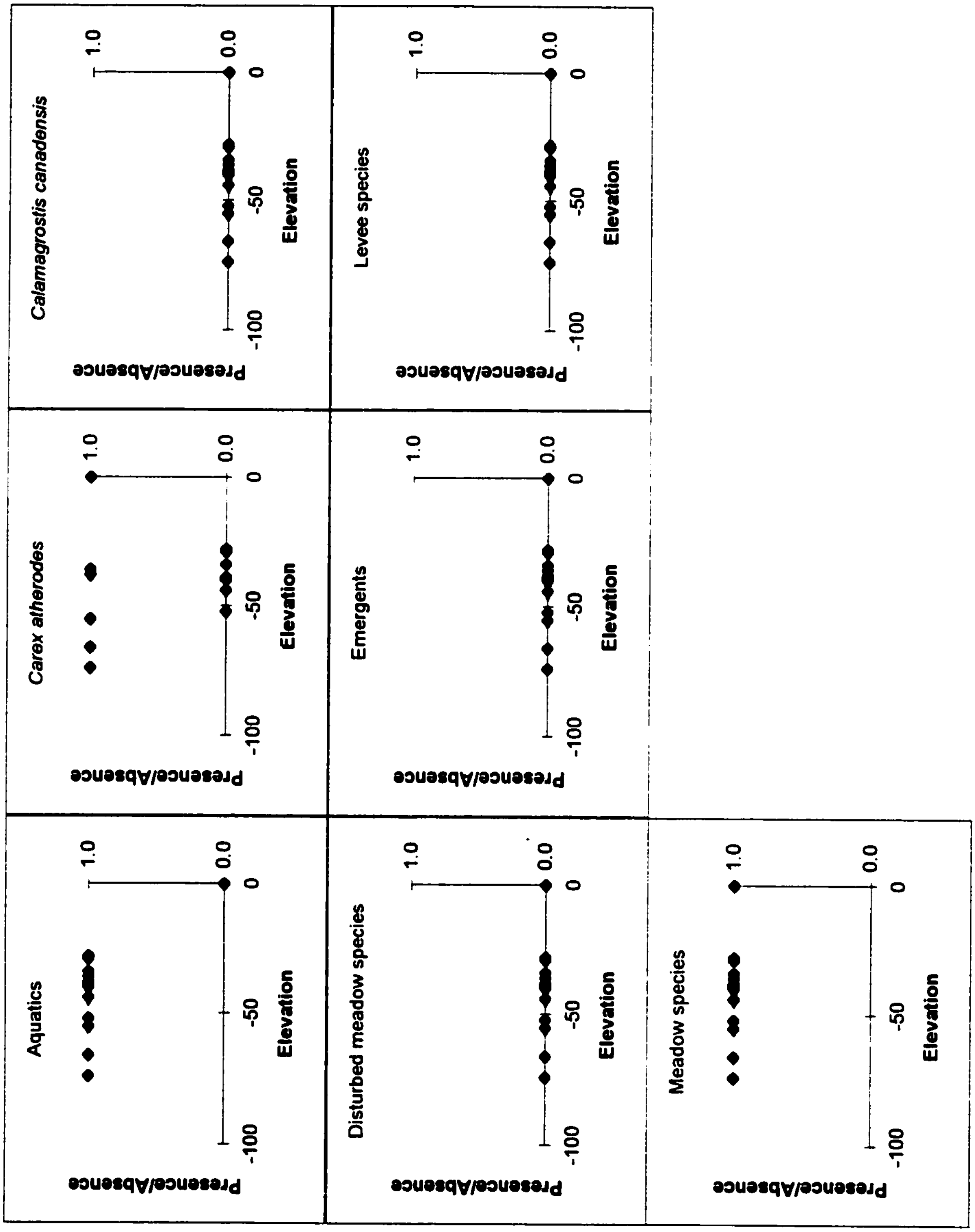

Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-100
-50
0

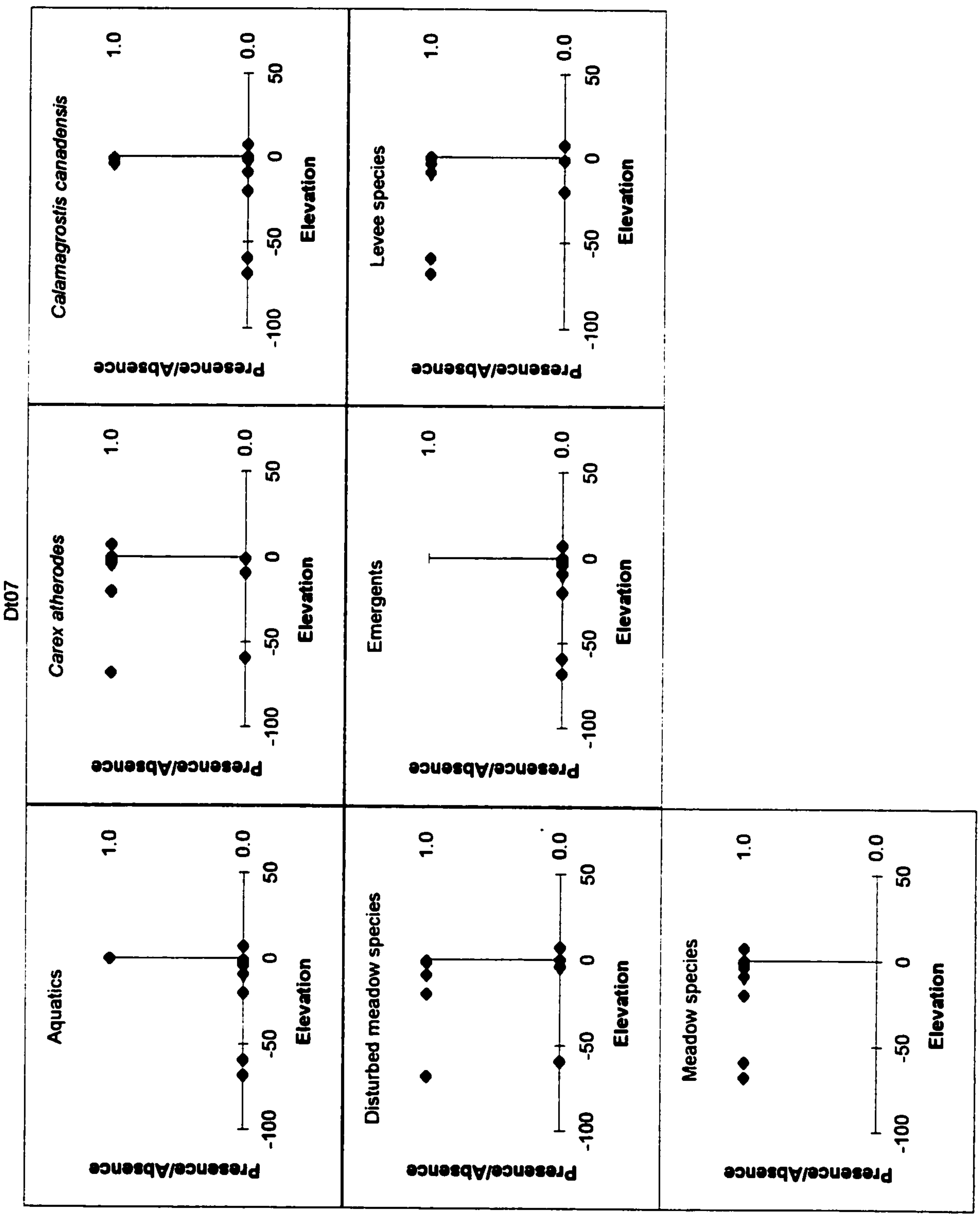


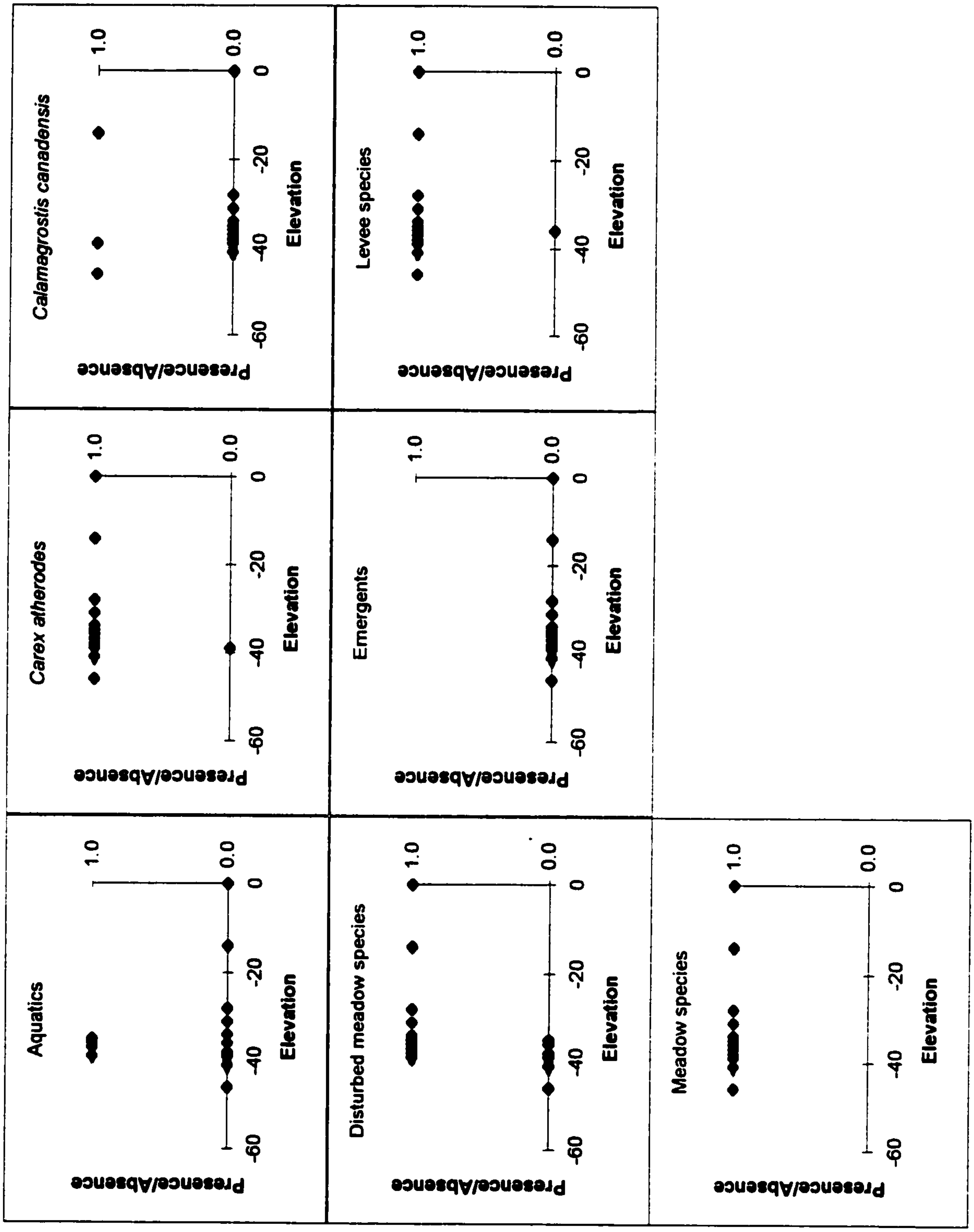
Dt04
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-100
-50
0



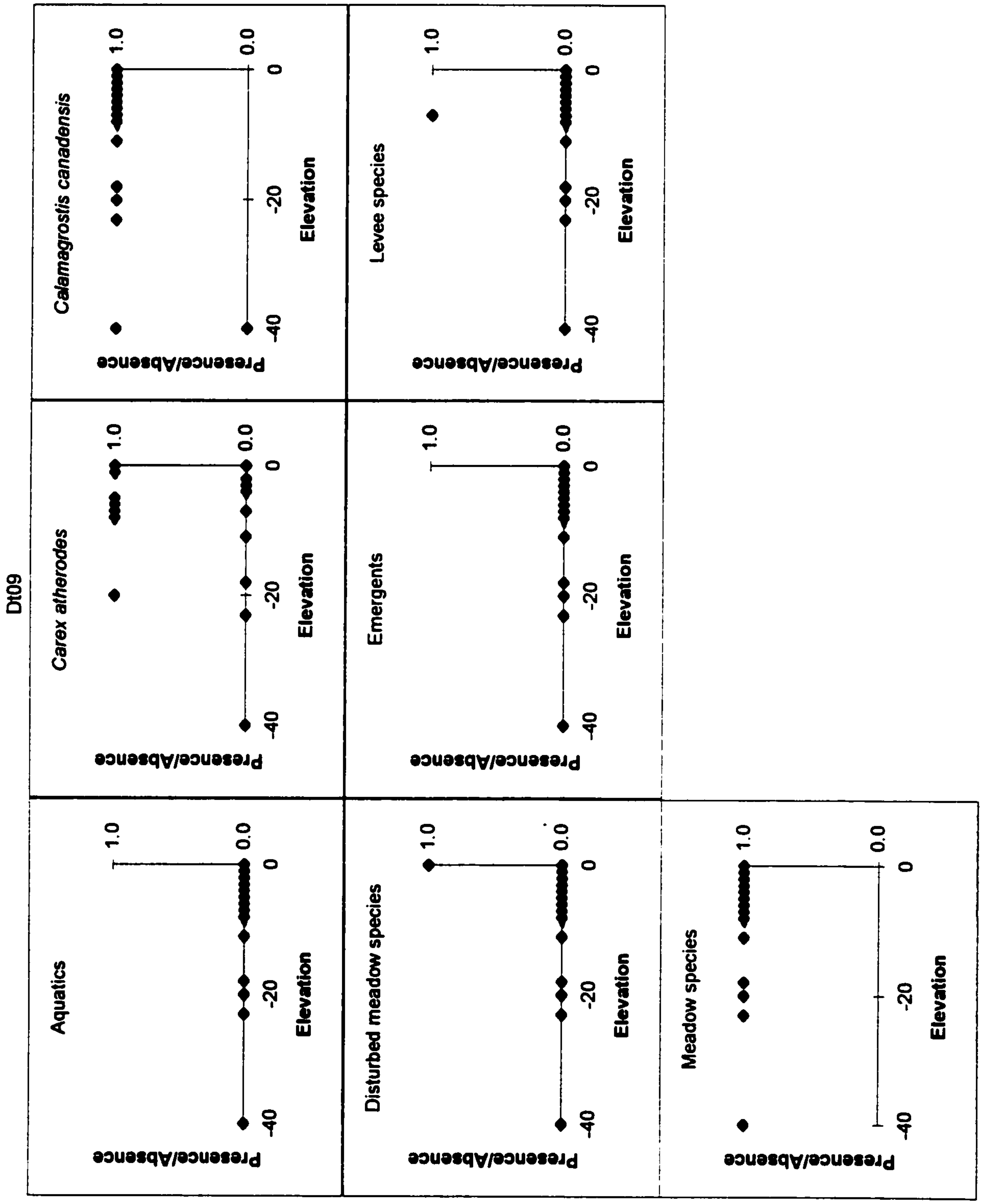
Dt05
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-100
-50
0

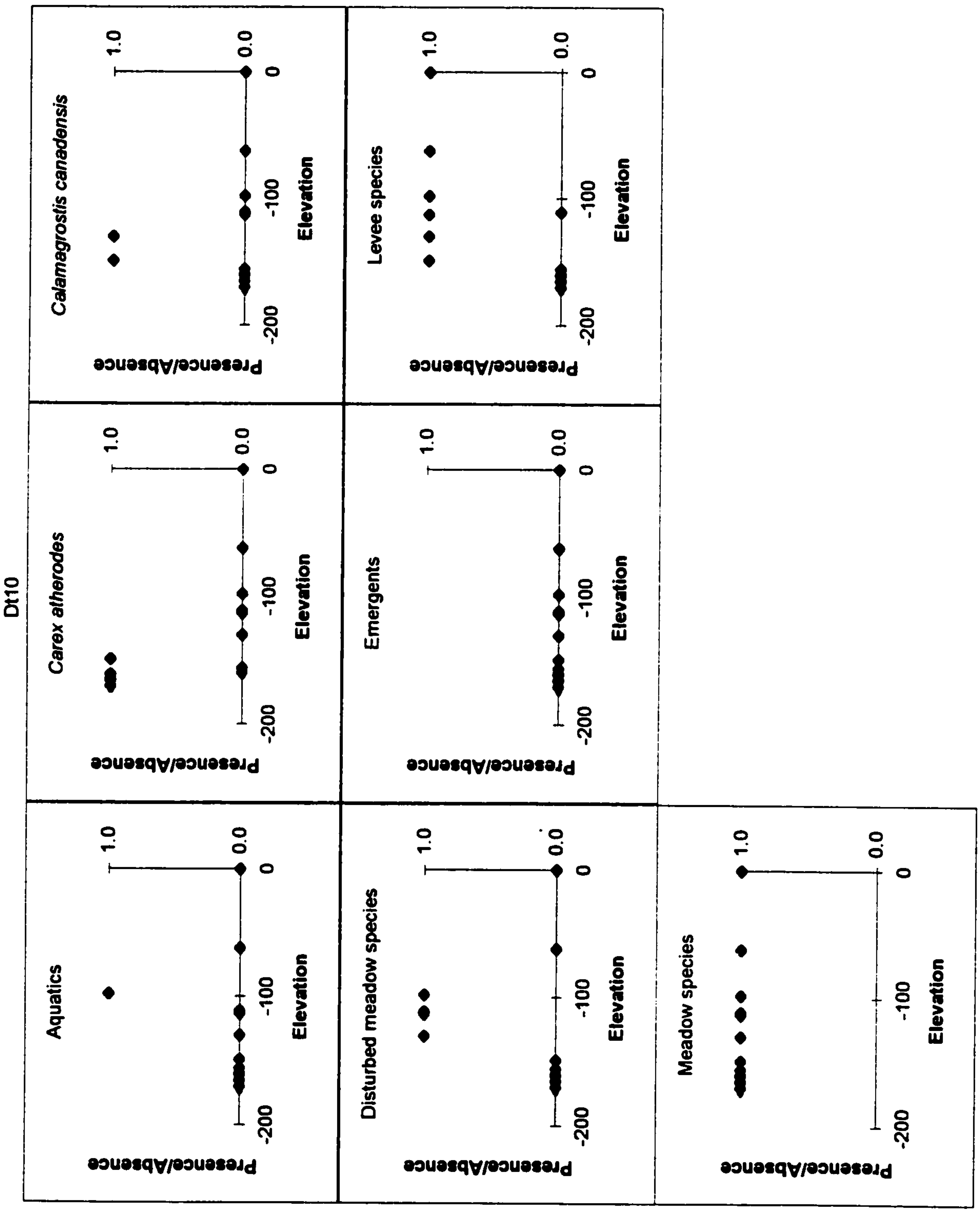

Dt06
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-100
-50
0

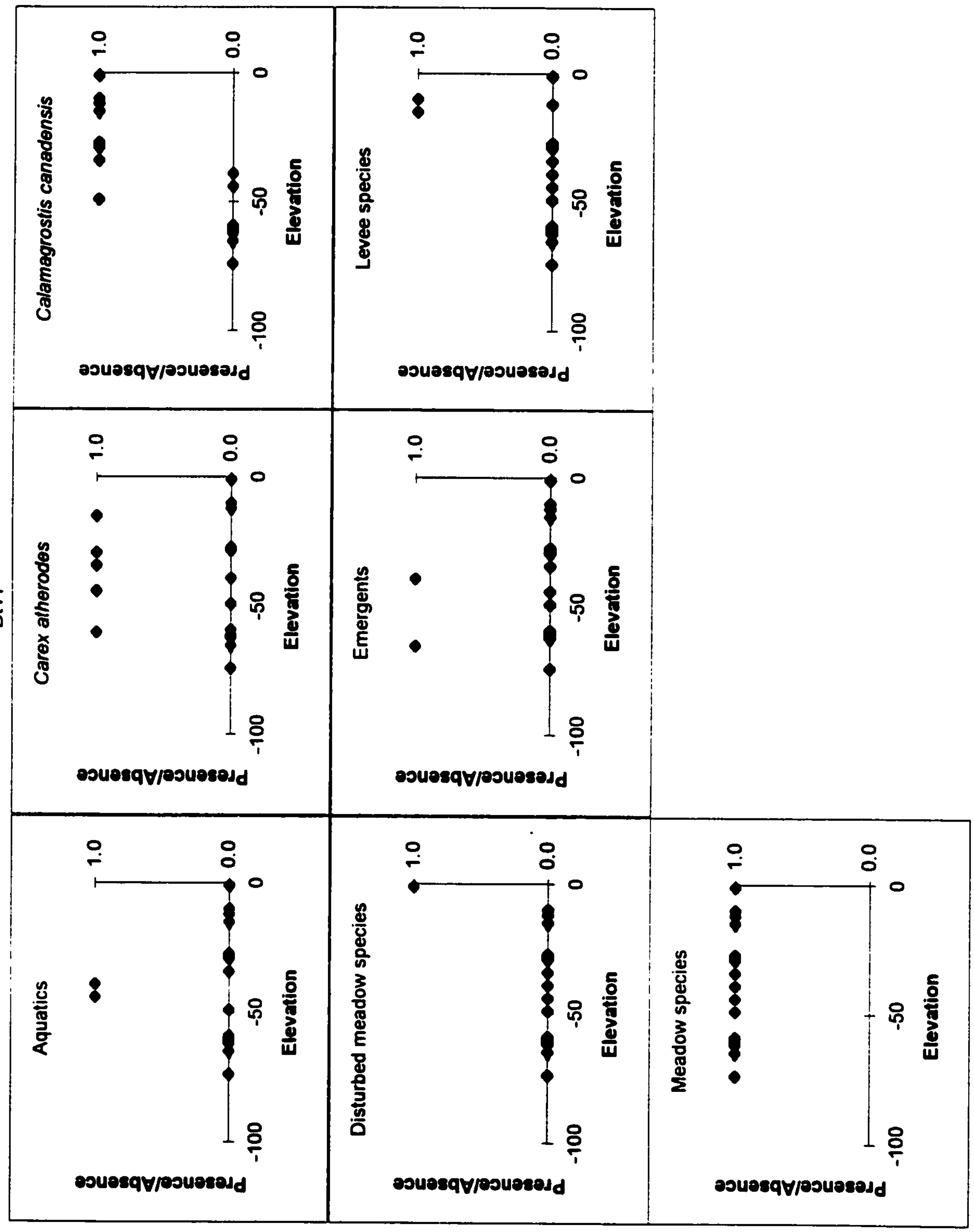

Dt07
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
1.0
0.0
Elevation
-100
-50
0
50

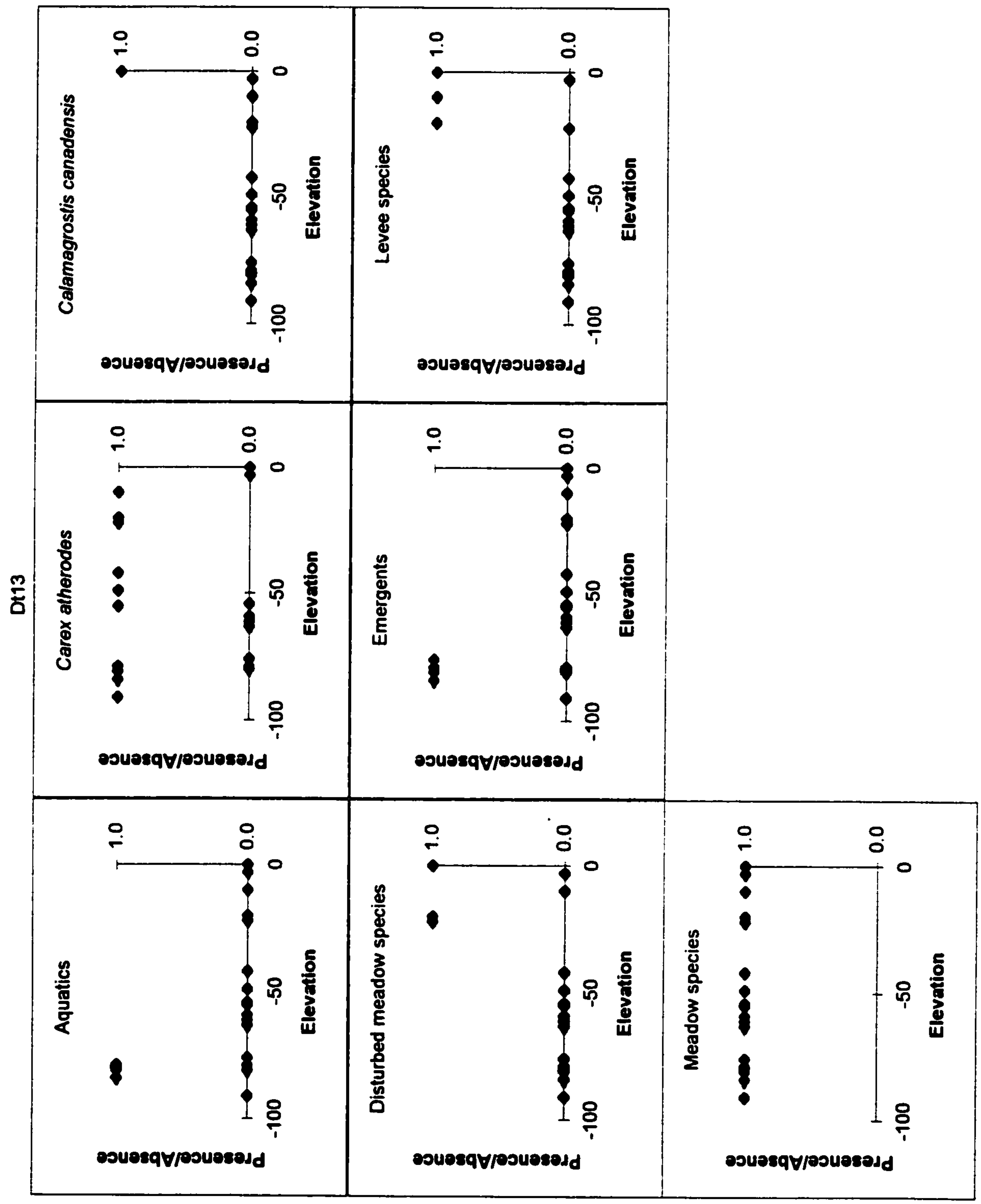


Dt08
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-60
-40
-20
0

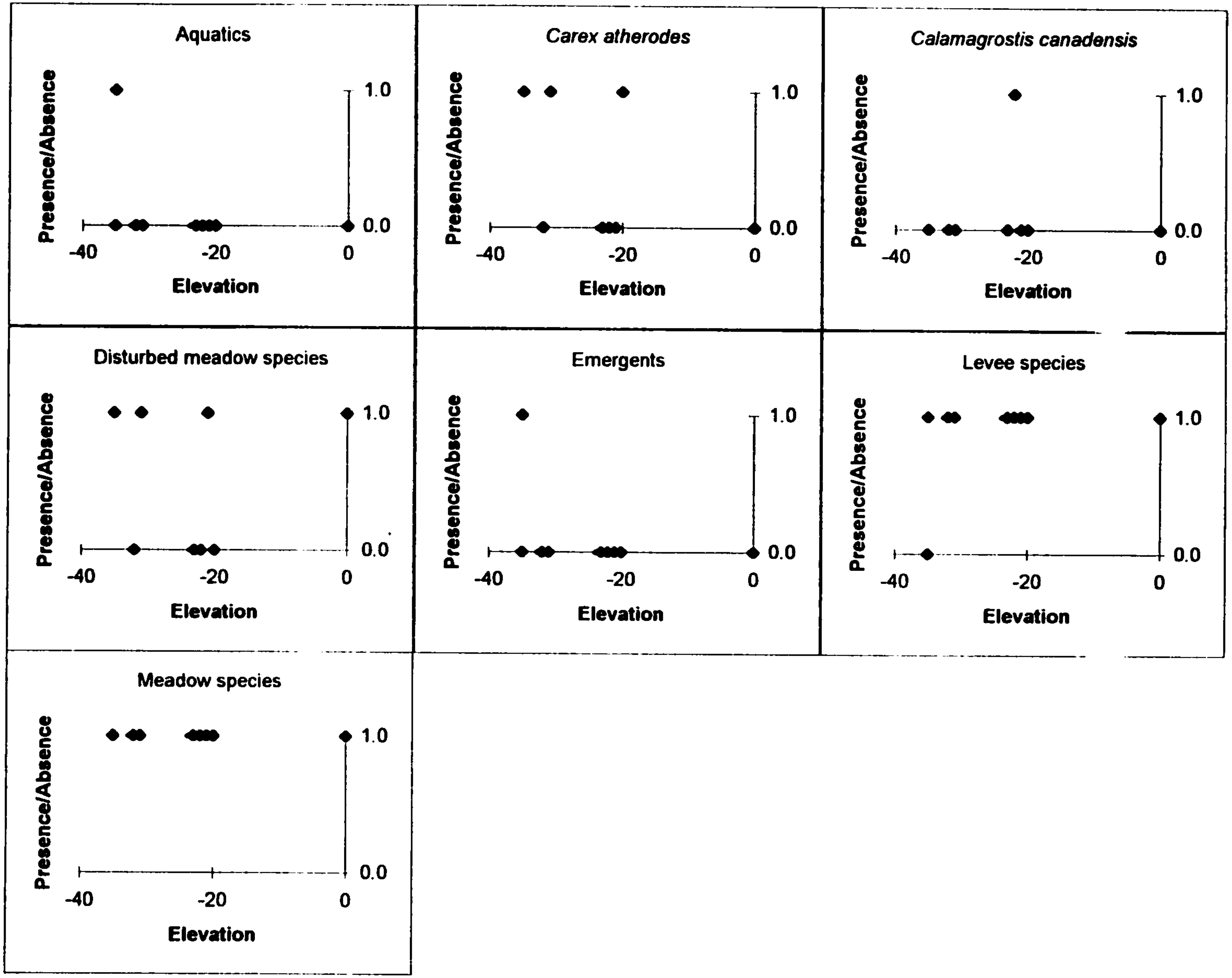

Dt09
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Elevation
1.0
0.0
0
-20
-40


Dt10
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Elevation
1.0
0.0
0
-100
-200

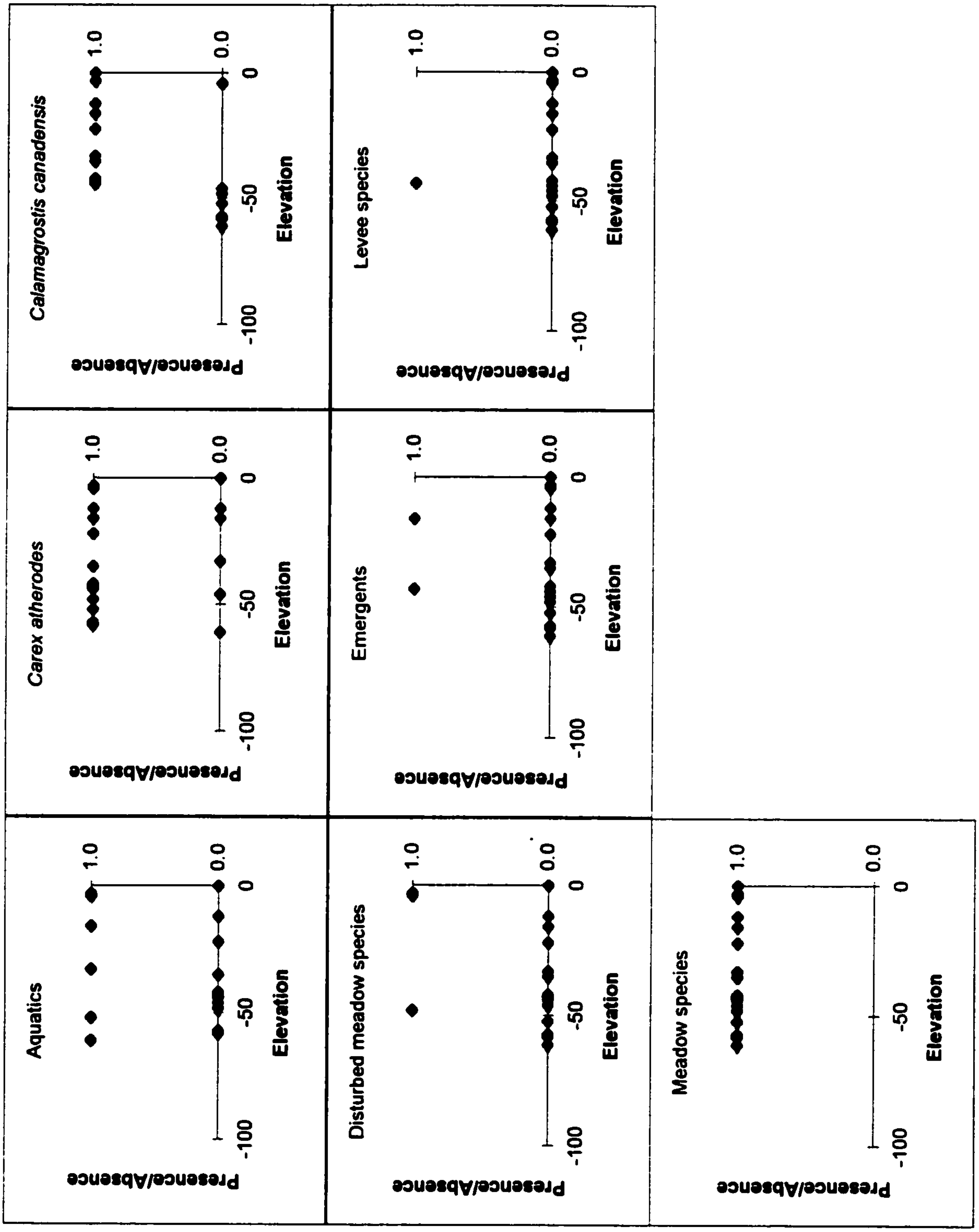

Dt11
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
1.0
0.0
-100
-50
0
Elevation

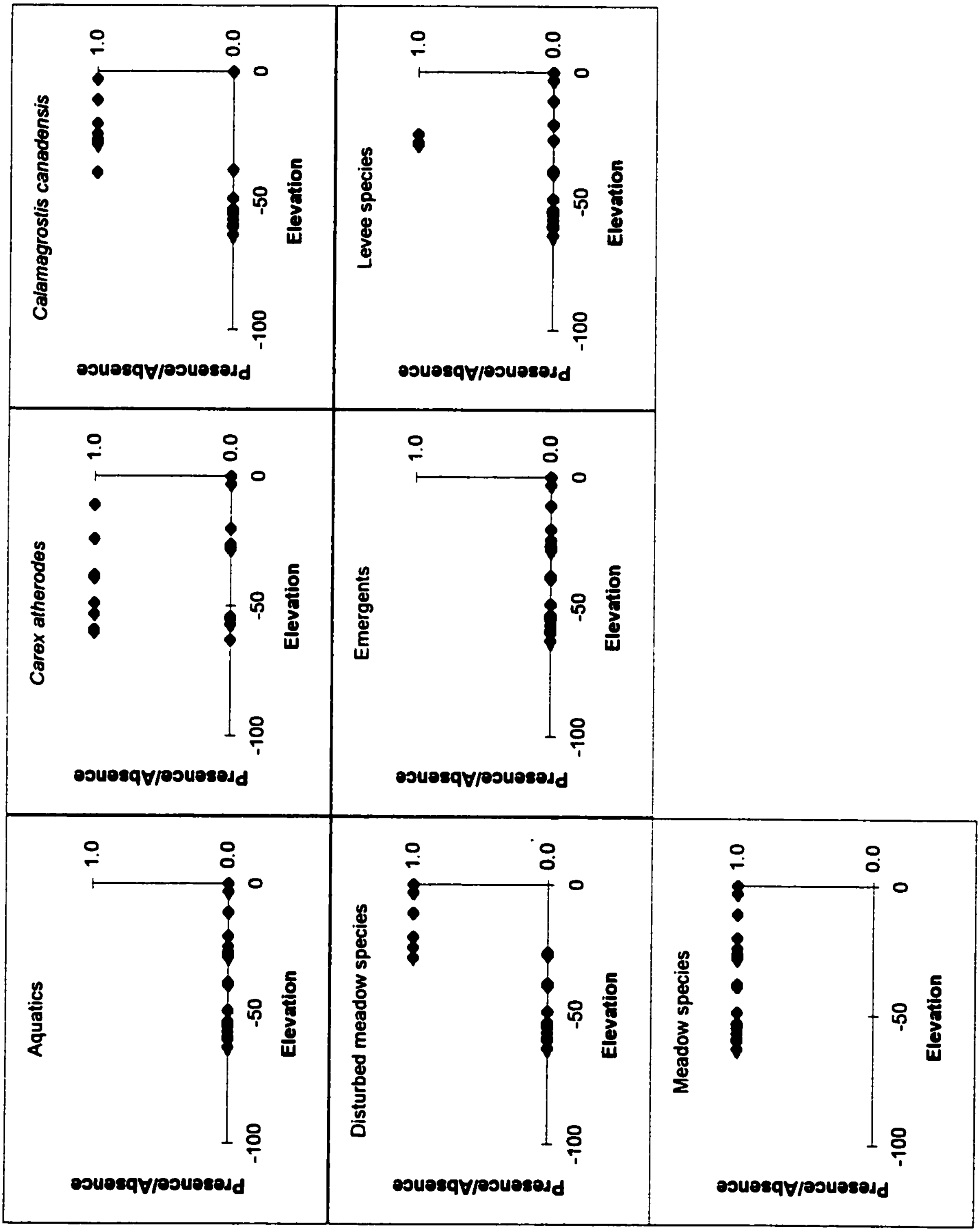

Dt13
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-100
-50
0

Dt14

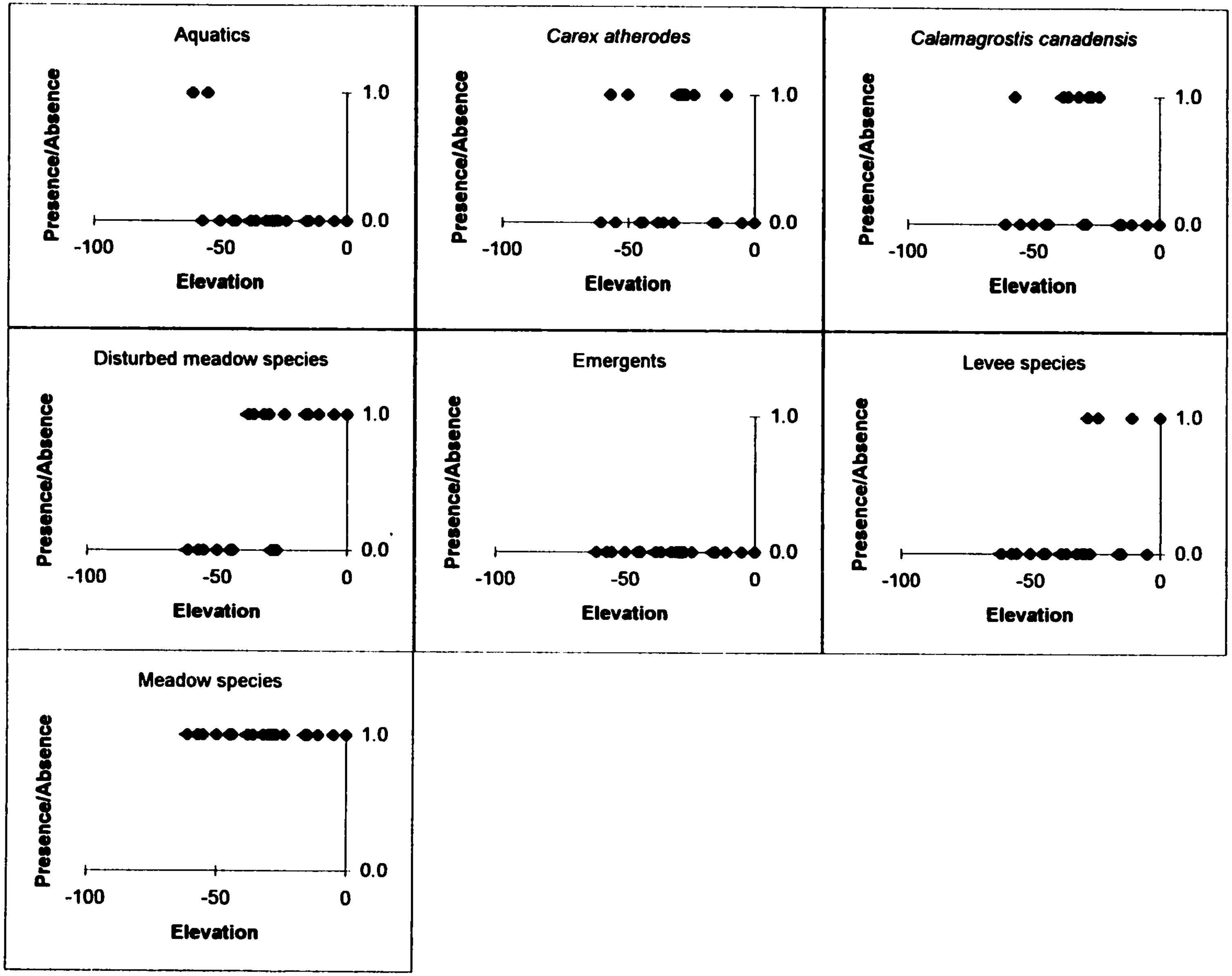

Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-40
-20
0

Dt15

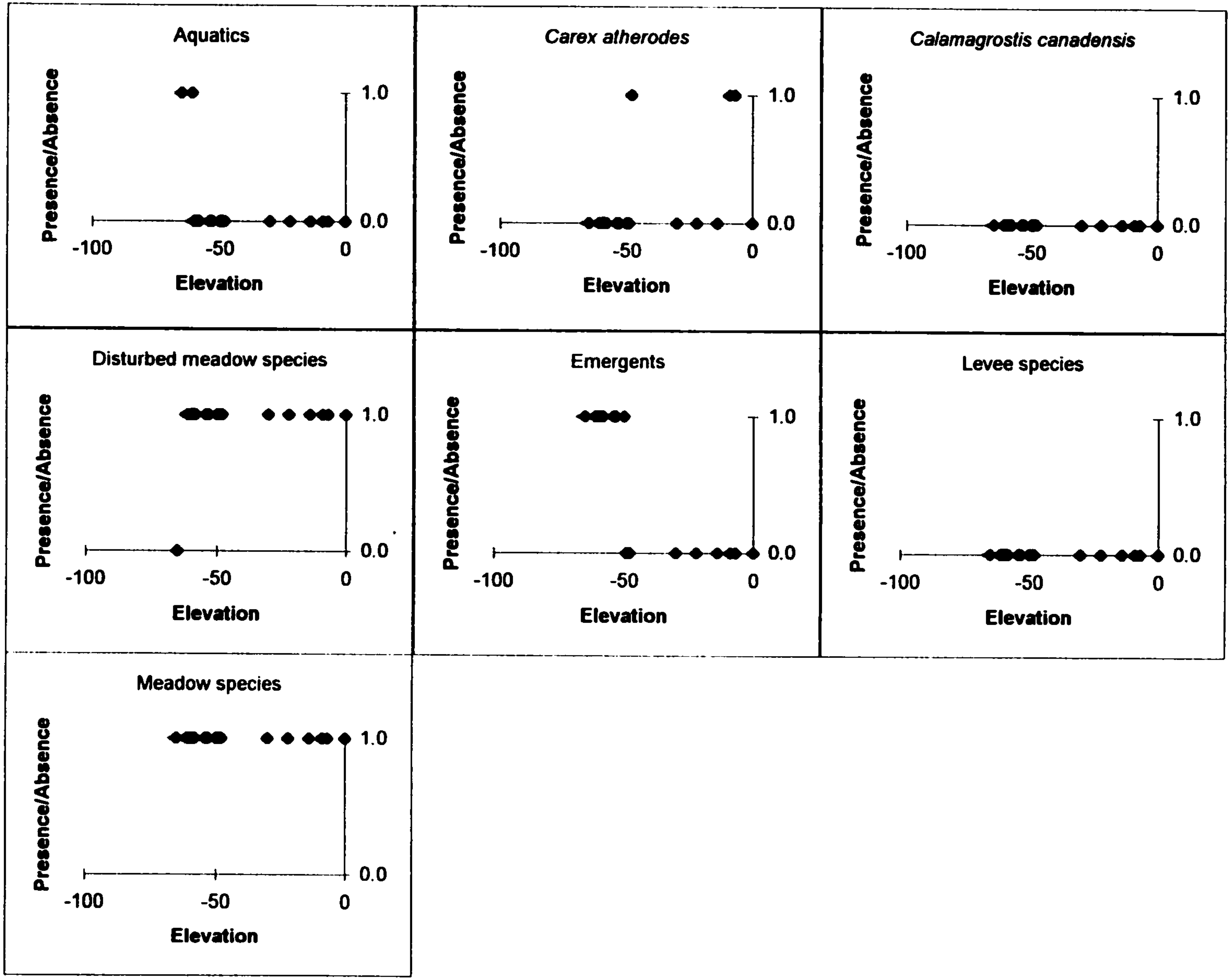

Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Elevation
1.0
0.0
0
-50
-100


Dt16
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-100
-50
0

Dt17

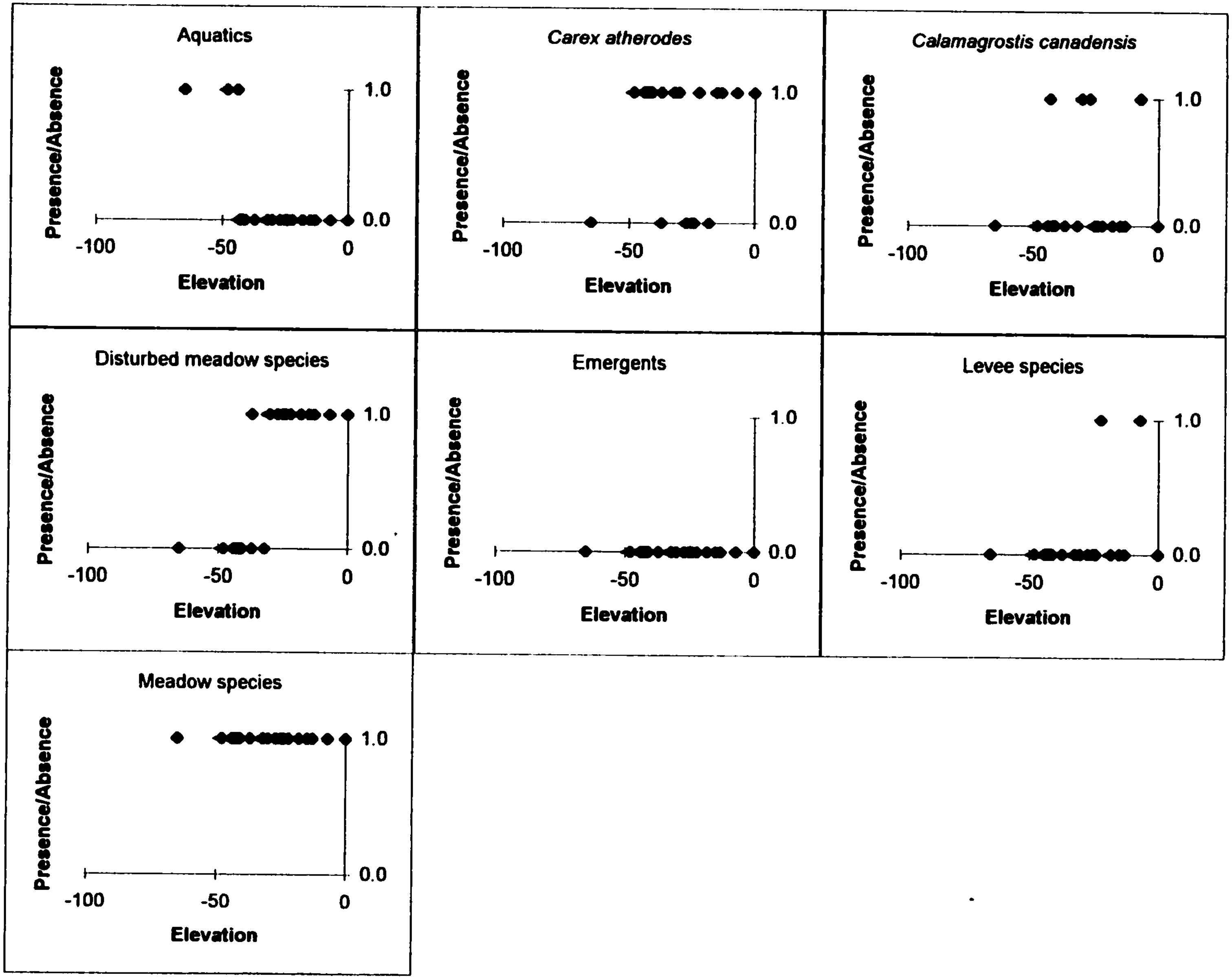

Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-100
-50
0

Dt19

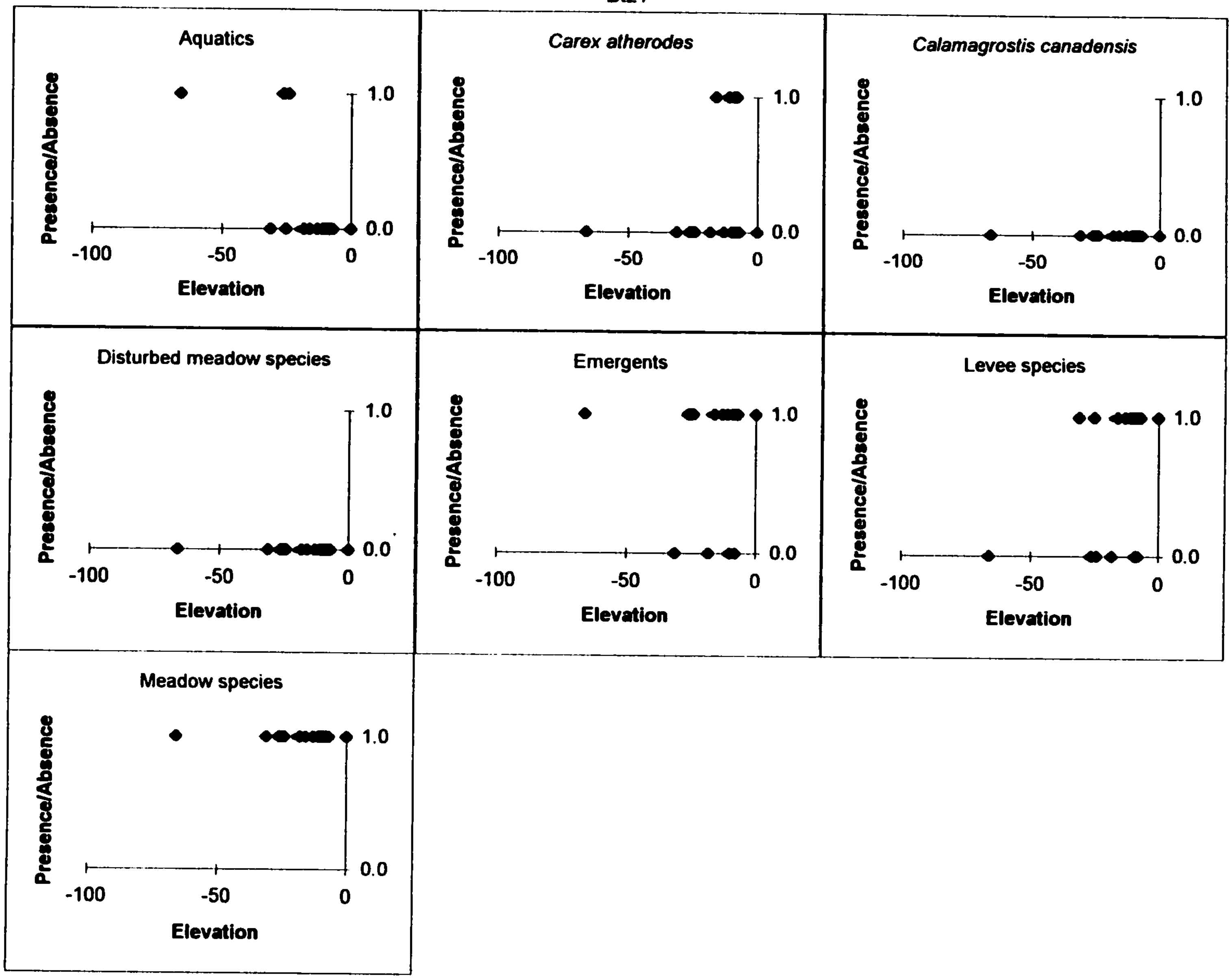


Aquatics
Presence/Absence
1.0
0.0
-100
-50
0
Elevation
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species

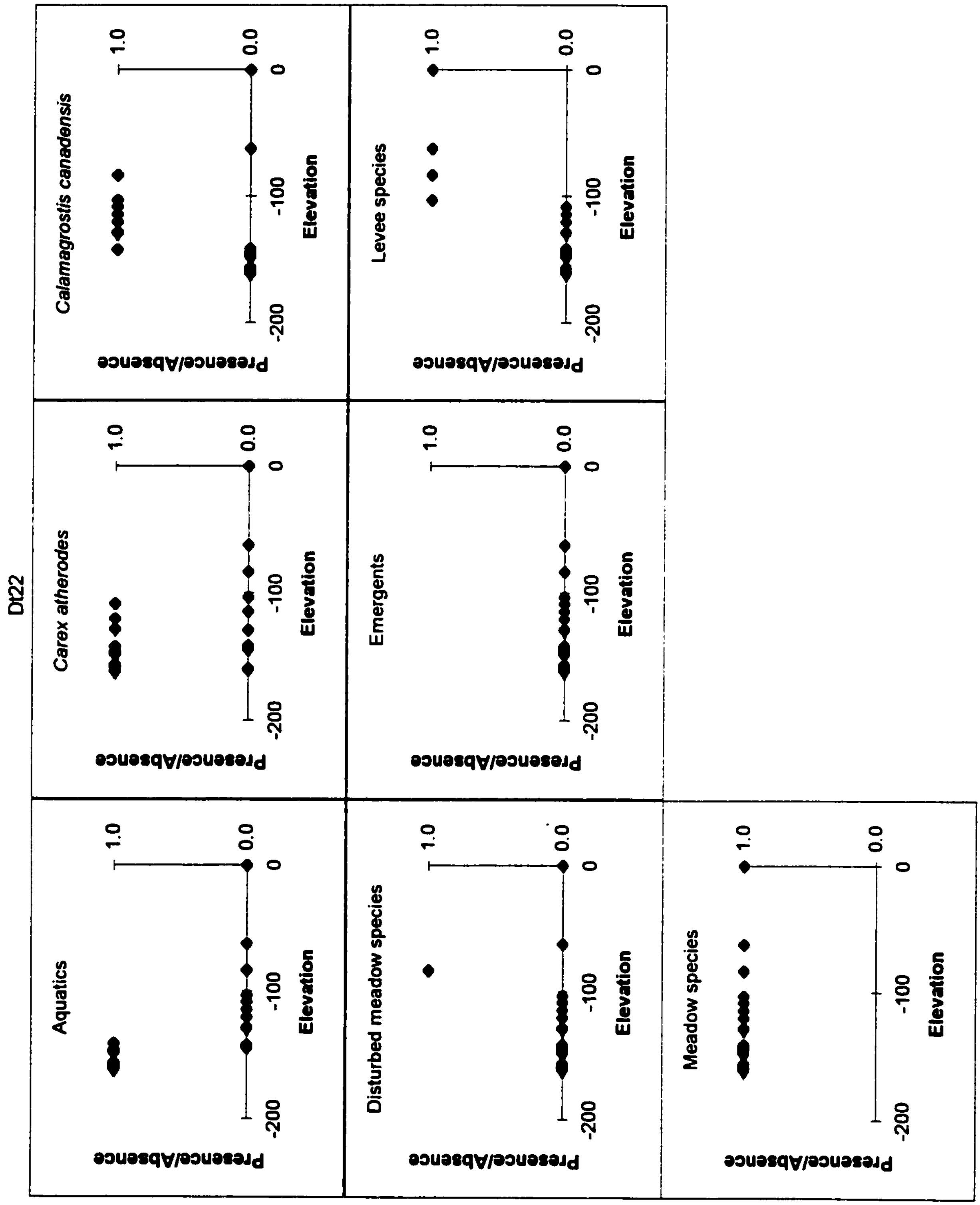
Dt20


Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
1.0
0.0
-100
-50
0
Elevation

Dt21

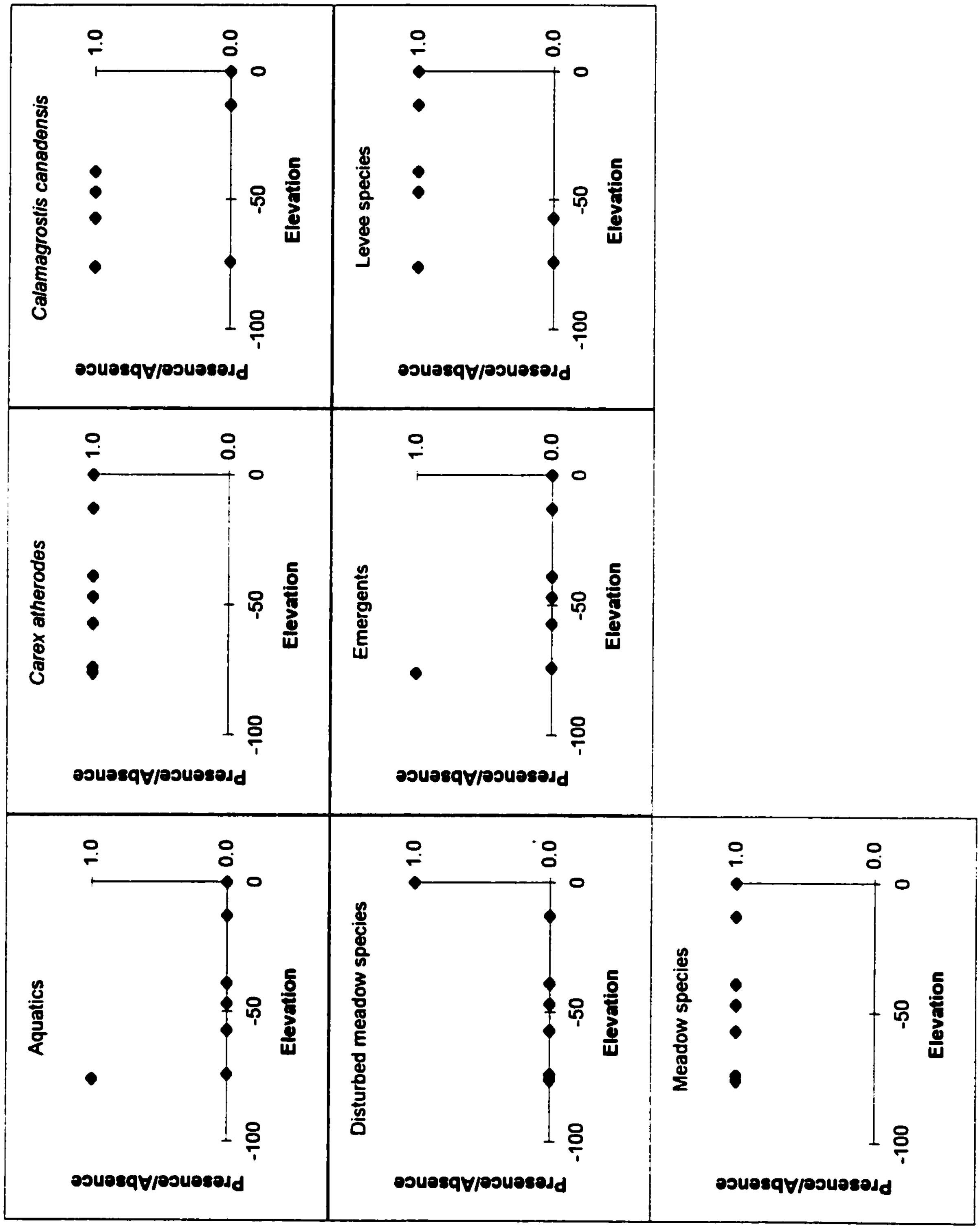


Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-100
-50
0

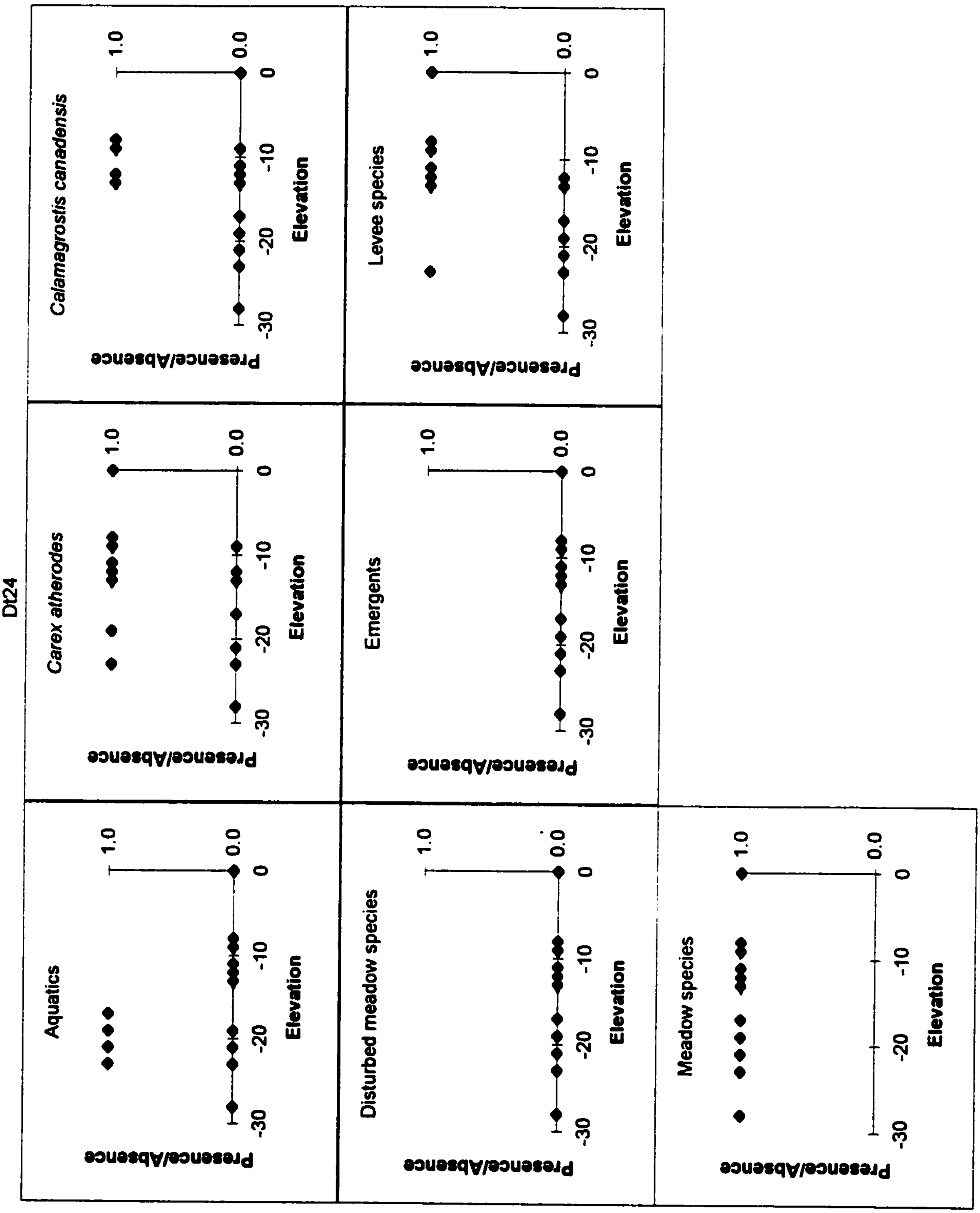


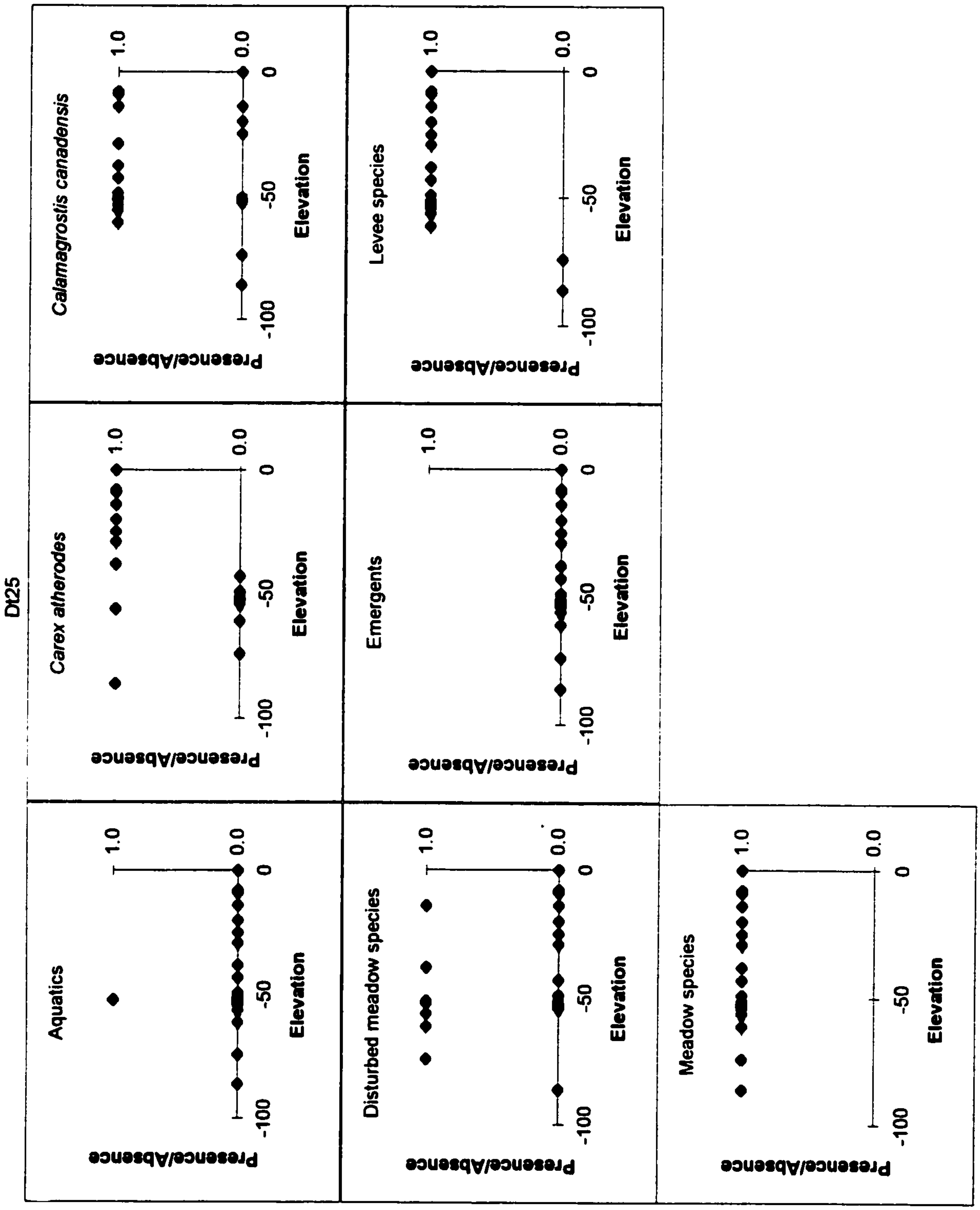
Dt22
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Elevation
1.0
0.0
0
-100
-200

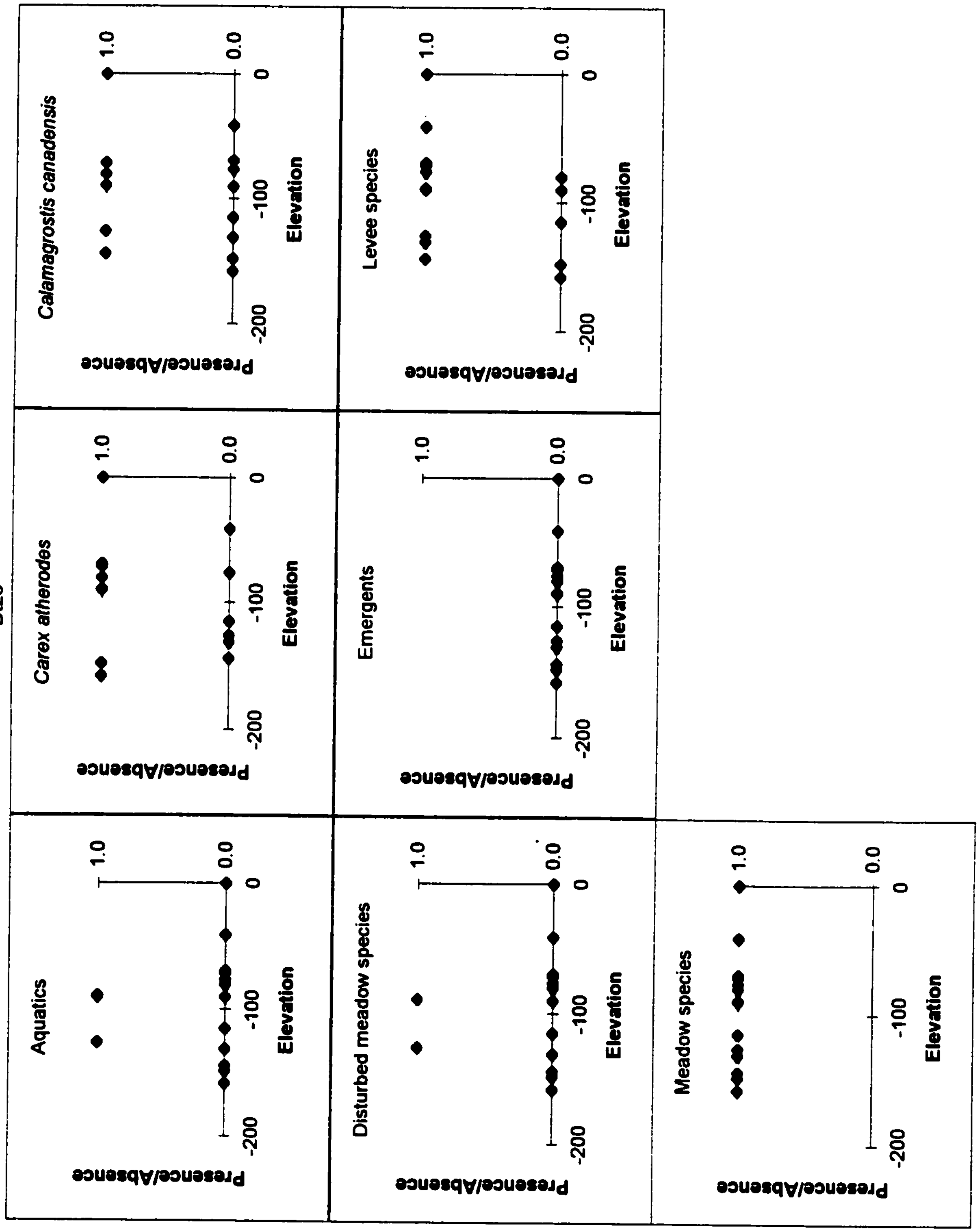
Dt23



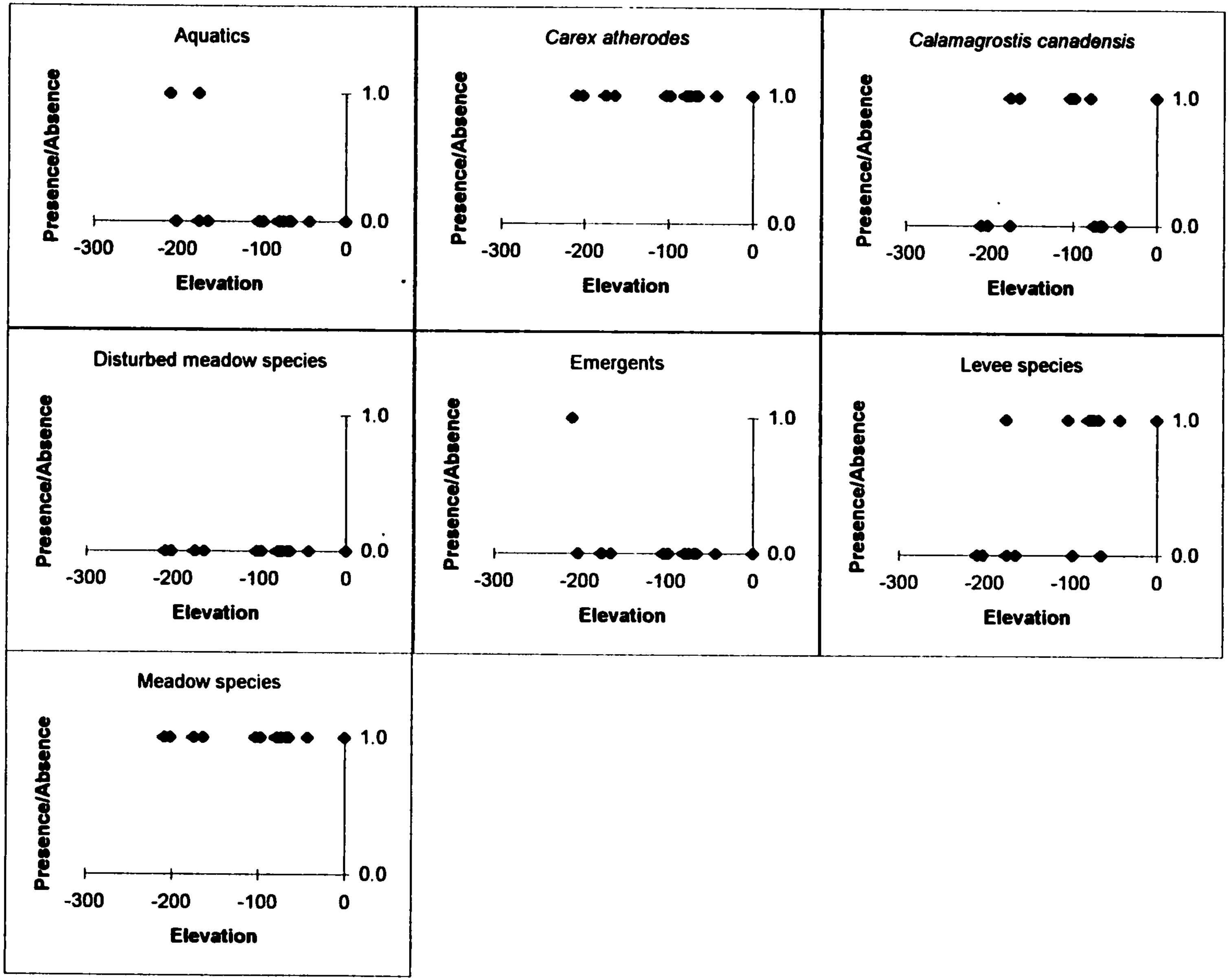
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Elevation
1.0
0.0
0
-50
-100


Dt24
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-30
-20
-10
0

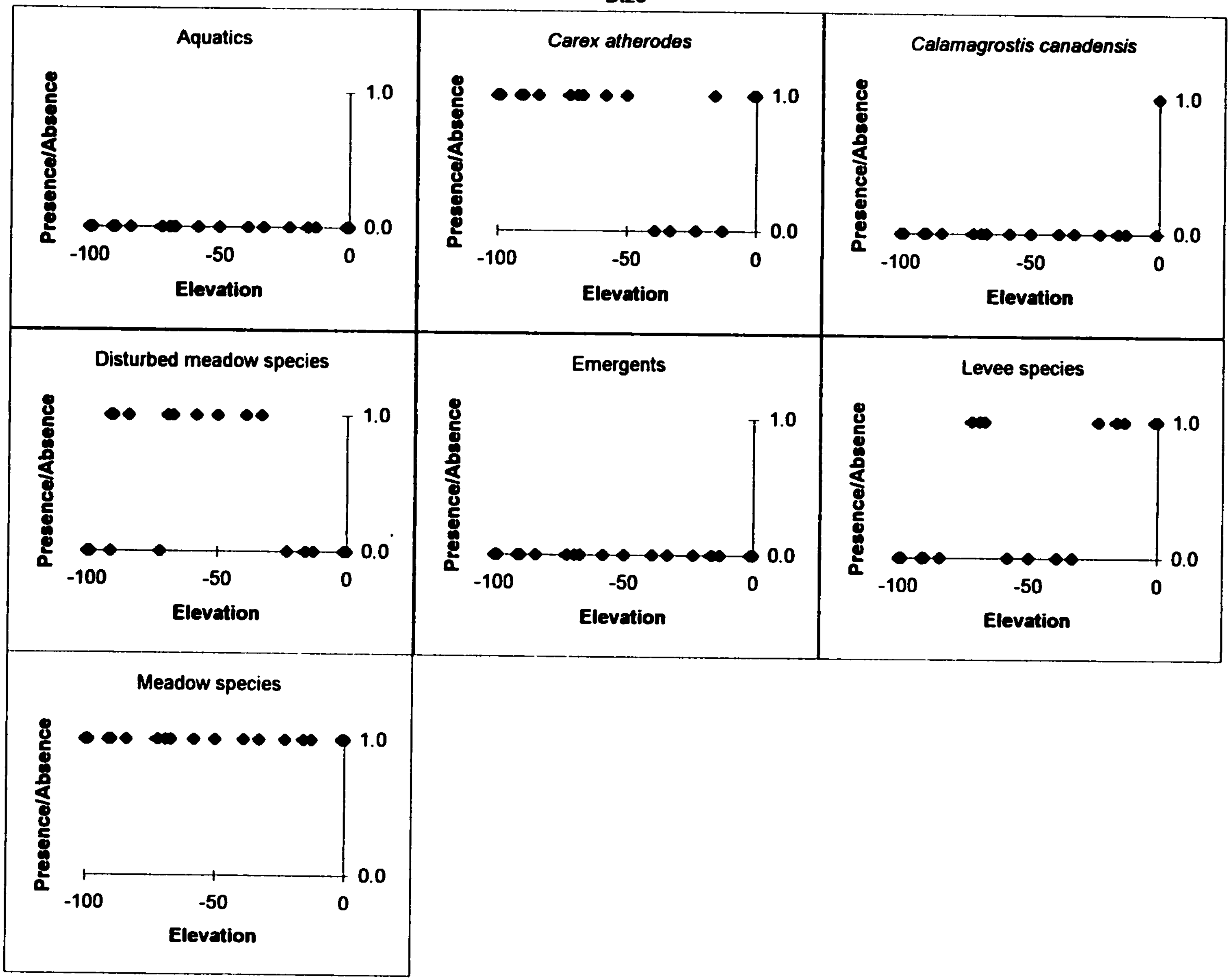

Dt25
Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Elevation
1.0
0.0
0
-50
-100


Dt26
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
0
-100
-200

Dt27

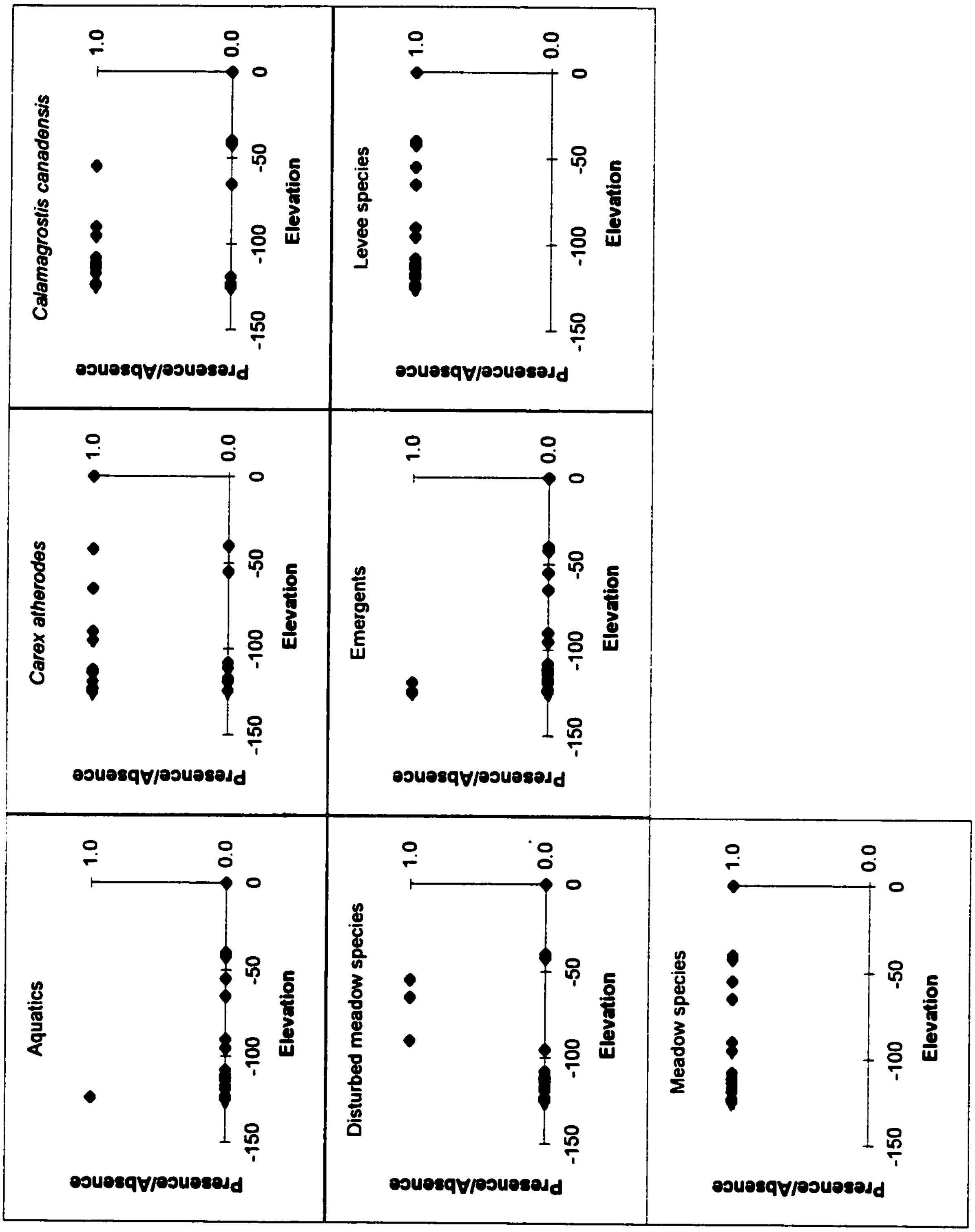

Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
1.0
0.0
-300
-200
-100
0
Elevation

Dt28

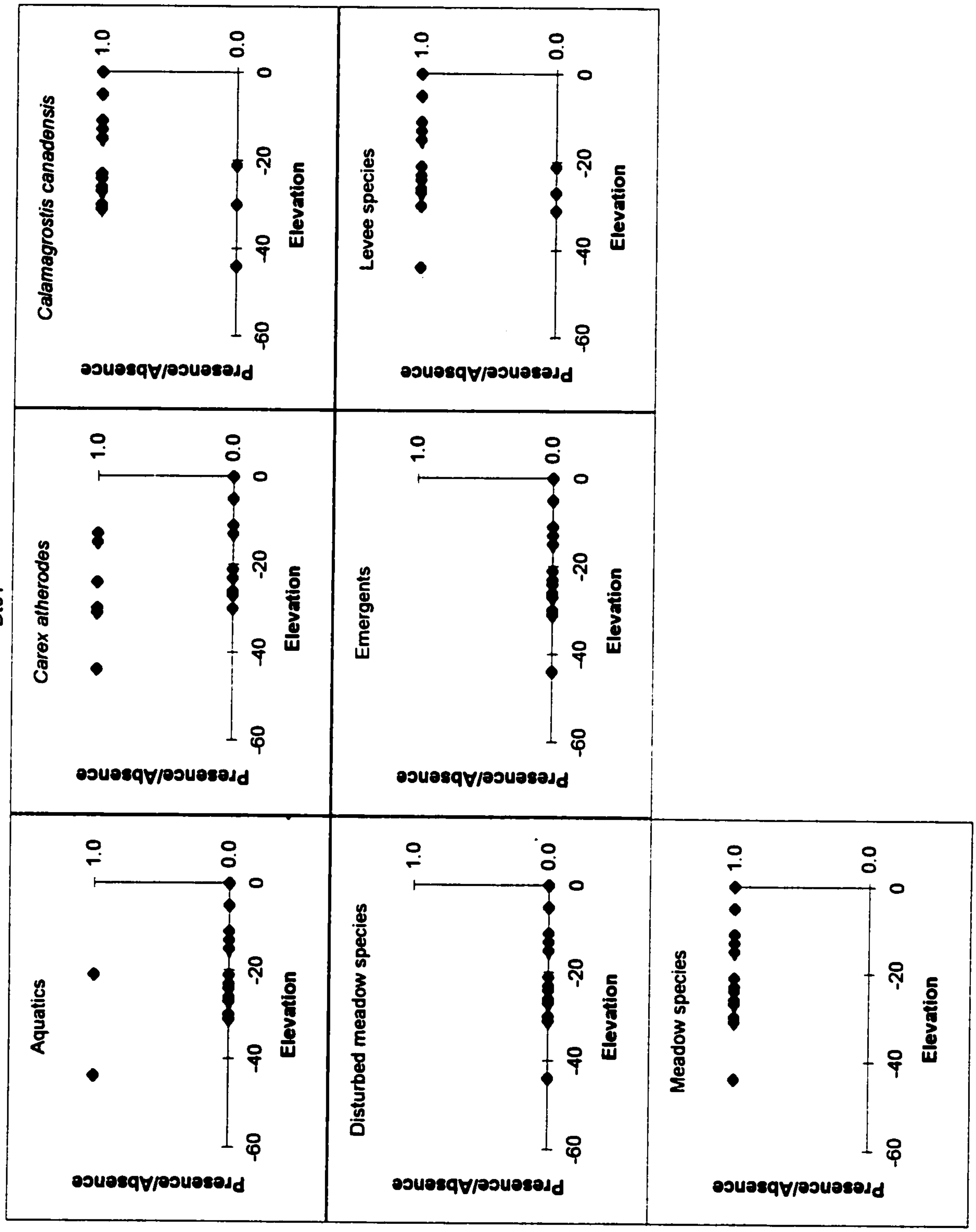


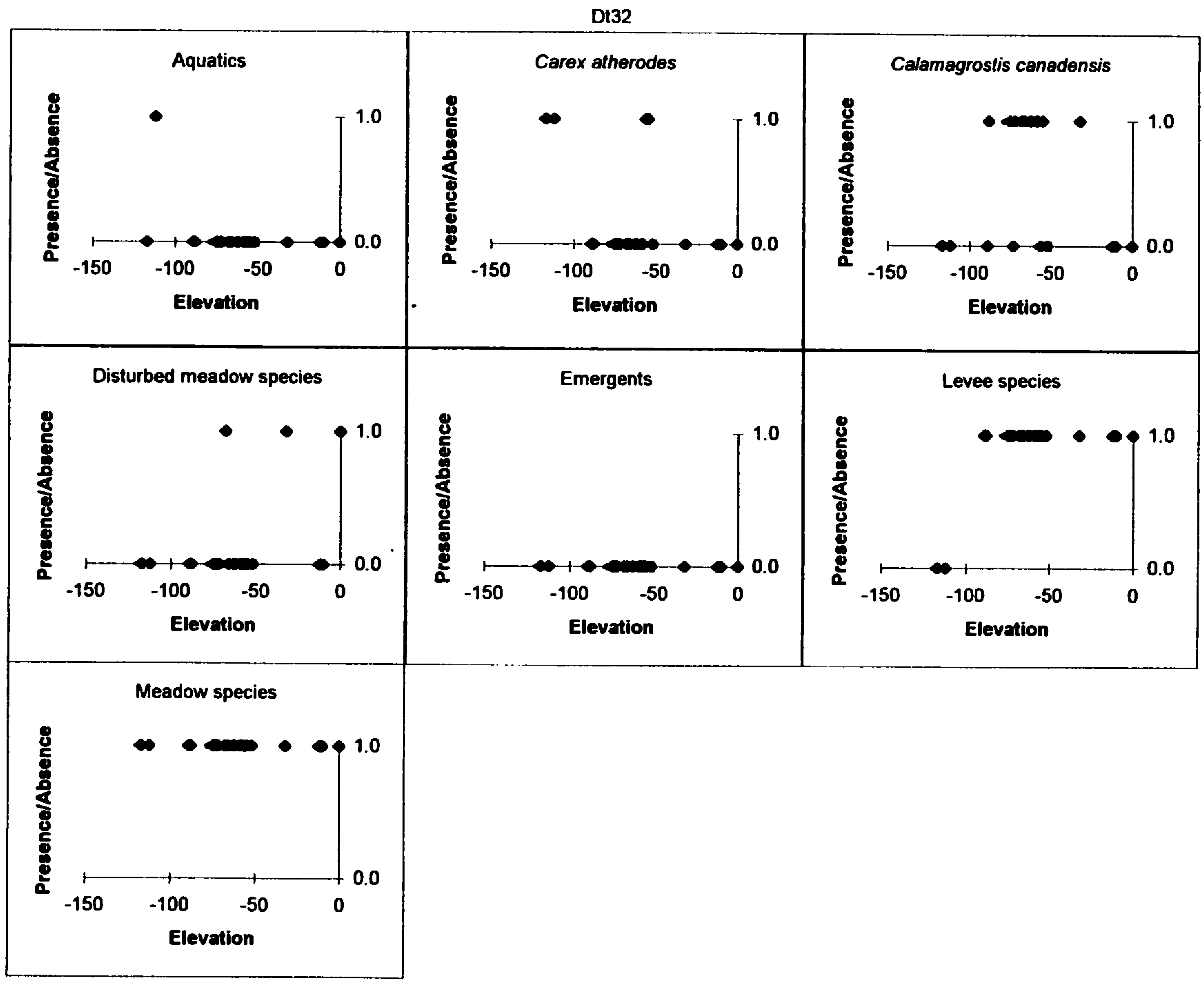
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
Elevation
1.0
0.0
-100
-50
0

Dt29


Aquatics
Disturbed meadow species
Meadow species
Carex atherodes
Emergents
Calamagrostis canadensis
Levee species
Presence/Absence
1.0
0.0
Elevation
-150
-100
-50
0

Dt31


Calamagrostis canadensis
Carex atherodes
Aquatics
Levee species
Emergents
Disturbed meadow species
Meadow species
Presence/Absence
Elevation
1.0
0.0
0
-20
-40
-60

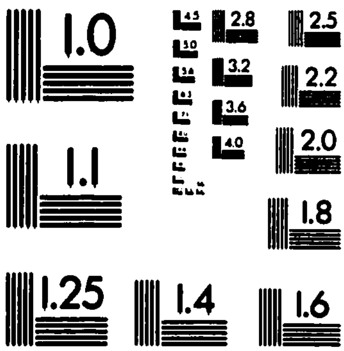

Dt32
Aquatics
Carex atherodes
Calamagrostis canadensis
Disturbed meadow species
Emergents
Levee species
Meadow species
Presence/Absence
1.0
0.0
-150
-100
-50
0
Elevation

Appendix 2. SAS Program used for meta-analysis.

```
THE META ANALYSIS PROGRAM (SAS)

*assume b1 b2 se1 se2 are set up as vectors*;

Proc IML;
A={
1.00  .085  .065  -.038 .073,
1.00  .145  .085  -.077 .056,
1.00  .062  .032  -.006 .028,
1.00  .100  .069  -.018 .053,
1.00  .082  .076  -.035 .030,
1.00  .143  .073  -.041 .031,
1.00  .117  .056  -.009 .009,
1.00  .105  .030  -.029 .012,
1.00  .124  .069  -.010 .020,
1.00  .173  .066  .017  .027,
1.00  .062  .034  -.030 .018,
1.00  .038  .025  -.035 .020,
2.00  -.017 .013  .019  .009,
2.00  .044  .025  .001  .009,
2.00  .020  .020  -.002 .009,
2.00  -.031 .041  .001  .010,
2.00  .020  .017  .002  .007,
2.00  -.011 .021  .010  .007,
2.00  -.009 .026  .002  .011,
2.00  .026  .023  .011  .021,
2.00  -.020 .015  .026  .012,
2.00  -.071 .103  .007  .061,
2.00  .013  .008  -.003 .006,
2.00  .015  .014  -.009 .013,
2.00  -.015 .017  .015  .012,
2.00  -.041 .044  .182  .077,
2.00  .018  .021  -.020 .025 };

b1 =  A[ 1:12,4];
b2 =  A[13:27,4];
se1 = A[ 1:12,5];
se2 = A[13:27,5];

*print b1, b2, se1, se2;

siga1 = ssq(b1 - sum(b1)/nrow(b1))/(nrow(b1) - 1);
siga2 = ssq(b2 - sum(b2)/nrow(b2))/(nrow(b2) - 1);

sigep1 = se1##2;
sigep2 = se2##2;

CapSig1 = J(nrow(b1),nrow(b1),siga1);
CapSig1 = CapSig1 + diag(sigep1);

CapSig2 = J(nrow(b2),nrow(b2),siga2);
CapSig2 = CapSig2 + diag(sigep2);

one1 = J(nrow(b1),1,1);
one2 = J(nrow(b2),1,1);

beta1 = inv(one1`*inv(CapSig1)*one1)*(one1`*inv(CapSig1)*b1);
```

```
varbeta1 = inv(one1`*inv(CapSig1)*one1);

beta2 = inv(one2`*inv(CapSig2)*one2)*(one2`*inv(CapSig2)*b2);
varbeta2 = inv(one2`*inv(CapSig2)*one2);

print "Beta w1", beta1,,;
print "Var Beta w1", varbeta1,,;

print "Beta w2", beta2;
print "Var Beta w2", varbeta2,,;

print / b1, se1, siga1, sigep1, CapSig1;
print / b2, se2, siga2, sigep2, CapSig2;

quit; *ends iml*;
run;
```

IMAGE EVALUATION
TEST TARGET (QA-3)



150mm

6"

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