Université de Montréal

# Spatial patterns in ecology:
# the influence of physical factors perceived at different scales and levels

par

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# Abstract

Pattern and process is a classic theme in ecology. The development of landscape ecology in the last two decades has brought an awareness of the explicit effects of spatial patterns on ecological processes. In addition, scale has been found to be associated with pattern and process. In landscape ecology, however, the processes which produce the pattern itself have not received much attention. Although traditional ecology has focused on processes that created the pattern, the ecological explanations have been largely phenomenological. Also, the role of physical factors on spatial patterns has not been emphasized in recent studies. Using GIS, remote sensing and spatial statistics, this thesis explores some spatial patterns in ecology, at a variety of levels and scales, through three case studies. The fundamental, but frequently obscure, role of physical factors in governing the spatial patterns and dynamics at different spatial scales and across different levels is emphasized.

The spatial pattern of coniferous and deciduous forest patches in the agricultural landscape is first investigated. The analyses reveal quite different spatial and dynamic forest patch patterns from the ones in natural landscapes. Spatially, coniferous patches are usually located on the margins of the overall forest patches, and they are connected to non-forest land-use types such as crop and pasture. Dynamically, the results reveal that on past abandoned land, conifers expand with increasing stand age, mostly by invasion from neighboring coniferous patches. Results show that the role of landscape physical factors on forest patch pattern has been modified by land use. Physical factors only indirectly influence the forest pattern because they strongly influence the land-use practices.

The role of physical factors on land-use patterns in the same study area is then further investigated. Results show that there are clear relationships between land-use types

and surface deposit types during the period of time studied. At the landscape level, crops are dominant on marine deposits, while forests are the dominant land use on moraine. Some of the transition types have an explicit deposit tendency. However, at the patch level, our analyses reveal very dynamic patterns. Also, more land-use changes occur at the boundaries between surface deposit types than in any other locations. They highlight the fact that the role of surface deposit is different at the path level and at the landscape level.

In case study three, the analyses not only further confirm the important role of physical factors at the species and community level, they also allow an in-depth analysis of the role of individual edaphic factors on the spatial structure of halophytic communities. Results show that there are two distinct vegetation gradients, one of which is determined by soil moisture, and the other by soil salinity. In addition, the analyses show that the relative importance of the two factors on the spatial structure of halophytic communities is scale-dependent.

From all three case studies, it can be concluded that no matter the location on the earth surface, the organisational level or the spatial scale, the ecological patterns have a physical basis. In addition, the relative importance of physical factors changes with scale, level and patch type. Obviously, biotic interactions or human and social-economic factors may be dominant at some scales and at some levels. However, knowledge of the inherent variability of the physical factors at different scales and levels provides a framework on which patterns and dynamics of landscapes and plant communities can be based.

# Résumé

La distribution spatiale des espèces et des populations de même que les processus agissant sur celle-ci constituent un des thèmes classiques à l'écologie. Au cours des deux dernières décennies, le développement de l'écologie du paysage a contribué à mieux comprendre l'effet de l'organisation spatiale sur les processus écologiques. L'échelle spatiale des phénomènes étudiés est reconnue dans ce contexte comme étant étroitement associée à l'organisation spatiale et aux processus qui sous-tendent celle-ci. Toutefois, l'écologie du paysage a porté peu d'attention jusqu'à maintenant aux processus qui déterminent les modèles spatiaux. Bien que l'écologie traditionnelle ait concentré ses efforts sur les processus qui régissent l'organisation spatiale des espèces et des populations, les explications fournies ne permettent pas de mesurer l'incidence réelle des mécanismes sous-jacents. Aussi, l'influence relative des facteurs physiques susceptibles d'agir sur l'hétérogénéité spatiale a fait l'objet de peu d'attention. Couplant les possibilités nouvelles des systèmes d'information géographique, de la télédétection et des analyses spatiales, cette thèse entend, à partir de trois études de cas, mettre en évidence le rôle fondamental des facteurs physiques régissant les dynamiques spatiales et temporelles et ce, suivant des échelles spatiales et des niveaux distincts.

La structuration spatiale des parcelles de forêts résineuses et feuillues situées à l'intérieur d'un paysage agricole fait l'objet d'un premier examen. L'analyse de ces parcelles suggère des dynamiques spatiales et temporelles très différentes de ce que l'on observe en milieu naturel. Au plan spatial, les parcelles de résineux se situent généralement en bordure des massifs forestiers tout en étant liées également à des classes d'utilisation du sol autres que forestières telles que les terres en culture et en pâturage. Au plan temporel, les résultats révèlent que les parcelles de conifères établies sur les terres en friche se développent principalement par la propagation des espèces

provenant de parcelles de forêt résineuse situées à proximité. Les résultats montrent que le rôle des facteurs physiques sur l'organisation spatiale des parcelles forestières est modifié par l'utilisation du sol. Ces facteurs influencent, quoique de façon indirecte, la structure spatiale des parcelles forestières dans la mesure où ils déterminent fortement les pratiques sous-jacentes aux formes d'utilisation du sol en présence.

A partir du même territoire d'étude, le rôle des facteurs physiques sur la structuration spatiale des formes d'utilisation du sol fait l'objet d'un examen plus approfondi. Pour la période d'étude, les résultats révèlent l'existence d'une relation étroite entre formes d'utilisation du sol et types de dépôts de surface. Au niveau du paysage, les superficies en culture dominent sur les dépôts marins alors que les zones boisées demeurent prédominantes sur les dépôts morainiques. Certains types de changement d'utilisation du sol sont étroitement associés à la nature des dépôts de surface. Nos analyses révèlent cependant la présence de modèles spatiaux très dynamiques au niveau de la parcelle. De plus, les changements d'utilisation du sol apparaissent plus clairement là où il y a transition entre types de dépôts de surface. Ces résultats mettent en lumière le rôle différentiel de ceux-ci au niveau de la parcelle et du paysage.

Dans la troisième étude de cas, les analyses confirment le rôle primordial des facteurs physiques au niveau des espèces et des communautés sur la base d'une analyse approfondie de l'influence des facteurs édaphiques sur l'organisation spatiale des communautés halophytiques. Les résultats révèlent la présence de deux gradients de végétation déterminés respectivement par l'humidité et la salinité des sols. Ces résultats montrent également que l'importance relative de ces facteurs varie suivant l'échelle spatiale considérée.

De ces trois études de cas, on peut conclure que quelque soient l'endroit sur la surface du globe, le niveau d'organisation ou l'échelle spatiale, les patrons écologiques conservent une base physique comme élément structurant. De plus, leur importance relative varie en fonction de l'échelle, du niveau d'organisation et du type de parcelle. Il importe de signaler que les multiples interactions de nature biotique ainsi que l'action de facteurs humains et socio-économiques sont appelés à devenir prédominant à certaines échelles spatiales et niveaux d'organisation. Toutefois, la compréhension de la variabilité des facteurs physiques selon différentes échelles et divers niveaux d'organisation fournit un cadre de référence à partir duquel les dynamiques spatiales et temporelles des paysages et des communautés végétales peuvent être abordées.

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# CHAPTER ONE

# Introduction

## *1.1 Pattern and process – a classic theme in ecology*

In ecology, the word "pattern" is used to describe the observable traits of a system and their configuration. Patterns can exist at various scales in time and space, and at all levels of ecological hierarchy, from organism, through population, community, ecosystem, landscape and region, to the level of the entire biosphere. A basic premise in ecology is that there are strong links between ecological pattern and ecological function and process. Understanding causes of patterns -- the biotic and abiotic processes of nature -- has long been and is still an important theme in ecology.

There has been a long tradition of interest in the spatial pattern and geographic distribution of organisms in ecology. The pioneer ecologist Von Humboldt (1769-1859) has described vegetation in terms of physiognomy and correlated the distribution of vegetation types with environmental factors (elevation, latitude and temperature). His work provided a major impetus to studies of the geographic distribution of plants and animals in the nineteenth century (McIntosh 1985). However, because of the complexity of the spatial patterning of ecological systems and the difficulty of quantifying them, most of these studies in the 19th century were qualitative. For simplicity, some ecological models still assume that biological organisms and their controlling variables are distributed in nature in a random or a uniform way (Legendre & Fortin 1989). For example, Clements' relay floristics succession theory and his climate climax concept viewed succession as a six-step process from nudation to climax, and held that the climax vegetation can be determined by macroclimate of the region. It stressed temporal dynamics but did not emphasize spatial pattern of vegetation.

In the first half of the 20th century, Alexander Stuart Watt (1892 - 1985) presented a revised concept of vegetation patterns in space and time in his paper entitled '*Pattern and process in the plant community*' (Watt 1947). The plant community was viewed as a dynamic mosaic of patches in different successional stages. Thus, space and time were linked by Watt for the first time on the broader scale that is now termed the landscape (Turner 1989). Watt introduced the concept that was later developed as the theory of patch dynamics ( Pickett & White 1985; van der Marrel 1993).

During the last thirty years, with the need to solve regional and global ecological and environmental problems, spatial pattern and dynamics have received increased attention. The development of landscape ecology (Turner 1989, Forman & Godron 1986) has brought an awareness of the explicit effects of spatial patterns on ecological processes. It even assumes that some ecological processes can be predicted by ecological patterns.

However, landscape ecology emphasizes the effects of spatial patterns on other ecological processes. The processes which produce the patterns have not received much attention. Although traditional ecology has focused on processes that created the patterns, the ecological explanations have been largely phenomenological. An observed pattern is matched with the predictions of a theory which postulates a certain linkage between pattern and process. The underlying mechanism has been largely overlooked (Wiens 1992). Obviously, there are still some 'gaps' in the linking of spatial patterns and processes.

## *1.2 The patch -- a link between spatial pattern and process*

Ecologists have recognized the spatial pattern or spatial heterogeneity for a long time. However, to a large degree, this recognition has been limited to distinguishing between homogeneous and heterogeneous vegetation or landscape, and evaluating heterogeneity as expressed in various statistical indices (Wiens 1992). Landscape ecology provides a new framework for the study of spatial pattern of ecological phenomena. In landscape ecology, patches represent relatively homogeneous areas which differ from their surroundings (Forman 1995). A landscape is composed of a mosaic of patches. The attributes of patches, such as size and shape, have widespread ecological implications for productivity, biodiversity, soil characteristics and water availability. Patches are also dynamic, and they have different causes or origins. Patch dynamics determine the changes of the whole mosaic. Therefore, the patch not only links the spatial pattern with other ecological processes, but it links the spatial pattern with the underlying process which governs the dynamics of the patch itself. From this point on, the patch can be thought of as a link between spatial patterns and processes.

There are different ways of classifying patches. Generally, patch boundaries are artificially imposed on an area. In fact, they are meaningful only when referenced to a particular scale, regardless of the phenomenon under consideration. Farina (1998) summarized five types of patches: 1, Structure patch: generally composed of a soil type overlapped by associations of vegetation; 2, Functional patch: an area which is homogeneous for a function or a physical descriptor, such as altitude, temperature, moisture, etc.; 3, Resource patch: mostly related to animal ecology, a landscape can be described as a combination of resource patches; 4, Habitat patch: may be defined as distinct plant community types which are generally larger than an individual's home range; 5, Corridor patch.

On the basis of causes or origins, Forman (1995) classified vegetation patches into the following five types. A "disturbance patch" results from the alteration or disturbance of a small area, whereas the inverse, a "remnant patch", appears when a small area escapes disturbance surrounding it. In contrast, an "environmental patch" (of vegetation) is caused by the patchiness of the environment, such as a rock or soil type. A "regenerated patch" resembles a remnant, but instead has reestablished on a previously disturbed site. Finally, "introduced patches" are created by people planting trees or grain, erecting buildings, and so forth.

In this research, we focused on land-use and vegetation patches. These patches are of the structure patch type and habitat patch type classified by Farina (1998) and include all five patch types described by Forman (1995). We classified the land-use patches as forest, crop, pasture, abandoned land, residential and water. Forest patches were further divided as coniferous forest and deciduous forest patches. The vegetation patches are identified by different plant community types according to the dominant species.

### *1.3 Scale -- an important factor to pattern and process*

There has been great variability in the meaning of "scale". The term "scale" as used in this thesis has two meanings. First, scale refers to physical dimensions of observed entities and phenomena. Things, objects or processes can be characterized and distinguished from others by their scale, such as the size of an object or the frequency of a process. Secondly, scale refers to the "scale of observation", the temporal and spatial dimensions at which phenomena are observed. The scale of observation encompasses both extent and grain (Forman and Godron 1986, Turner et al. 1989, Wiens 1989). Extent represents the overall area encompassed by an investigation. Grain is the size of the individual units of observation. Grain can be equated with resolution. Extent and grain define the upper and lower limits of the "view port" of a study. Any inferences about scale-dependency in a system are constrained by the extent and grain of investigation (Wiens 1989). The pattern and process in ecology are associated with scale in two ways. First, the pattern detected in ecology is a function of scale. Many studies have shown that the spatial pattern may change considerably with scale (e.g. Turner et al. 1989; O'Neill et al. 1991; Wu and Loucks 1995). Secondly, the ecological processes and parameters which govern the pattern also shift with scale. Processes and parameters important at one scale may not be as important or predictive at another scale. Therefore, results of pattern analysis need to be presented with explicit specification of scale or over multiple scales.

There are some ambiguities in the use of scale related concepts. "Level" refers to level of organization in a hierarchically organized system (Allen & Starr 1982). The terms "scale" and "level" are often used loosely and interchangeably since a change in scale often necessitates consideration of new levels of organization (see O'Neill & King 1998). The term level used in this thesis either refers to the predefined levels in ecology, i.e., organism, population, ecosystem, landscape and region, etc., or the levels in landscape organization, i.e., landscape level and patch level.

A fine scale to an ecologist is a large scale to a geographer or cartographer, who express scale as a ratio (e.g. 1:100 is a larger scale than 1: 1,000). Withers and Meentemeyer (1999) suggested using "broad scale" to replace "large-scale" (i.e., large extent), and using "fine scale" to replace "small-scale" (i.e. small extent). "Large-scale" in cartography is best expressed as "large map-scale" and "small-scale" is best expressed as "small map-scale". This thesis conforms to these suggestions.

### *1.4 The role of physical factors -- the focus of this research*

Ecological patterns are governed by the interaction of underlying processes and factors. These factors can be classified as physical (environmental or abiotic) factors, biotic factors, human activities, historical events and disturbances, etc. Clearly, the relative importance of different factors in regulating patterns varies with spatial scale and time scale (e.g. Allen & Starr 1982; Meentemeyer & Box 1987; Turner et al. 1989; Levin 1992; Wiens 1992; and many others). However, the physical factors have not been appropriately evaluated for their influence on ecological patterns at different levels, such as population, community and landscape. At the community level, there is a view that abiotic factors merely determine which species are eligible to participate in biotic interactions, or the sense that abiotic factors were important only in historical times, and that they play minor roles at present (see Dunson and Travis 1991). Similarly, at the landscape level, human activity is emphasized. However, how physical attributes of landscape elements constrain land use and determine land cover changes has been largely overlooked.

The general hypothesis of this thesis is that no matter the location on the earth surface, the organisational level or the spatial scale, the ecological patterns have a physical basis. An empirical investigation about the effects of physical factors on the ecological patterns was undertaken using data from different locations, across different organisational levels and at different scales. In order to contrast the role of physical factors, two rather extreme locations were selected: (1) an agro-forested landscape where physical factors are assumed to be less important than human activities on the land-use pattern, (2) an arid and salty landscape where physical factors are normally considered much more important than the biological factors on the spatial structure of its plant communities.

The specific research problems addressed in this thesis include:

(1) How are deciduous and coniferous patches distributed in the agricultural landscape? Which factors are important to the patterns? How do surface deposits influence the patterns? What implications can the results have on landscape management (Case study one)?

(2) How do surface deposits influence the spatial pattern and dynamics of land use? How do the land-use pattern and the role of surface deposits change from the whole landscape level to the local patch level? Which approaches can be adopted to combine the analyses at the whole landscape level and at the local patch level (Case study two)?

(3) Which edaphic factors are important to the spatial structure of halophytic plant communities? How do the roles of these factors change with the spatial scales? Compared to the biotic factors, what percentage of the spatial structure can be explained by the edaphic factors? What implications for soil salinization control can be derived from this study (Case study three)?

(4) Finally, what general conclusions about spatial patterns and the role of physical factors may be reached from these investigations?

## 1.5 Northeastern America and Central Asia -- two study sites

To answer these questions, two distinct study sites were selected. One is located in the south of the province of Quebec, Canada, the other is located in the Xinjiang Autonomous Region of China. In the first site, I focused on the landscape level analysis, while in the second site, the focus was on the plant community and organism levels.

*1.5.1 Study site in Canada*

The first study site is located in the Godmanchester county of Haut-Saint-Laurent regional county municipality, in the southernmost part of the Province of Québec, Canada (Fig.1-1). The Haut-Saint-Laurent is bounded by the St. Lawrence River to the North and New York State (USA) to the South (Fig. 1-1). It belongs to the humid mid-cool temperate ecoclimatic region of Canada, with warm summers and relatively mild winters (Ecoregions Working Group 1989). Annual average temperature is 6.1°C in Huntingdon (altitude 75 m) and average seasonal temperature ranges from -10°C in January to 20.8°C in July. The average frost-free period is 140 days. The annual sum of degrees during days of growth (average temperature over 5°C) is approximately 2093 (Wilson 1971). Precipitation is evenly distributed throughout the year with a slight increase in summer, the mean total being between 961 mm - 975 mm (Anon. 1982).

Geomorphologically, the area lies on a bed of dolomite, limestone and shale of the Beekmantown group, represented by the Beauharnois formation (Globensky 1981). Glacial recession left numerous moraine islets and morainic ridges lying parallel to the St. Lawrence river (Bariteau 1988), whereas lowlands, which are mostly cultivated, are covered with rich marine clay deposits of the post-glacial Champlain Sea. In some areas there are also large biogenic (peaty) deposits.

This area is part of the maple-hickory region (Grandtner 1966) of the deciduous forest region of the Great Lakes and St. Lawrence river system (Rowe 1972). Mesic forests are generally dominated by sugar maple (*Acer saccharum* Marsh.), with bitternut hickory (*Carya cordiformis* [Wang.] K.Koch), ironwood (*Ostrya virginiana* [Mill.] K.Koch), basswood (*Tilia americana* L.) and American beech (*Fagus grandifolia* Ehrh.). Red maple (*Acer rubrum* L.), trembling aspen (*Populus tremuloides* Michx), and gray birch (*Betula populifolia* March) can be found on disturbed upland sites as well as on xeric sites with white pine (Meilleur et al. 1994). Red ash (*F. pennsylvanica*, Marsh), red maple and silver maple (*A. saccharinum*) are found on poorly drained sites. In the last century, this region has been extensively exploited for timber (Bouchard et al. 1989; Simard & Bouchard 1996). Today, the remnant forest patches stand out from a matrix of agricultural land mostly occupied by dairy farms.

*1.5.2 Study site in China*

The second study site is located in the Xinjiang Autonomous Region of China (Fig. 1-2), where a long-term ecological monitoring project on the dynamics of vegetation, soil water, and salinity is in progress. Its geographic position is 86°57'10" E, 44°19'02" N. The annual average temperature is 6.8 °C, the monthly average temperature is -16.9 °C in January and 25.6 °C in July. The annual precipitation is only ca. 170 mm, but the potential evaporation is ca. 2300 mm, giving a P:E ratio of 0.07. Geomorphologically, the study site is located on the lower fringe of the alluvial fan of the Hutubi River, which is part of the Zhungeer basin whose central portion is occupied by the Guerbantonggute desert.

The study site lies in a transition zone between oases and the desert. Temperate desert vegetation dominated by the semi-shrub *Reaumuria soongorica* is distributed on the well-drained plain connected to the alluvial fan. On the upper and middle area of the alluvial fan are new or old oases. Due to the large amount of salt in the soil, as well as the relatively high water table, not only salt desert, but also salt marsh vegetation is distributed extensively in this transition zone. It provided an ideal location to analyze the relationships between the spatial structure of halophytic communities and edaphic factors. In addition, because this is the only zone with high potential for agricultural development which remains in this extremely arid region, it has been the object of several research projects in grassland management and soil salinization control in China.

The study site extends over a 2.6 $km^2$ area. The topography is undulating and elevation varies between 446.0 and 449.5 m above sea level; the southeastern part of the area is at a higher altitude than the western part. In the upper part, the water table is 1.5 - 2.5 m below the soil surface, whereas in the lower part, the water table is 0.7 - 1.5 m below the soil surface. Salt content in the ground water varies from 2.3 to 38.5 g/L. Soil salinity varies spatially. Electrical conductivity of the first soil layer (0 - 30 cm) ranges between 0.1 and 0.9 S/m. Salts are generally sodium sulfates or sodium chlorides. In some areas where the pH and alkalinity are relatively high, there are also sodium carbonates. The pH of the first soil layer is 8.2 - 9.9 and hydrolytic alkalinity is 0.1 - 1.8 meq/100g soil. Soil texture is usually fine sand or light loam with a clay layer occurring at 30 - 120 cm depth. The thickness of the clay layer varies from 25 to 120 cm. The spatial variation of the plant communities in the study area is notable. The extremely xerohalophytic species such as *Reaumuria soongorica, Nitraria sibirica* and *Suaeda physophora*, occur in the upper parts, while in the lower parts the communities are dominated by hydrohalophytic species such as *Aeluropus littoralis*, *Limonium gmelinii* and *Tamarix ramosissima*. Between the upper and lower parts, xerohalophytic species such as *Kalidium foliatum* and *Halocnemum strobilaceum* dominate most of the area.

### *1.6 GIS, remote sensing and spatial statistics -- methodology of this research*

There are two general approaches to the studies of spatial pattern, one is by categorical maps, the other is by a collection of samples taken at specific spatial locations (point data) (Gustafson 1998). The two approaches are combined and their advantages are explored in this thesis. Because both approaches depend heavily on the development of relevant tools, such as remote sensing, GIS and spatial statistics, all of these tools were also adopted in this thesis. In addition, some frameworks for analyzing the patterns and the role of physical factors are developed in this study.

Specifically, in case studies one and two, the categorical map approach is mainly used. The spatial pattern of coniferous and deciduous forest patches was acquired from LandSat TM data, while the land-use pattern was acquired from aerial photographs. Remote sensing digital image processing techniques were used to identify the overall forest patches, as well as the coniferous and deciduous forest patches. Various GIS modeling methods, canonical correspondence analysis (CCA), logistic regression and multiple linear regression analysis were used to explain the patterns. In case study three, both a point data approach and a category map approach were used. The halophytic community patterns were detected from both the field point data and the field category maps. CCA, correlograms (with Moran's I) and Mantel correlograms were used to analyze the role of edaphic factors and to determine how they change with the spatial scales.

### *1.7 Organization of the thesis -- three case studies*

The research questions were explored through three case studies. They are: 1, deciduous vs. coniferous forest patch pattern analysis in southern Quebec (site 1); 2, land-use pattern and dynamics analysis in south Quebec (site 1); and 3, spatial structure analysis of plant communities in Xinjiang, China (site 2) (Table 1-1). In order to achieve a better understanding of the role of physical factors in determining spatial patterns in ecology, these case studies were selected to span different scales, as well as different levels of ecological hierarchy.

Accordingly, the main body of the thesis is composed of three chapters presented as scientific papers. At the end, a general conclusion chapter summarizes the findings of the thesis.

Table 1-1. Research design of this thesis.

| | Case study 1 | Case study 2 | Case study 3 |
|---|---|---|---|
| Patch type | General forest type (deciduous vs. coniferous) | land-use type | Plant community type |
| Extent | 137 $km^2$ | 95 $km^2$ | 2.6 $km^2$ |
| Grain size (resolution) | 30 m | 15 m | 2 m |
| Methods and tools | Remote sensing of LandSat TM data; GIS analyses; Regression analysis. | GIS analyses; CCA analysis. | Spatial statistics; CCA analysis; Cluster analysis; GIS analysis. |
| Potential applications | Landscape planning & management | Landscape management | Salinization control |
| Specific research questions | See p. 7 | See p. 7 | See p. 7 |

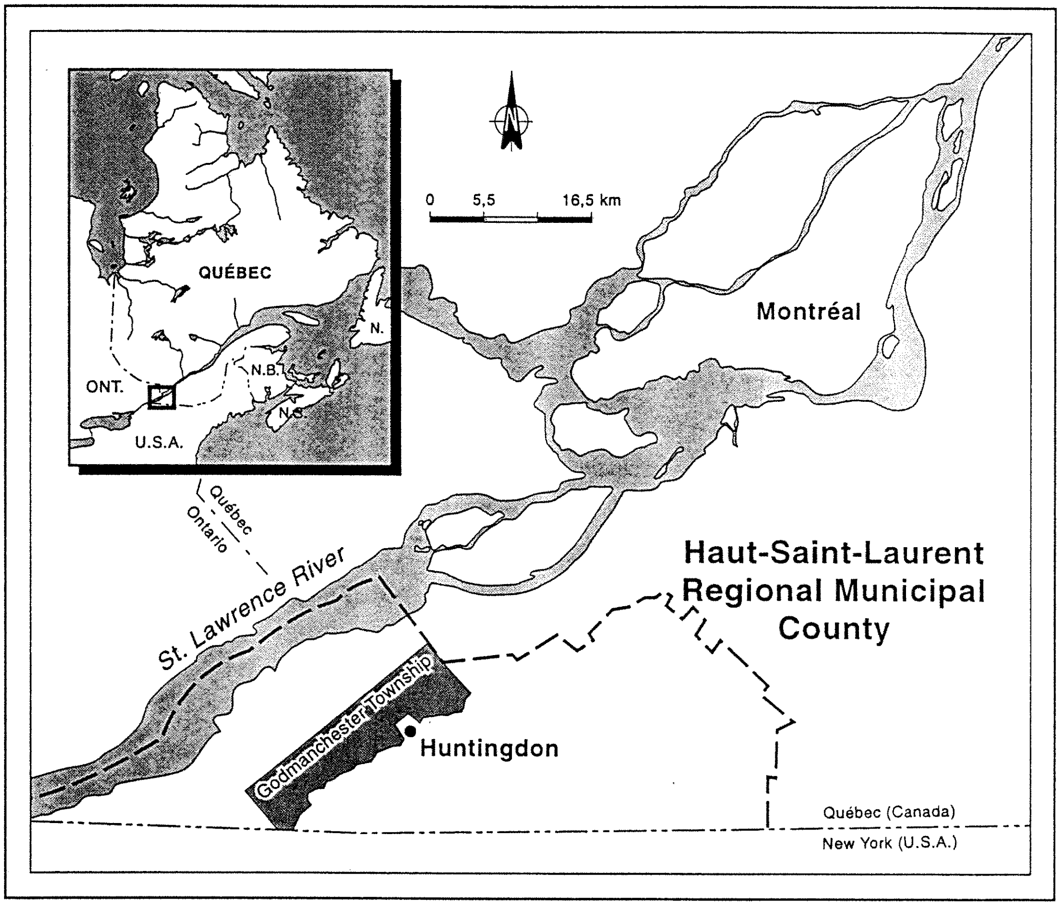


Figure 1-1. Study site in Canada.

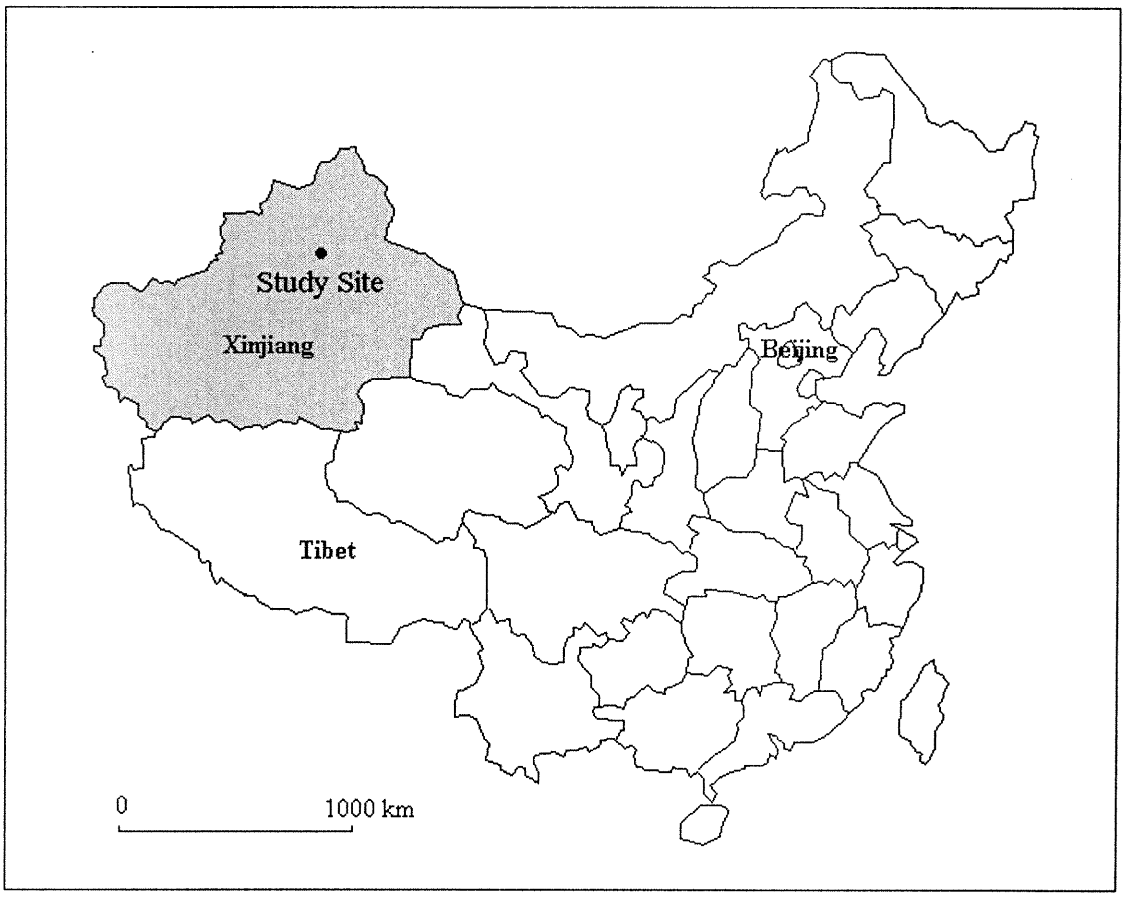


Figure 1-2. Study site in China

# CHAPTER TWO

## Spatial pattern of coniferous and deciduous forest patches in an agricultural landscape: the influence of land use and physical attributes

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### *Abstract*

In agricultural landscapes, most studies have investigated the influence of the spatial pattern of forest patches on other ecological phenomena and processes, such as animal movement and biodiversity. However, few have focused on explaining the spatial pattern of the forest patches themselves. Understanding how these patterns relate to the processes that generate them is fundamental in developing a sound theory of landscape ecology, and in devising rational management strategies. In this paper, the pattern of the overall forest patches, as well as the pattern of deciduous and coniferous patches in an agricultural landscape of Southern Quebec, Canada, were analyzed and related to landscape physical attributes and land use, using remote sensing, geographic information systems and statistical methods.

Results show that the role of landscape physical attributes on forest patch pattern has been modified by land use. In the study area, coniferous or deciduous patches are not associated with a specific surface deposit. In addition, physical attributes explain only a small proportion of the abundance of conifers on past abandoned land compared with land-use factors. Physical attributes only indirectly influence the forest pattern because they strongly influence the land-use practices.

Our results reveal a conifer recovery process with the abandonment of agriculture land. On past abandoned land, conifers expand with increasing stand age, mostly by invasion from neighboring coniferous patches. Spatially, coniferous patches are usually located on the margins of the overall forest patches, and they are connected to non-forest land-use types such as crop and pasture, the latter being the most important. By showing the importance of some coniferous forest types that did not exist in the precolonial forest, a new perspective emerges when landscape, especially, land-use dynamics are taken into account.

*Key Words*: agricultural landscape, Canada, forest patch, geographical information system, land use, physical attributes, Quebec, remote sensing, spatial pattern.

## 2.1 Introduction

The pattern of forest patches in the matrix of agricultural lands has long been, and is still an important research topic in landscape ecology. Most studies have investigated the influence of the spatial pattern (location, shape and size) of forest patches on other ecological phenomena and processes, such as animal movement and biodiversity (Harris 1984; van Dorp and Opdam 1987; Bolger et al. 1991; van Apeldoorn et al. 1994; McIntyre 1995; and many others). Few, however, have focused on explaining the spatial pattern of the forest patches themselves (Burgess and Sharpe 1981; Sharpe et al. 1987). Understanding how these patterns relate to the processes that generate them is fundamental in developing a sound theory of landscape ecology, and in devising rational management strategies.

It is well known that in a human-dominated landscape, land use is a major determinant of the spatial pattern of the forest patches. In addition to directly altering the type of forest patches and their spatial pattern, such as by plantation and clear cutting, land use can also trigger secondary succession through field abandonment, or modify the natural forest succession processes, such as by grazing or selective cutting (Curtis 1956; Burgess and Sharpe 1981; Sharpe et al 1987; Foster 1993). In vegetation science, the influence of land use on vegetation has been widely documented at the species, community and landscape levels (Peterken 1993; Hermy 1994; Koerner et al. 1997; Foster 1992; White and Mladenoff 1994; Whitney 1987). In addition, the characteristics of secondary succession stages on abandoned fields have been identified in different forest regions (e.g. Oosting 1942; Keever 1983 and others in North Carolina Piedmont). However, studies on explicit patterns and dynamics of forest patches in the agricultural landscape are rare. The applicability of the forest succession pathways in the agricultural landscape, where forest has been fragmented into relatively small isolated patches, also needs to be examined. In addition, the theories about forest pattern and dynamics at the landscape level, such as the shifting mosaic (Bormann and Likens 1979) and patch dynamics (Pickett and White 1985) are confined to the natural landscape. Further investigations are needed to link the vegetation dynamics and the pattern of forest patches in the agricultural landscape.

In this paper, we explore the pattern of forest patches in an agricultural landscape of southern Quebec, where forest patches occupy approximately 30% of the whole landscape. Like many other agricultural landscapes of eastern North America, most of the forest patches in the study area recovered from the abandoned agricultural land. Nowadays, these forest patches are mainly used as a source of firewood or as pastureland (Domon 1989). A prominent pattern which draws our attention, is the creation of numerous coniferous patches dominated by white cedar (*Thuja occidentalis* L.), and few dominated by white pine (*Pinus strobus* L.), or by a mixture of white pine and white cedar on upland mesic sites. Although white cedar grows in a wide variety of environmental conditions, it is usually associated with wetland habitats (Fowells 1965; Blanchet 1982; Johnston 1990). Curtis (1944, 1946) first reported that white cedar can form pure stands in old fields in Maine. He suggested that cattle browsing was favoring white cedar over deciduous competitors. In our study site, de Blois and Bouchard (1995), using quantitative methods, showed that cattle grazing has played a significant role in the appearance of white cedar stands on mesic sites. Similar to white cedar, white pine can grow on nearly all the soils within its range (Wilson and McQuilkin 1965). However, it generally competes best on well drained sandy soils of low to medium site quality (Wendel and Smith 1990). It was reported that in New England white pine frequently pioneers on abandoned agricultural land, but only on the well-drained to excessively drained deposits (Wendel & Smith 1990). In our study site, white pine is usually distributed on thin, dry bedrock or mixed with white cedar on abandoned land (Meilleur et al. 1994). In order to better understand the creation and dynamics of conifer patches of all species in the agricultural setting, aside from research at the species and community level, further investigation is also required at the landscape level.

Using remote sensing, geographic information systems and statistical methods, the patterns of the overall forest patches, as well as the patterns of deciduous and coniferous patches, were analyzed and related to the landscape's physical attributes and land use. The main objective of this paper is to reveal the pattern of these two broad forest types, especially conifers, at the landscape level and to explore the factors which govern the forest patch pattern in the agricultural landscape. Among the landscape's physical attributes, we have emphasized surface deposit, as it is the most stable feature over time (Bouchard et al. 1985). In order to better understand the influence of land use on the forest patch pattern, we investigated the effects of both present and past land-use types. The current investigation is part of a long-term multidisciplinary project which has produced several ecological and land management studies in the same area (for an overview see Bouchard and Domon 1997) and, in particular, complements the study of Pan et al. (1999) which analyzed the overall land-use pattern for the same landscape. This investigation is intended to give some insight into the dynamics and patterns of forest patches at the landscape level. It will also facilitate agricultural landscape planning and management.

## *2.2 Study area*

The study area covers about 137 $km^2$ and is located in the Godmanchester county, of the Haut-Saint-Laurent regional county municipality, in the southernmost part of the Province of Québec, Canada (Fig.2-1). The Haut-Saint-Laurent is bounded by the St-Lawrence River to the North and New York State (USA) to the South. The region has a humid continental climate with a cool summer. Annual average temperature is 6.1°C in Huntingdon (elevation 75 m), and average seasonal temperature ranges from -10°C in January to 20.8°C in July. The average frost-free period is 140 days. The annual sum of degrees during days of growth (average temperature over 5°C) is approximately 2093°C (Wilson 1971). Precipitation is evenly distributed throughout the year with a slight increase in summer, the mean total being between 961 mm and 975 mm (Anon. 1982).

Geomorphologically, the area lies on a bed of dolomite, limestone and shale of the Beekmantown group, represented by the Beauharnois formation (Globensky 1981). Glacial recession left numerous moraine islets and morainic ridges lying parallel to the St. Lawrence river (Bariteau 1988), whereas lowlands, which are mostly cultivated, are covered with the nutrient-rich marine clay deposits of the post-glacial Champlain Sea. In some areas there are also large biogenic (peaty) deposits.

This area is part of the sugar maple-hickory zone (Grandtner 1966) of the deciduous forest region of the Great Lakes - St. Lawrence River area (Rowe 1972). Mesic forests are generally dominated by sugar maple (*Acer saccharum* Marsh.), with bitternut hickory (*Carya cordiformis* [Wang.] K.Koch), ironwood (*Ostrya virginiana* [Mill.] K.Koch), basswood (*Tilia americana* L.), and American beech (*Fagus grandifolia* Ehrh.). Red maple (*Acer rubrum* L.), trembling aspen (*Populus tremuloides* Michx), and gray birch (*Betula populifolia* March) can be found on disturbed upland sites as well as on xeric sites with white pine (Meilleur et al. 1994). Red ash (*Fraxinus pensylvanica* Marsh), red maple and silver maple (*A. saccharinum*) are found on poorly drained sites. In the last century, this region has been extensively exploited for timber (Bouchard et al. 1989; Simard and Bouchard 1996). Today, the remnant forest patches stand out from a matrix of agricultural land, mostly occupied by dairy farms.

## 2.3 Methods

### *2.3.1 Data set development*

*Forest Patches* ---- A cloud-free LANDSAT5 Thematic Mapper (TM) data set of August 19, 1995 was selected to interpret the pattern of forest patches in the study area. The TM data set was georectified and registered to a Universal Transverse Mercator (UTM) coordinate system, by using road intersections and other prominent visible features on the existing 1/50,000 digital topographical map from Geomatics Canada. A two-step unsupervised classification procedure was adopted for producing the forest patch map. Considering the relatively high variability of the forest communities, this data set was first aggregated into as many as 225 natural spectral classes. These spectral classes were produced from the TM bands 1-5 and 7 using a clustering algorithm (i.cluster), followed by a maximum likelihood classifier (i.maxlik) in the GRASS (USA CERL 1991). To facilitate the labeling procedure from the 225 classes to the final three classes, the class means of these spectral classes were used as input for a principal component transformation (PCT). Based on the spectral similarity of these classes, shown on the two dimension ordination diagram of the PCT, and with the help of available aerial photographs (1:15,000 black and white 1993 aerial photographs), previous forest maps (which include 1:20,000 forest maps [1984] from the Forest Inventory Service of the Quebec Government, and 1:10,000 forest maps [Domon 1989]), as well as more than 500 vegetation sample plot data from 1986-1997 (Meilleur et al. 1994; Saucier 1986; de Blois and Bouchard 1995), these spectral classes were grouped into the final three classes: (1) coniferous forest, (2) deciduous forest, and (3) others. Coniferous forest mainly includes pure or dominant stands of white cedar or white pine. Deciduous forest is dominated by various pioneer, successional and climax deciduous trees. For simplification, the mixed deciduous and coniferous forest was merged with the coniferous type if the percentage of conifer coverage was >50% of the total coverage; otherwise, it was merged with the deciduous forest type. The non-forest type (others) is dominated by crop and pasture.

The accuracy of the classification was assessed by field validation and aerial photography interpretation. A random sampling of 50 pixels of each class was selected across the study area for checking the classification accuracy. The classification accuracy was calculated by error matrix. The overall imagery classification accuracy was estimated to be 94.6% for the whole study area. The classification was correct for 90.0 % of the coniferous forest, 94.0% of the deciduous forest and 100% of the non-forest. The smoothed data, with a 3 × 3 mean filter was used for the subsequent analyses.

*Surface deposit, topography, and past and present land use* ---- An available data set with surface deposit, topography, as well as past (1958, 1965, 1973 and 1983) and present (1993) land-use maps was joined to the data set of the forest patches, and used to analyze the relationships between forest patch pattern and past and present land use and surface deposit. The three main types of surface deposits (Bariteau 1988) are marine (46.27% of the study area), glacial moraine (35.82% of the study area), and biogenic deposits (7.68% of the study area). The past and present land-use layers, which were interpreted from 1:15,000 black and white aerial photographs, include six types: forest, crop, residential, abandoned land, water, and pasture. Detailed descriptions of the development of these maps can be found in Pan et al. (1999).

### *2.3.2 Spatial pattern analysis of the forest patches*

In order to reveal the pattern of overall forest patches, as well as of the deciduous and coniferous forest patches, an analysis was performed at two levels. One is at the level of the overall forest patches (i.e. merging the coniferous forest patches and deciduous forest patches into a single forest type); the other is at the level of two different types of forest patches (deciduous and coniferous). The shape, size and number characteristics of each patch type, as well as their spatial adjacency were investigated with FRAGSTATS (McGarigal and Marks 1995), GRASS (USA CERL 1991), and some other programs created for this study.

We used the mean shape index (MSI), the area-weighted mean shape index (AWMSI) (McGarigal and Marks 1995), and the fractal dimension to describe the shape of the forest patches. MSI measures the average perimeter-to-area ratio for a particular patch type without weighting patches according to their size, while AWMSI weights patches according to their size (for detailed explanations and equations, see McGarigal and Marks 1995). By comparing the MSI and the AWMSI, we can determine if large patches are more irregular in shape than the average. Fractal analysis was used to investigate in detail how patch shape varies with patch size. The principle being that if there are multiple reasons for the origin of a patch type, and in particular if these processes operate at different scales, the patches of different size should have different shapes (Krummel et al. 1987; Pastor and Broschart 1990). Successive linear regressions of log (Perimeter) against log (Area) of the patches of each forest type were performed by removing the smallest and adding the next largest patches (Lovejoy 1982; Krummel et al. 1987). The fractal dimension (D) of a geometric shape was then equal to twice the slope of the regression line. For smooth shapes, D=1, whereas for more complex shapes, D approaches the value 2.

In the spatial adjacency analysis, three kinds of forest patches were identified according to the connectivity of the deciduous patches and coniferous patches. One is the composite patch, which is formed by adjacent coniferous and deciduous patches; the other two types are unitary coniferous patches and unitary deciduous patches, which are composed of a single coniferous patch or a single deciduous patch respectively. Whether coniferous patches are completely surrounded by deciduous patches was also examined.

*2.3.3 Spatial analysis of the pattern of forest patches on surface deposit and land use*

A series of GIS overlay analyses were carried out to investigate the distribution of forest patches on previous land use and surface deposit. The basic premise is that if coniferous and deciduous patches segregate according to some surface deposit types or past land-use types, then they should be associated with that type to a greater or lesser degree than would be expected at random (Pastor and Broschart 1990). We also investigated the proportional difference of the forest type (i.e. the percentage of coniferous or deciduous forest on the total forest area) among different surface deposits and different past land uses. In addition, from the five land-use maps we derived a layer showing five forest recovery phases, i.e. (1) old forest land, which was forest before 1958; (2) forest recovered between 1958-1965; (3) forest recovered between 1965-1973; (4) forest recovered between 1973-1983, and (5) forest recovered between 1983-1993. We then overlaid the layer of the five forest recovery phases with the present forest patch layer to investigate the proportional difference of forest patches with different ages. In order to compare the difference in neighboring land-use types surrounding the deciduous and coniferous patches, a layer with a two pixel-wide (60m) boundary around each patch was created. This layer was then overlaid with the present (1993) land-use layer. The percentage of each land-use type within the boundary was calculated.

*2.3.4 Regression analysis of land use and landscape physical attributes with occurrence and abundance of coniferous patches*

In order to identify the relative contributions and combinations of landscape physical attributes and land use that explain the occurrence as well as the abundance of conifers, the reforestation from the land abandoned in 1958 was investigated. First, we identified 262 patches of abandoned land from the 1958 land-use map. We then excluded those patches which have been deforested again from 1958 onward with the land-use maps of 1965, 1973, 1983, 1993. After this step, 83 patches were kept for analysis. By overlaying the layer with 83 abandoned land patches to the layer with present forest patches, we classified the abandoned land patches into two categories, i.e. the patches with conifers (47 patches) after 37 years, as well as the patches without conifers (36 patches) after 37 years. Furthermore, the percentage of conifers on the total forest area for each abandoned land patch was also identified. Similarly, by overlaying the layer with 83 abandoned land patches to the layers of surface deposit and topography respectively, the physical attributes were retrieved. It includes the percentage of each surface deposit type, the number of different surface deposits, the average elevation, and the range of elevation in each abandoned land patch. With the GIS buffer and overlay manipulation, the past land-use information, which includes the percentage of each land-use type around the abandoned land patches (60 m), the number of different neighboring land uses, and the area and shape (Fractal Dimension) of each abandoned land patch were also retrieved. Logistic regression and multiple linear regression analysis (SAS Institute Inc. 1988) were used respectively to explain the occurrence and abundance of conifers with the above retrieved land use and physical attributes.

## 2.4 Results

### *2.4.1 Overview of the spatial pattern of the forest patches*

Forest occupies only 29.9% of the total landscape area. It is fragmented by agriculture into as many as 422 patches. The forest patch density is 3.1 patch / 100 ha. The mean forest patch size is 9.6 ha and 70% of the forest patches are less than 1.0 ha in size. The forest patch shape becomes more complex with the increase of the patch size, as the mean shape index (MSI) is 1.3 while the area-weighted MSI (AWMSI) is 6.3.

### *2.4.2 Coniferous vs. deciduous patches*

Analysis at the level of coniferous vs. deciduous patches highlighted the difference between the two patch types. Deciduous forest patches are dominant. They constitute 82% of the total forest area, while coniferous patches occupy only 18% of the total forest area. In addition, coniferous forest patches are relatively small and their shapes are relatively simple (Table 2-1). However, fractal analysis of the two kinds of patches show that the curves of the fractal dimension against the log of area are very similar (Fig. 2-2a and Fig. 2-2b). When the area is less than 0.54 ha (log (A) = 8.6 $m^2$), the fractal dimension fluctuates around 1.2; when the area is greater than 0.54 ha, the fractal dimension gradually increases to 1.3-1.4. This may indicate that different factors influence the shape of the small and the large patches for both forest patch types.

Three adjacency properties are revealed by the analysis of the spatial adjacency of the deciduous and coniferous patches. First, landscape fragmentation does not isolate the distribution of coniferous patches from deciduous patches. Actually, isolated coniferous forest patches are rare and their sizes are small (Table 2-2). Second, in most of the composite patches, deciduous forests are dominant. Results showed that of the 101 composite patches, only 15 patches have >60% coniferous area and only 7 patches have >70% coniferous area. Finally, the coniferous patches which are completely surrounded by deciduous forest are few and their size is small. Only about 29% of the coniferous forest patches (164 patches) are completely surrounded by deciduous forest. Their mean sizes are 0.58 ha and they occupy 14% of the total coniferous forest area. In other words, most of the conifer patches are located on the margins of the overall forest patches and are connected to other land-use types such as crop and pasture.

*2.4.3 Spatial pattern of the forest patches in relation to the pattern of past and present land use*

Two salient patterns are identified through the analysis of the relationships between the present forest pattern and past land use. First, the percentage of the present conifers in the total forest area is higher on relatively older aforested land than on newer aforested land (Table 2-3). This indicates the expansion of conifers with the increase of the forest stand age. Second, 67.9% of the conifer area in the aforested land from 1958 onward are coalesced with the conifer patches distributed on the old forest land (before 1958). In other words, only 32.1% of the conifer areas in the aforested land after 1958 are distributed separately from the old conifer patches. They represent 44.0% of the total number of conifer patches. This result reveals the importance of neighboring conifer patches on the origin of the conifer patches. The above two patterns not only indicate conifer expansion, but also suggest a likely mechanism: the invasion from the neighboring conifer patches, rather than the creation of new patches, is an important process of conifer expansion.

Without considering the difference of the surface deposit, results show that no matter whether the past land use was crop, abandoned land or pasture, the coniferous and deciduous proportion of present forest is almost the same. However, considering the difference of the surface deposit, results show that on clay deposits, the percentage of coniferous forest is obviously higher in those forests which are restored from the pasture (26.60% of the total forest area), than in those restored from crop (11.06% of the total forest area). This result indicates that past land-use type plays a more important role in conifer distribution on clay deposits than on morainic deposits.

The present neighboring land-use types are surrounding the two kinds of forest patches in different proportions. Results show that 66.66% of the coniferous forest boundaries are composed of deciduous forest, whereas only 42.22 % of the deciduous forest boundaries are occupied by coniferous forest. This difference may reflect the area difference between the two types of forest. The interesting result is that the percentage of crop land use surrounding the conifer patches is much lower than the percentage of crop land use surrounding the deciduous patches, while the pasture and abandoned land occupy the same percentage around both types of forest patches (Table 2-4).

*2.4.4 Spatial pattern of the forest patches in relation to the pattern of surface deposit*

There are strong positive associations between both deciduous and coniferous forest patches and the morainic deposit, and negative associations between the two types of forest patches and the marine deposit. In the study area, although clay deposits occupy a larger area than moraine, only 10.7% of the coniferous forests and only 14.6 % of the deciduous forests are distributed on clay deposits, whereas 76.7% of coniferous forest and 65.8% of deciduous forests are distributed on glacial deposits. Nevertheless, there are still different proportions of the coniferous forests on different surface deposit types. Our analyses show that on clay deposits, coniferous forest occupies 14.8% of the total forest area, whereas on glacial deposits, it occupies 20.4% of the total forest area.

*2.4.5 Combined effect of past land use and landscape physical attributes on conifers*

Logistic regression failed to select any significant physical attribute or land-use factors explaining the presence of conifers on the past abandoned land. However, multiple linear regression selected 10 factors explaining the relative abundance of conifers on the past abandoned agricultural patches (Table 2-5). Among them, five factors, i.e., patch area of abandoned land, number of different neighboring land uses, percentage of pasture in neighboring land use, number of different surface deposit types, and percentage of glacial deposits, are all significant. Land-use factors appear to explain much more variance than the selected landscape physical attributes (Table 2-5). The most significant factor which explains the abundance of conifers is the patch area of abandoned land. This indicates that if conifers successfully colonized, their development largely depended on the available abandoned land area. The results also show the importance of the presence of diversified land uses around the abandoned land, as well as of the presence of pasture.

### *2.5 Discussion and conclusions*

Although the vegetation of Haut-Saint-Laurent was mostly composed of sugar maple, hemlock and American beech (Brisson et al. 1988), there have been vast conifer forests mostly composed of white pine in the precolonial forest of the study area (Sellar 1888; Simard & Bouchard 1996). Because of high economical value, conifers were depleted from the forest in the last century (Simard & Bouchard 1996). Our analyses reveal a recovery process of conifers with the abandonment of agricultural land. On past abandoned land, conifers expand with increasing stand age, and a major mode of expansion is by invasion from the neighboring coniferous patches. The factors explaining the pattern of conifers in the present landscape are different from those in the precolonial period. Nowadays, coniferous patches are usually located on the margins of the overall forest patches, and they are connected to non-forest land-use types such as crop and pasture.

In the Haut-Saint-Laurent agricultural landscape, physical attributes explain only a small proportion of the abundance of conifers on abandoned land compared with land-use factors. In addition, coniferous or deciduous patches are not associated with a specific surface deposit. Physical attributes influenced the forest pattern only indirectly, because they strongly influenced the land use practices. In the past several decades, because of the high agricultural potential of clay deposits, most of the forest area on the clay deposits has been transformed into agricultural land (Pan et al. 1999). As a result, most of the present forests are confined to glacial deposits. Therefore, we can still see a strong determinism of physical factors at both the overall forest level, and at the deciduous vs. coniferous level. Most forests, no matter if coniferous or deciduous, are distributed on glacial deposits rather than on clay deposits.

In our study area, at the species level, Leduc et al. (1992) showed that the spatial distribution of more than half of the tree species which they studied did not track the measured environmental variables (geomorphology, drainage, stoniness of the soil). At the community level, Meilleur et al. (1994) showed that 23 out of 47 forest community types are not statistically significantly associated with any surface deposit features. At the landscape level, our results also show that physical attributes only indirectly influenced the forest pattern by influencing the land-use practices. All of the above results clearly show that the role of the physical factors have been modified by human land use in different manners and intensities. In order to explain the forest patch pattern, human land use must be taken into account.

Present spatial patterns of land use play obvious roles in the deciduous vs. coniferous patch pattern. Because of the edge effect, the boundary environments of the forest islands are different from the core environments (Ranney et al. 1981; Forman 1995). The core environments are more similar to those of natural forests. Therefore, natural gap-phase replacement processes may not be mediated by the agricultural land-use pattern. Our results show that conifer patches are usually in contact with the non-forest land-use types, and only some small conifer patches are completely surrounded by deciduous patches. This pattern suggests that the boundary environments are more suitable for conifers, and that the factors controlling the conifer patches are not the same for the large patches located at the margins of the forest island, compared to the few small patches which are completely surrounded by deciduous forest. The fractal dimension analysis results, where the shape of large and small patches are different, support this interpretation. In natural gap-phase replacement of deciduous forest, conifers such as white pine or white cedar occur rarely. This can explain why there are only some small coniferous patches completely surrounded by deciduous forest. Conversely, the boundary environment of the forest patch is not only relatively open, but provides easy access for various types of human disturbances, such as cattle grazing, which are more favorable to the colonization and development of coniferous species, such as white cedar. The important role of diversified land-use types around the abandoned land on the abundance of conifers is in agreement with this interpretation. Therefore, the land-use pattern, which produces two kinds of forest island environment, plays a direct role on the deciduous vs. coniferous forest patch pattern. The dynamics of the proportion of conifers in each forest patch should be mainly determined by the maintenance of those coniferous patches at the margins of the overall forest patches, and the direct interactions at the boundaries of the two types of patches.

The role of pasture on conifers is obvious. Our results show that on clay deposits, the proportion of coniferous forest is higher when they are restored from abandoned pasture than when restored from abandoned crop land use. In addition, the occurrence of pasture around abandoned land has a significant effect on the abundance of conifers. De Blois and Bouchard (1995) found that in mesic sites, large and nearly monospecific stands of white cedar occur in similar habitats as the ones colonized by sugar maple. Their analyses showed that cattle grazing has played a significant role in the appearance of white cedar stands on mesic sites. Our results at the landscape level support their conclusion.

Our results also indicate the important role of the biotic properties of white cedar on the expansion of conifers. White cedar has strong invasion ability with vegetative propagation. In the study site, vegetative reproduction accounts for at least 60 to 80% of all standing trees within cedar stands (de Blois and Bouchard 1995). The result that the predominant mode of expansion of conifers is by invasion from neighboring conifer patches indicated that vegetative propagation must play a more important role than seed dispersal. Vegetative propagation produces a genetic homogeneity within stands (Lamy et al. 1999). Once cultivated land is abandoned, the neighboring white cedar can rapidly invade through vegetative propagation. In addition, the colonial dense conifer patches may also prohibit the invasion of later successional trees and contribute to the maintenance of conifer patches as seen with other colonial species (Peterson and Squiers 1995). Our results clearly show the invasion of abandoned land by conifers within about 40 years. This is particularly interesting in a landscape that was perceived as being essentially deciduous (Dansereau 1946, 1959; Grandtner 1966). These pioneering studies had emphasized the relationships between vegetation types and environment variables. However, by showing the importance of some coniferous forest types, that did not exist in the precolonial forest, a new perspective emerges when landscape and, especially, land-use dynamics are taken into account.

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Table 2-1. Characteristics of coniferous vs. deciduous forest patches

| Forest patch type | Area (ha) | Percent of landscape (%) | Number of patches | Average patch size (ha) (SD) | Patch shape MSI* | AWMSI* |
|---|---|---|---|---|---|---|
| Coniferous | 733.77 | 5.39 | 564 | 1.301 (3.0) | 1.23 | 1.786 |
| Deciduous | 3336.54 | 24.51 | 703 | 4.764 (53.55) | 1.29 | 7.447 |

* MSI = Mean Shape Index; AWMSI = Area Weighted Mean Shape Index.

Table 2-2. Characteristics of the three adjacent types of forest patches.

| Patch type | Number of patches | Patch size (ha) (SD) | Percent of total forest area (%) |
|---|---|---|---|
| Unitary coniferous | 21 | 0.167 (0.10) | 0.086 |
| Unitary deciduous | 300 | 0.815 (1.64) | 6.008 |
| Composite | 101 | 37.854 (183.71) | 93.906 |

Table 2-3. Coniferous and deciduous forest proportion of total forest area on the land recovered in different periods.

| Forest type | 1958-1965 (%) | 1965-1973 (%) | 1973-1983 (%) |
|---|---|---|---|
| Coniferous | 24.81 | 16.20 | 15.82 |
| Deciduous | 75.19 | 83.80 | 84.18 |

Table 2-4. Land-use proportion within the boundaries of the two types of forest patches.

| Forest patch | Forest (%) | Crop (%) | Abandoned land (%) | Pasture (%) |
|---|---|---|---|---|
| Coniferous | 66.66 | 17.18 | 10.75 | 4.00 |
| Deciduous | 42.22 | 36.50 | 13.93 | 4.47 |

Table 2-5. Results of the multiple regression analysis for the abundance of conifers in the abandoned land. The order of physical factors and land use is according to the forward selection option.

| Physical factors and land use | Partial $R^2$ |
|---|---|
| Patch area of abandoned land | 0.2423** |
| Number of different neighboring land uses | 0.2202** |
| Percentage of pasture in neighboring land use | 0.1308* |
| Number of different surface deposit types | 0.1303* |
| Percentage of glacial deposit | 0.0624* |
| Elevation range | 0.0297 |
| Percentage of residential area in neighboring land use | 0.0201 |
| Percentage of crop area in neighboring land use | 0.0182 |
| Average elevation | 0.0083 |
| Percentage of forest area in neighboring land use | 0.0115 |

* $0.01<p<0.05$; ** $p<0.01$.

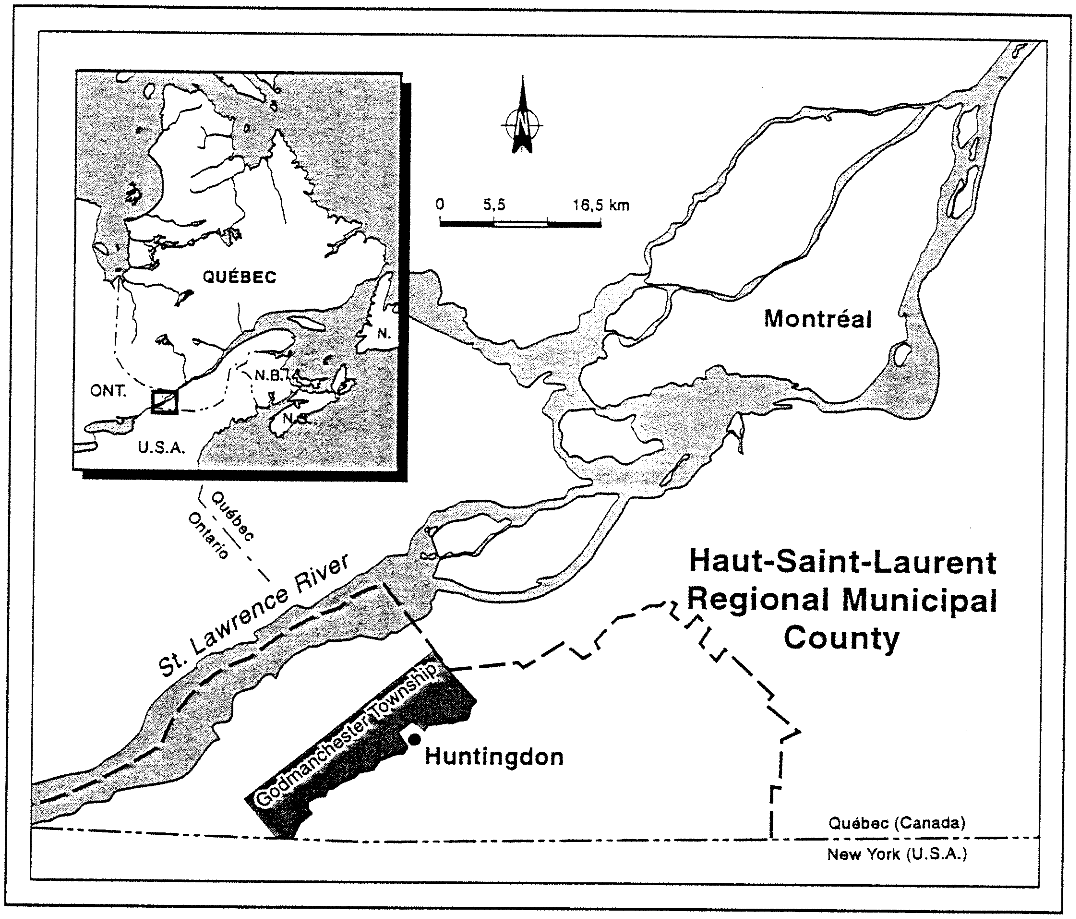


Figure 2-1. Location of the study area

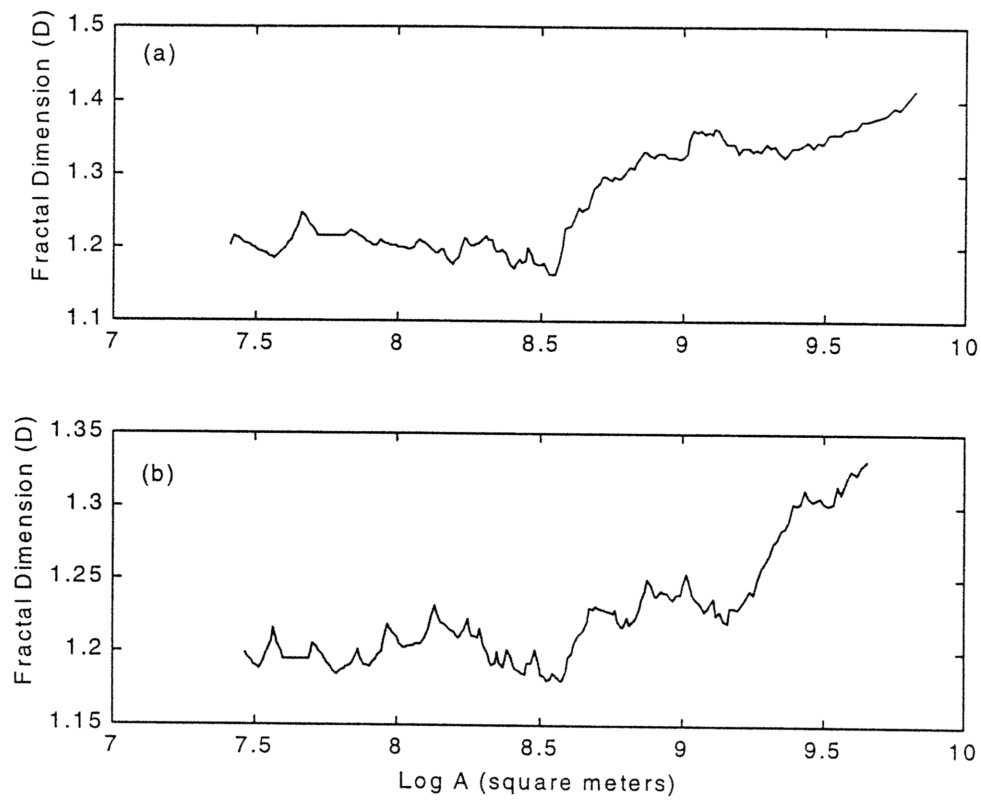


Figure 2-2. Changes of fractal dimension (D) against log of area ($m^2$) for deciduous (a) and coniferous patches (b).

# CHAPTER THREE

## Temporal (1958-1993) and spatial patterns of land use changes in Haut-Saint-Laurent (Quebec, Canada) and their relation to landscape physical attributes

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***Abstract***

In the last few years, landscape researchers have sought to understand temporal and spatial patterns of landscape changes in order to develop comprehensive models of land cover dynamics. To do so, most studies have used similar methods to quantify structural patterns, usually by comparing various landscape structural indices through time. Whereas the necessity for complementary approaches which might provide insights into landscape dynamics at some finer scale relevant to local managers has been expressed, few studies have proposed alternative methodologies. Moreover, the important relationship between the physical constraints of the landscape and land use dynamics has been seldom emphasized. Here we propose a methodological outline which was applied to the study of a rural landscape of Southern Quebec, Canada, to detect spatial and temporal (1958 to 1993) patterns of land cover changes at field, patch and landscape level. We then relate these patterns to the underlying physical structure of landscape elements using GIS and canonical correspondence analyses. We use the different geomorphological deposit types as stable discriminant factors which may constrain land use.

Canonical correspondence analyses showed relations of land use and land use changes to the physical attributes of the landscape elements, whereas spatial analyses revealed very dynamic patterns at finer spatial and temporal scales. They highlighted the fact that not only the physical attributes of the landscape elements but also their spatial configuration were important determinants of land use dynamics in this area. Thus more land use changes occurred at the boundary between geomorphological deposit types than in any other locations. This trend is apparent for specific small-size changes (e.g. forest to crop), but not for the large-size ones (e.g. abandoned land to forest). Although land use

changes are triggered by socioeconomic forces in this area, these changes are nevertheless constrained by the underlying physical landscape structure. A thorough comprehension of historical changes will enhance our capability to predict future landscape dynamics and devise more effective landscape management strategies.

*Keywords:* Canonical correspondence analysis; geographical information system; geomorphological deposit; landscape index; land use change, patch and field scale, physical attribute, Quebec.

### 3.1 Introduction

In the last few years, landscape researchers have sought to understand temporal and spatial patterns of landscape changes in order to develop comprehensive models of land cover dynamics (e.g., Baudry 1993; Iverson 1988; Medley et al. 1995; Simpson et al. 1994; Turner & Ruscher 1988; and many others). In most regions, these changes are thought to be driven by the complex interactions of physiographic and socioeconomic factors (Forman 1995; Zonneveld 1995). Indeed human activity is a major force in shaping regions, whereas the underlying physical structure of a landscape often constrains land-use (Bouchard et al. 1985; Domon et al. 1993; Iverson 1988). A thorough comprehension of the patterns, the causes and both the social and ecological consequences of historical changes will enhance our capability to predict future landscape dynamics and devise more effective landscape management strategies (Kienast 1993). This is especially important in rural settings where conflicts often arise between the multiple social, economic and ecological functions of the landscape (agriculture, forestry, recreation, biodiversity conservation etc.) (Merriam 1988; Turner et al. 1996).

Most studies aimed at understanding rural landscape dynamics have used similar analytical approaches to quantify structural patterns, usually by comparing various overall landscape structural indices through time and/or for different physiographic regions. Few, however, have focused on the relationship between the physical constraints of the landscape and land use patterns. Iverson (1988), for example, showed in a study of land use changes in Illinois USA that most of the present land use patches were poorly correlated with natural characteristics of the landscape and Baudry (1993) concluded that farmers' decisions were more important than physical factors in explaining land use changes in a rural European setting. Simpson et al (1994), on the other hand, emphasized changes at the physiographic region level and correlated greater geomorphological diversity with greater land cover dynamism at the landscape scale. Clearly more data are needed to understand how stable physical attributes of landscape elements really constrain land use and determine land cover changes, so that some generalization can be made over a range of similar landscapes.

Whereas most studies have brought a significant contribution to the development of a general rural landscape model, they also have emphasized the necessity for complementary approaches which might provide insights into landscape dynamics at some finer scale relevant to local managers (Hulshoff 1995). Landscape indices can be used to detect broader patterns of changes at the landscape scale, but their use must be complemented by some other analyses in order to extract fine-scale aspects of spatial and temporal patterns. This was recognized by many researchers including Kienast et al. (1993) who proposed a spatio-temporal data model which allows the user to generate information about land cover dynamics for each landscape element. When such analytical tools are combined with general information about changes in landscape structure and when the resulting patterns of land cover changes are related to the fine-scale physical characteristics of the landscape, significant insights can be gained into regional landscape dynamics.

In order to resolve these issues, we propose a methodological outline which was applied to the study of a rural landscape of Southern Quebec, Canada, in order to detect spatial and temporal patterns of land cover changes at field, patch and landscape level from 1958 to 1993. We then relate these patterns to the underlying physical structure of landscape elements. We use the different geomorphological deposit types within the landscape as a stable discriminant factor which may constrain land use, and we focus on very dynamic patches at the boundary between different deposit types. The current investigation is part of a long-term multidisciplinary project which has produced several ecological and land management studies in the same area (for an overview see Bouchard & Domon 1997) and, in particular, complements the study of Paquette and Domon (1997) who analyzed the relationship between landscape dynamics and physical factors in the 19th century for the same landscape.

### *3.2 Study area*

Our study area is located in the Haut-Saint-Laurent regional county municipality in the southernmost part of the Province of Québec, Canada. The Haut-Saint-Laurent covers an area of 1148 $km^2$ (Fig. 3-1) and is bounded by the St-Lawrence River to the North and New York State (USA) to the South. It belongs to the humid mid-cool temperate ecoclimatic region of Canada with warm summers and relatively mild winters (Ecoregions Working Group 1989). Annual average temperature is 6.1°C in Huntingdon (altitude 75 m) and average seasonal temperature ranges from -10°C in January to 20.8°C in July. Precipitation is evenly distributed throughout the year with a slight increase in summer, mean total being between 961 mm - 975 mm (Jean & Bouchard 1991). This area is part of the hickory-maple region of the deciduous forest region of the Great Lakes and St. Lawrence river system (Braun 1950). In the last century, this region has been extensively exploited for timber (Bouchard et al. 1989; Simard & Bouchard 1996). Today the remnant forest patches stand out from a matrix of agricultural land mostly occupied by dairy farms.

For the purpose of this study, we selected a landscape (sensu Forman 1995) of 95 $km^2$, which includes most of the municipality of Godmanchester. We chose this area because it represents the general geomorphology features of the whole Haut-St-Laurent (Fig. 3-1). The area lies on a bed of dolomite, limestone and shale of the Beekmantown group, represented by the Beauharnois formation (Globensky 1981). Glacial recession left numerous moraine islets and morainic ridges lying parallel to the St. Lawrence river (Bariteau 1988), whereas lowlands are covered with rich marine clay deposits of the Champlain Sea. In some areas there are also large biogenic (peaty) deposits.

## 3.3 Methods

### *3.3.1. Database development*

Using SPANS GIS software (INTERA TYDAC 1991) we developed a spatial database which included primarily five temporal land use layers - 1958, 1965, 1973, 1983 and 1993 (Fig. 3-2) - a geomorphological deposit layer (Bariteau 1987, 1988) (Fig. 3-1), and a topography layer. Although the area includes as many as 7 different types of deposit, moraine (42.05%), marine (43.34%) and biogenic deposits (10.80%) occupy more than 95% of the total area. Therefore our results are only shown for these three deposit types.

The establishment of the database included the following procedures. We first interpreted the land use from 1:15000 black and white aerial photographs. In order to minimize possible interpretation errors, all aerial photographs were taken between May and June. In addition, all interpretation work was carried out by the same person and the land cover classification system included only 6 types: forest, crop, residential, abandoned land, water, and pasture. Field boundaries, defined by the property boundaries marked by fencerows or ditches, were also digitized and used for field level analyses. Digitization of the five temporal land use maps, geomorphological deposit map and topography map was carried out using TYDIG (INTERA TYDAC 1991) software and maps were registered into a uniform projection. The resolution of the original raster data is 15.66 × 15.66 meters per cell, which is equivalent to the quad level 13 of the quad tree format in SPANS.

### *3.3.2 GIS analyses and landscape indices computation*

Spatial analyses were carried out to 1. describe structural landscape patterns and overall land use changes over time and measure the rate of change; 2. relate overall land use dynamics to physical features of the landscape; and 3. identify fine-scale spatial and structural patterns of patch dynamics in relation to the physical features of the landscape.

From the five temporal land use layers, four land use transformation layers were extracted by respectively overlaying the successive land use layers, namely, 1958-1965, 1965-1973, 1973-1983, and 1983-1993. These four layers recorded the type of land use changes that occurred in these time periods. The transition matrix for every successive layer was then built to measure the rate of land use change in different time intervals. The four land use transformation layers were used for subsequent analyses with GIS and for the canonical correspondence analyses.

To extract fine-scale information on patch dynamics, all five temporal land use layers were overlaid together. Different maps depicting dynamics at the patch scale were prepared by further sorting the overlaid result with a program created for this study. The idea of this procedure is very similar to the spatio-temporal data model in the vector based GIS (see Kienast 1993). With this procedure, two basic patch layers were produced. In the first one, patches were coded by their dynamic course type; i.e., at this point a patch was defined by its land use history over time. In the second layer, patches were coded by their sizes. Patches were also classified into categories according to the number of times they had changed - one, two, three or four times - over the time series. Data could then be generated by this model to relate patch dynamics to geomorphological features of the landscape.

To analyze temporal and spatial patterns of land use changes in relation to different geomorphological deposit types and distance to the geomorphological deposit boundary, the five temporal land use layers, the four transformation layers and the two basic patch layers were each overlaid with the geomorphological deposit layer and the geomorphological boundary layer. We derived the geomorphological deposit boundary layer by creating buffer zones of different widths around deposit patches (Burrough 1986). The buffer layer had 6 categories, 1 to 5 respectively representing different distances (1-5 cells) to the boundary by cells, 6 representing any distance larger than 5 cells. The electivity index (Jacobs 1974; Jenkins 1979; Pastor & Broschart 1990) was then calculated to examine the relationships between the land use change and deposit boundary. The formula was:

$$E_{ij} = \ln[(r_{ij})(1-p_j) / (p_j)(1-r_{ij})]$$

where $E_{ij}$ was the electivity index for dynamic course type i to deposit boundary category j, $r_{ij}$ was the proportion of dynamic course type i on deposit boundary category j and $p_j$ was the proportion of the landscape occupied by deposit boundary category j. An electivity index greater than 0 indicates a preference by the dynamic course type for the deposit boundary category. The electivity indices were tested against the chi-square distribution according to the formula:

$$\chi^2 = E_{ij}^2 / [1/x_{ij} + 1/(m_j - x_{ij}) + 1/y_i + 1/(n_t - y_i)]$$

where $x_{ij}$ was the area of dynamic course type i on deposit boundary category j and $y_i$ was the total area of dynamic course type i in the landscape, $m_j$ was the area of boundary category j and $n_t$ was the area of the entire landscape. The electivity indices for the total changed area to the deposit boundary were also calculated in the same way.

Because it is important to minimize the effect of possible positional errors incurred when interpreting and digitizing maps, especially when fine-scale changes are considered, we adopted two procedures. First, we filtered out small patches (less than 2 cells) after every overlay operation. Secondly, we decreased the resolution when doing the multivariate analyses (see below). The above analyses were mainly carried out on GRASS (USA CERL 1991) combined with other programs created for this study.

Finally, landscape structural indices were derived using SPAN (Turner 1990; Turner & Ruscher 1988) and SAS (SAS institute 1988). The data sets with the original resolution were used for SPAN analyses. Area, amount of edge, patch number and average size as well as four other landscape indices (dominance, diversity, contagion and fractal dimension) were computed over the time series. For detailed meaning and equations see O'Neill et al. (1988) and Turner & Ruscher (1988).

### *3.3.3 Multivariate analyses*

Canonical correspondence analysis (CCA) (ter braak & Prentice 1988) was used to evaluate the relations of land use and land use changes over time to physical attributes. CCA is an ordination technique that forces the land use axes (or land use change axes) to be linear combinations of physical attributes. Five land use matrices, one from each temporal land use layer, and four land use change matrices, one from each land use transformation layer, were generated by sampling individual grid cells in the study area. Each of these matrices was related to a physical attribute matrix which included the geomorphological deposit type, elevation, and distance to the deposit boundary for each grid cell. In order to reduce the effect of possible positional errors, we decreased the resolution of the maps. The dominant land use or physical attribute was assigned to each cell. The percentage of the constrained eigenvalue on the total variance (trace) was used to assess the strength of the relationships between the different land use data sets and the explanatory variables. Monte Carlo permutation tests were conducted to assess the effectiveness of the canonical axis in showing these relationships and to determine the significance of a specific physical attribute. Note that all stable grid cells or cells which were classified as residential or water were excluded from the analyses of the four land use change data sets as we focused on the transition of agroforested land use. These analyses were done with CANOCO 3.1 (ter Braak 1987).

## 3.4 Results

### *3.4.1 General patterns of landscape structure*

Overall, crop was the dominant land-use during the study period and showed little variation in terms of % coverage of the study area (Fig. 3-3). Landscape structural indices revealed a fluctuation in crop patch number at the landscape level (Fig. 3-3). At the crop field level, however, the coalescence process was evident (Table 3-1). This reflected the intensification of agricultural practices in the study area. Following crop, forest was the next most abundant land use type (Fig. 3-3). Its area consistently increased from 24.6% in 1958 to 34.5% in 1993, but forest patch size and number fluctuated with time (Fig. 3-3).

Abandoned land occupied from 5.3% to 13.6% of the total area (Fig. 3-3). From 1958 to 1973 it showed a sharp decrease in both area and patch number, then an increase from 1973 to 1983. With the exception of 1973, patch size of the abandoned land also decreased. Finally, the proportion of pasture also varied with time (Fig. 3-3). There was a little increase in the area, patch size and patch number from 1958 to 1965, followed by a sharp decrease from 1965 onwards.

The transition matrix (Table 3-2) highlights the dominant dynamic events during the study period and reveals two distinct transition phases. From 1958-1973, the lowest retention frequency was abandoned land, and the highest changing rate was from abandoned land to forest. From 1973-1993, however, the lowest retention frequency was pasture, and the highest changing rate was from pasture to abandoned land. The area of changes also fluctuated through time. The percentage of the changed area was 9.1% from 1958 to 1965, 14.9% from 1965 to 1973, 13.9% from 1973 to 1983 and 5.8% from 1983-1993.

The complexity of patch shape was shown by the fractal dimension (FD). Surprisingly, the FD of crop was consistently higher than that of forest, abandoned land and pasture. Generally, FD fluctuated with time, and diversity and contagion, except for a fluctuation in 1973, decreased with time.

*3.4.2 The relationship between physical attributes and land use dynamics*

There were clear relationships between land use types and geomorphological deposit types during the study period (Fig. 3-4). Our data show that, overall, crop was dominant on marine deposit, followed by forest (Fig. 3-4). By contrast, forest was the dominant land-use on moraine, and crop was second. On biogenic deposit (Fig. 3-4) the dominant category changed with time. Abandoned land fell from the first position in 1958 to the second position in 1965 and to the third position afterward, whereas forest increased from the second position in 1958 to the first position in 1965-1993 and crop increased from the third position in 1958 and 1965 to the second position in 1973-1993. Diversity was lower and dominance was higher on marine deposit than on biogenic deposit and moraine, although on biogenic deposit diversity steadily decreased. This reflects the highest potential of marine deposit or biogenic deposits for intensive agricultural practices in the region and the constraints imposed by glacial deposit on such activities. Note also that the area of changes was larger on moraine than on any other deposit for the study period. 62.6% of the changed area was on moraine compared to 20.7% on marine deposit, though moraine and marine deposits have almost the same total area.

Results of CCA of the five temporal land use data layers with physical attributes confirm these observations (Table 3-3). All first axes are positively correlated with moraine and negatively correlated with marine deposit. From the ordination diagrams (Fig. 3-5), we observe that crop has a low score on the first axis and distributes near marine deposit, whereas forest has a high score and correlates with moraine. The correlation coefficients of the remaining variables are small. Monte Carlo permutation tests confirm the overall significance of the canonical ordination ($p<0.01$) and the significance of the first axes ($p<0.01$). The importance of geomorphological deposits was further confirmed by significance test ($p<0.01$) for partial CCA where the other variables were used as covariables in the analysis. The overall influence of elevation and of distance to geomorphological deposit boundary on land-use type remains non-significant ($p>0.01$). The strength of the relationship between deposit type and land use type reached its peak in 1958-1965.

The results of CCA of the four land use transformation layers with physical attributes reveal interesting dynamic events (Fig. 3-6). Although eigenvalues and correlation coefficients are small compared to the results of the land use data sets, Monte Carlo permutation tests confirm the significance of geomorphological deposit types on land-use changes ($p<0.01$). Furthermore elevation and deposit boundary were also significant in some transition periods. The role of elevation was significant ($p<0.01$) except for the period 1973-1983. The role of distance to deposit boundary was significant in 1958-1965. The ordination diagrams (Fig. 3-6) show that some of the transition types had explicit deposit tendency. On moraine, abandoned land went to forest or pasture in 1958-1965 and in 1973-1983. On marine deposit, crop, abandoned land and pasture were the dynamic land-uses in 1965-1973.

*3.4.3 Fine-scale temporal and spatial patch dynamics*

The above results underline the fact that land use changes did not distribute randomly in space or time. On moraine, the area of land use changes was larger than on other locations whereas different types of land use changes tended to occur in specific physical conditions and at specific time. The following steps were carried out in order to understand more thoroughly the influence of the underlying physical configuration of the landscape on land use changes and describe the fine-scale temporal and spatial patch dynamics.

First, the distribution of frequency percentage of the dynamic patches with different sizes in relation to deposit types (Table 3-4) shows that, as size increases, so does the frequency percentage on biogenic deposit. Small size dynamic patches mainly distributed on moraine and marine deposit, whereas large ones mainly distributed on moraine and biogenic deposit.

The classification of the dynamic patches into four categories, i.e. 1. patch changed only one time, which occupied 52.76% of the total changed area; 2. patch changed two times (35.63%); 3. patch changed three times (10.31%) and 4. patch changed four times (1.30%) revealed an important feature of the landscape. Almost half of the dynamic parcels were quite unstable and shifted from one land use to another more than one time in the four time intervals.

The distribution of the dynamic courses on different deposits (Table 3-5) confirms that both the first and the second dominant changes, i.e. the natural reforestation of already abandoned land and the abandonment of pasture, occurred on moraine. Clearly these changes tended to occur mainly on large rather than small patches of moraine.

Finally, in the whole study period, the electivity indices for the total changed area decrease consistently with the increase of the distance to the deposit boundary (Table 3-6).

When the distance is larger than 3 cells, the index becomes negative. This reveals that more land use changes occurred within the distance of 3 cells (47 m) to the geomorphological deposit boundary than in other locations. Moreover, most of small-size dynamic courses such as from forest to crop and from pasture to crop had obvious boundary tendency (Table 3-5); whereas the large-size dynamic courses, the dominant courses from abandoned land to forest and from pasture to abandoned land did not have this tendency. Regardless of the difference of the categories, the distribution of the frequency percentage of the dynamic patches with different size along the geomorphological boundary (Table 3-4) shows that these boundary-oriented changes were obvious for dynamic parcels with small size (< 1.5 ha).

## 3.5 Discussion

### *3.5.1 Socioeconomic determinants of temporal landscape dynamics*

Our analyses reveal three important dynamic processes. Although we need to investigate further the correlation between the patterns we observed and specific socioeconomic factors, previous works in the study area (Domon 1990; Domon et al. 1993) as well as comprehensive studies on agriculture in Quebec (Boudreau et al. 1997; Morisset 1987; Séguin 1980) suggest that such processes have their roots in socioeconomic changes. First, from 1958-1973, the dominant dynamic process was the natural reforestation of already abandoned lands. This natural process driven by succession was initiated in the 1930's when, as records show, area under cultivation began to decline during the economic depression (Boudreau et al. 1997). Concurrent significant changes in agricultural practices which led to a concentration of crops on marine deposit also contributed to this process (see below). Accordingly, most forest fragments in the area are relatively young and successional species are abundant (Meilleur et al. 1993). Similar patterns were observed in other landscapes of North America where reforestation was triggered by socioeconomic changes (Dunn et al. 1991; Foster 1992; Simpson et al. 1994; Turner & Ruscher 1988).

The period from 1973-1993, on the other hand, was marked by the abandonment of pasture. This event coincided with significant changes in agricultural production in southern Quebec. Overall, dairy production became more efficient, going from 2862 liters/head/year in 1966 to 4386 liters/head/year in 1985, whereas milk demand reached a ceiling in 1970 (Bureau de la statistique du Québec 1986). In this context, milk producers were encouraged to turn to grain production (Domon 1990). In Huntingdon county, which includes our study area, grain producing area increased from 1000 ha in 1971 to 8700 ha in 1986 (Statistiques Canada 1971; 1986). All these factors combined to effectively reduce grazing on specific sites. This trend had dramatic consequences for the diversity of ecological communities which had been under intense grazing pressure. Hence, the numerous cedar stands on mesic sites in this otherwise deciduous landscape have their origin in the abandonment of grazing practices and many fallow lands are dominated by dense thickets of thorny shrubs which may effectively reduce invasion by more valuable forest species (de Blois & Bouchard 1995).

Another significant pattern which emerges from the analysis at the field level is the coalescence of crop patches, a phenomena also closely related to the increase in grain production. It is a direct consequence of the intensification of agricultural practices which resulted in the dominance of corn. Since fencerows were one of the main features used to map field boundaries, this result also indirectly monitors an overall decrease of these important landscape elements. This trend is currently being analyzed directly in an ongoing study by Schmucki et al. (unpubl.) on temporal and structural changes of fencerows in the same area. Such transformations may have ecological consequences on biodiversity and other ecological processes which remain to be fully assessed (Baudry & Merriam 1988; Fahrig & Merriam 1985; Forman & Baudry 1984).

Apart from these main dynamic patterns, our results reveal numerous temporal changes which highlight the intensely dynamic character of this landscape. Yet these patterns do not clearly emerge from the overall landscape indices such as fractal dimension, diversity, dominance or contagion, because they may be the result of numerous changes at the patch scale which might cancel out each other at the landscape scale. They strongly suggest, however, that modifications of socioeconomic factors and policies had a direct and immediate influence on land management by individual owners. A fine temporal and spatial scale analysis at the patch level therefore becomes essential to understand and appreciate fully the dynamic nature of this landscape.

### *3.5.2 Physical determinants of spatial landscape dynamics*

In a study of landscape dynamics in the 19th century for the same area, Paquette & Domon (1997), using spatially relevant information from census records, found no significant relationship between improved agricultural land and surface deposits and concluded that early settlers were farming indiscriminately either on the clay plain, on small morainic islets or ridges or even on peaty deposits, depending on the availability of the land. Data show that, at that time, agricultural activities occupied more than 70% of the landscape. Most of the forested areas had been harvested from 1800 to 1880 (Simard & Bouchard 1996) as population in this area reached a first peak in the mid-19th century. Agricultural activities, however, probably began on moraine because of its relatively good drainage conditions compared to the clay plains (Roy et al. 1998). Conversely, the patterns of land use that we observed in the second part of the 20th century are characterized by a strong physical determinism, as the various human activities were becoming more and more related to the underlying physical potentials and constraints of the landscape. Two significant events concurred to trigger these important changes. First of all, early pedological studies, while confirming the strong potential of clay soils for agriculture, also highlighted the fact that drainage was a problem (Mailloux & Godbout 1954). Consequently, governmental programs were implemented to improve drainage conditions on clay soils so as to increase their agricultural potentials. In the administrative unit which includes our study area, 41% of class A soils were drained between 1964 and 1984 (Domon 1990). Moreover, with the intense mechanization of agricultural practices, the stony moraines became less attractive to farm and forests began to recolonize these abandoned area. Finally, with the strong shift to grain production in the 1970's, increasing pressure was put on the available land on marine deposit.

The fine-scale spatial analysis of dynamic patterns highlights important trends which only confirm the strong relationship between the physical characteristic of the landscape and land use patterns. Some land use changes, such as from forest to crop, or from pasture to crop, tended to occur near deposit boundaries, whereas the dominant patterns, as from abandoned land to forest or from pasture to abandoned land were more likely to happen on moraine (Fig. 3-7). The boundary-oriented changes were obvious for dynamic parcels with small size (< 1.5 ha). As land use patterns were already strongly established in the first part of the 20th century in this area, there were few possible improvements to be made or area to be gained for agriculture on the rich marine deposit. The only leeway was near moraine islets where some fine-scale adjustments could be made. Our data suggest that edges between forest (or pasture or abandoned land) and crop were quite dynamic in this period. It is interesting to note that, in the last few years, with excellent prices for grain, one can still observe crops creeping up into small moraine islets in the landscape. In fact, the higher fractal dimension that was observed for crop might be partially explained by the fact that crop covers more area than any other land use and that it often has to circumvent numerous small morainic islets in the landscape, which would result in irregular edges. Thus, not only the physical characteristic of the landscape elements but also their spatial configuration are important determinants of land use dynamics in this area. We need to assess the ecological consequences of these recurrent disturbances at forest fragment edges which may impact both interior and edge species (Murcia 1995; Sparks et al. 1996). This process may also have important consequences for ecological flows at landscape boundaries (Hansen & di Castri 1992; Johnston & Bonde 1989; Wiens 1995).

### *3.5.3 Analysis methods*

The use of a geographic information system was essential for our overlay processing and multivariate analyses allowed us to evaluate effectively the different role of physical factors on overall land use structure and changes. Landscape indices, however, were more efficient in showing broader scale measures of pattern and in the detection of large temporal changes, but, as was also noticed by Hulshoff (1995) for a Dutch landscape, were less useful in the detection of fine-scale aspects of spatial patterns. Our analysis of patch dynamics and its relation to the spatial configuration of the stable geomorphological features of the landscape provided new insights into rural landscape dynamics and has several advantages over the single use of landscape indices patterns, one of which being that patch's location and history can both be extracted and displayed graphically. We believe that a combination of several approaches, (landscape indices, multivariate analyses, and patch dynamic extraction) will provide more comprehensive information on both temporal and spatial dynamics of landscapes which exhibit instability at small spatial and temporal scales but show relative stability at larger ones.

One always has to be cautious about drawing strong inferences when analyzing fine-scale patterns because of the potential errors inherent in the interpretation and overlay of land use maps. Regarding this matter, Chrisman (1989) identifies two basic types of error which are commonly present with digital map data. First, the misplacement of boundaries between parcels of different land cover types (positional error), and second, the assignment of parcels of land to inappropriate cover types (attribute classification error). Cherrill & McClean (1995) point out that the second kind of error is more serious than the first one. In our study classification errors were kept to a minimum by insuring constancy in photo interpretation, by reducing land use type categories to those that were easier to interpret, by double checking dubious land use transformation, and by validating recent photo interpretation in the field. Nevertheless, after each overlay procedure, we noticed that some very small patches were produced. We believe that most of these small patches might have been linked to positional error when digitizing and registering the maps. We found that removing these small patches had no significant effect on the values reported for land use changes and other landscape indices. However, to minimize the error, we not only filtered out the small patches after each overlay procedure, but also decreased the resolution when doing multivariate analyses.

### *3.6. Conclusion*

In a study of landscape dynamics in two contiguous Ohio landscapes for the 1940-1988 period, Simpson et al. (1994) reported that moraine landscape, owing to the lower inherent agricultural productivity of their soils, were showing more dynamism and diversity than the till plain. Our results corroborate these findings at finer scale and suggest that land use dynamics are driven not only by the proportion but also by the spatial arrangement of marine and glacial deposits in this rural area. Furthermore, we determined that land-use patterns in the second part of the 20th century were characterized by a strong physical determinism. This contrasts with the findings of a previous study in the same area which did not show any correlation between land-use types and the physical characteristics of the landscape in the 19th century (Paquette and Domon 1997). It also suggests that, although land use changes are triggered by socioeconomic forces and made possible by technological advancement -both factors varying in time-, these changes are nevertheless possible within the physical constraints of the underlying landscape structure. In some cases, however, these constraints can be overcome when the investment is worthwhile, as when demand for agricultural products is good and productive land is at a premium. Moreover, our study highlights the fact that one has to be cautious when interpreting patterns of apparent relative stability at the landscape scale which might hide greater dynamism at some finer spatial scale. Finally we believe that the methods used to investigate land use dynamics in this paper can benefit both the ecologist and the manager working at the regional level. Whereas the former will benefit from the understanding of patterns which might affect biodiversity and other important ecological processes in rural landscapes, the latter will be better equipped to develop effective management strategies and programs aimed at reconciling and enhancing both agricultural and forest productivity. In our area, we can anticipate, based on their physical and spatial characteristics, which sites are more liable to be stable and which sites are more liable to change. We are using this knowledge, in conjunction with information on the ecological requirements of forest species, to direct human interventions aimed at restoring the forest productivity of selected sites (Cogliastro et al. 1993; 1997) while preserving essential ecological processes. We are also currently using our land-use model to investigate the interrelation between physical factors, past and present land-use patterns, the spatial configuration of landscape elements, and plant species diversity in this landscape (de Blois et al. unpubl.).

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Table 3-1. Landscape indices for crop at the field level.

| Index | 1958 | 1965 | 1973 | 1983 | 1993 |
|---|---|---|---|---|---|
| Crop area ($km^2$) | 49.222 | 48.166 | 50.398 | 48.375 | 48.586 |
| Patch number | 1964 | 1906 | 1670 | 1695 | 1598 |
| Average patch size (ha) | 2.51 | 2.53 | 3.02 | 2.85 | 3.04 |
| Edge length (km) | 1003.64 | 979.74 | 958.85 | 952.03 | 934.28 |

Table 3-2. Land use transition proportion (%) in the whole region.

| Land use | Forest | Crop | Residential | Abandoned land | Water | Pasture |
|---|---|---|---|---|---|---|
| | | | | 1965 | | |
| 1958 | | | | | | |
| Forest | 96.93 | 0.86 | 0.01 | 1.13 | 0.00 | 1.08 |
| Crop | 0.66 | 95.96 | 0.16 | 1.24 | 0.03 | 1.94 |
| Residential | 0.24 | 3.09 | 95.53 | 0.21 | 0.05 | 0.87 |
| Abandoned land | 34.87 | 2.53 | 0.03 | 56.69 | 0.00 | 5.87 |
| Water | 0.15 | 1.49 | 0.11 | 0.03 | 98.15 | 0.07 |
| Pasture | 5.39 | 4.55 | 0.08 | 6.80 | 0.00 | 83.18 |
| | | | | 1973 | | |
| 1965 | | | | | | |
| Forest | 90.03 | 4.87 | 0.14 | 2.23 | 0.01 | 2.72 |
| Crop | 0.90 | 95.57 | 0.56 | 0.65 | 0.04 | 2.27 |
| Residential | 6.86 | 31.05 | 52.92 | 0.69 | 0.55 | 7.93 |
| Abandoned land | 40.90 | 13.45 | 0.58 | 37.07 | 0.01 | 7.99 |
| Water | 0.07 | 7.73 | 0.26 | 0.24 | 91.53 | 0.17 |
| Pasture | 5.40 | 25.01 | 0.69 | 11.46 | 0.00 | 57.44 |
| | | | | 1983 | | |
| 1973 | | | | | | |
| Forest | 92.15 | 3.50 | 0.59 | 2.92 | 0.00 | 0.78 |
| Crop | 1.01 | 91.85 | 1.56 | 2.72 | 0.07 | 2.71 |
| Residential | 4.37 | 15.93 | 74.78 | 2.57 | 0.04 | 2.11 |
| Abandoned land | 20.01 | 8.46 | 1.13 | 68.73 | 0.02 | 1.55 |
| Water | 0.41 | 2.01 | 0.46 | 0.03 | 95.94 | 0.03 |
| Pasture | 6.10 | 18.76 | 1.89 | 32.14 | 0.01 | 41.01 |
| | | | | 1993 | | |
| 1983 | | | | | | |
| Forest | 98.24 | 1.24 | 0.08 | 0.36 | 0.00 | 0.07 |
| Crop | 0.54 | 97.07 | 0.14 | 0.77 | 0.03 | 1.30 |
| Residential | 0.39 | 2.66 | 96.43 | 0.25 | 0.12 | 0.13 |
| Abandoned land | 20.21 | 8.08 | 0.10 | 71.12 | 0.00 | 0.49 |
| Water | 0.32 | 0.90 | 0.32 | 0.22 | 98.24 | 0.00 |
| Pasture | 4.03 | 10.08 | 0.49 | 29.86 | 0.00 | 55.54 |

Table 3-3. Correlations of physical attributes with the first and second canonical axes of the ordination analyses for land use data sets.

| | 1958 | | 1965 | | 1973 | | 1983 | | 1993 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Axis I | Axis | Axis I | Axis II | Axis I | Axis II | Axis I | Axis II | Axis I | Axis II |
| Biogenic deposit | 0.145 | 0.184 | 0.189 | 0.273 | 0.197 | 0.163 | 0.089 | 0.193 | 0.065 | 0.122 |
| Marine deposit | -0.603 | -0.033 | -0.639 | -0.024 | -0.620 | 0.019 | -0.621 | -0.040 | -0.614 | -0.032 |
| Morainic deposit | 0.525 | -0.075 | 0.535 | -0.137 | 0.511 | -0.115 | 0.576 | -0.073 | 0.583 | -0.039 |
| Deposit boundary | -0.137 | 0.116 | -0.113 | 0.143 | -0.059 | 0.076 | -0.132 | 0.073 | -0.132 | 0.053 |
| Elevation | 0.328 | -0.006 | 0.340 | -0.054 | 0.362 | 0.013 | 0.362 | 0.013 | 0.372 | 0.009 |

Table 3-4. The distribution of frequency percentage of the dynamic patches with different size in relation to deposit types and distances to deposit boundary.

| Patch size (ha) | Patch number | Deposit type | | | Deposit boundary (cell) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Biogenic | Marine | Morainic | <1 | 1-2 | 2-3 | 3-4 | 4-5 | >5 |
| <0.25 | 3151 | 0.07 | 0.33 | 0.60 | 0.31 | 0.21 | 0.12 | 0.06 | 0.05 | 0.24 |
| 0.25-0.50 | 521 | 0.11 | 0.31 | 0.58 | 0.19 | 0.20 | 0.16 | 0.10 | 0.08 | 0.26 |
| 0.50-1.00 | 407 | 0.14 | 0.30 | 0.56 | 0.17 | 0.18 | 0.17 | 0.11 | 0.10 | 0.27 |
| 1.00-1.50 | 224 | 0.19 | 0.30 | 0.51 | 0.16 | 0.17 | 0.17 | 0.14 | 0.12 | 0.25 |
| 1.50-2.00 | 106 | 0.15 | 0.28 | 0.57 | 0.15 | 0.16 | 0.16 | 0.15 | 0.13 | 0.25 |
| 2.00-3.00 | 121 | 0.25 | 0.23 | 0.52 | 0.13 | 0.14 | 0.15 | 0.16 | 0.16 | 0.26 |
| 3.00-4.00 | 59 | 0.29 | 0.24 | 0.47 | 0.14 | 0.15 | 0.16 | 0.15 | 0.15 | 0.26 |
| 4.00-5.00 | 27 | 0.30 | 0.24 | 0.46 | 0.15 | 0.14 | 0.15 | 0.14 | 0.14 | 0.27 |
| >5.00 | 71 | 0.40 | 0.15 | 0.45 | 0.14 | 0.14 | 0.15 | 0.15 | 0.14 | 0.28 |

Table 3-5. Characteristics of the main dynamic courses.

| Dynamic course | Total area (cell) | On biogenic deposit (cell) | On marine deposit (cell) | On morainic deposit (cell) | Patch number | Patch size (cell) | Electivity[a] Deposit boundary (cell) | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | 0-1 | 1-2 | 2-3 |
| 1 Abandoned land to forest | 24743 | 2996 | 1907 | 19667 | 271 | 91.3 | 0.03 | -0.05 | -0.04 |
| 2 Pasture to abandoned land | 7888 | 248 | 887 | 5923 | 84 | 93.9 | -0.03 | 0.04 | -0.01 |
| 3 Crop to pasture to crop | 4213 | 607 | 1757 | 1641 | 409 | 10.3 | 0.27* | 0.21* | 0.17* |
| 4 Crop to abandoned land | 3537 | 245 | 2064 | 1109 | 343 | 10.3 | 0.16* | 0.12* | 0.19* |
| 5 Pasture to forest | 3489 | 172 | 200 | 3024 | 257 | 13.6 | -0.15* | -0.10 | -0.02 |
| 6 Abandoned land to crop | 3025 | 1243 | 1188 | 488 | 256 | 11.8 | 0.14* | 0.04 | -0.01 |
| 7 Forest to crop | 2929 | 502 | 1213 | 1176 | 1017 | 2.9 | 1.07* | 0.59* | -0.17* |
| 8 Pasture to crop | 2787 | 119 | 928 | 1693 | 329 | 8.5 | 0.33* | 0.32* | 0.09 |

[a] See text for electivity definitions.
* Significant at $p<0.01$.

Table 3-6. Electivity indices for the total changed area[a].

| Deposit boundary (cell) | 1958-1965 | 1965-1973 | 1973-1983 | 1983-1993 | The whole period |
|---|---|---|---|---|---|
| 0-1 | 0.14* | 0.34* | 0.37* | 0.05* | 0.27* |
| 1-2 | 0.09* | 0.22 | 0.24* | -0.01 | 0.17* |
| 2-3 | 0.01 | 0.03 | 0.07* | -0.13* | 0.02 |
| 3-4 | 0.03 | -0.11* | -0.07* | -0.17* | -0.08* |
| 4-5 | -0.12* | -0.19* | -0.15* | -0.14* | -0.12* |

[a] See text for electivity definitions.
* Significant at $p<0.01$.

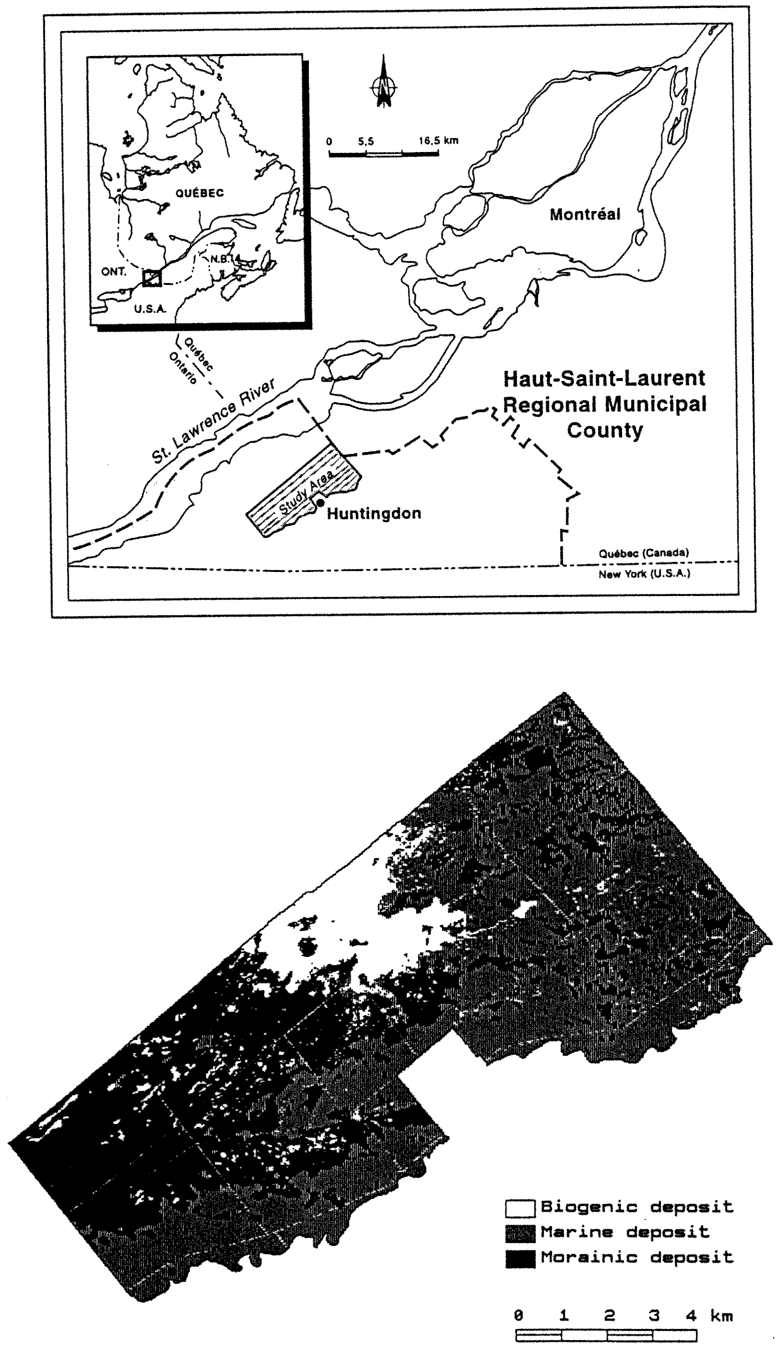



Figure 3-1. Location of the study area and main geomorphological deposit types.

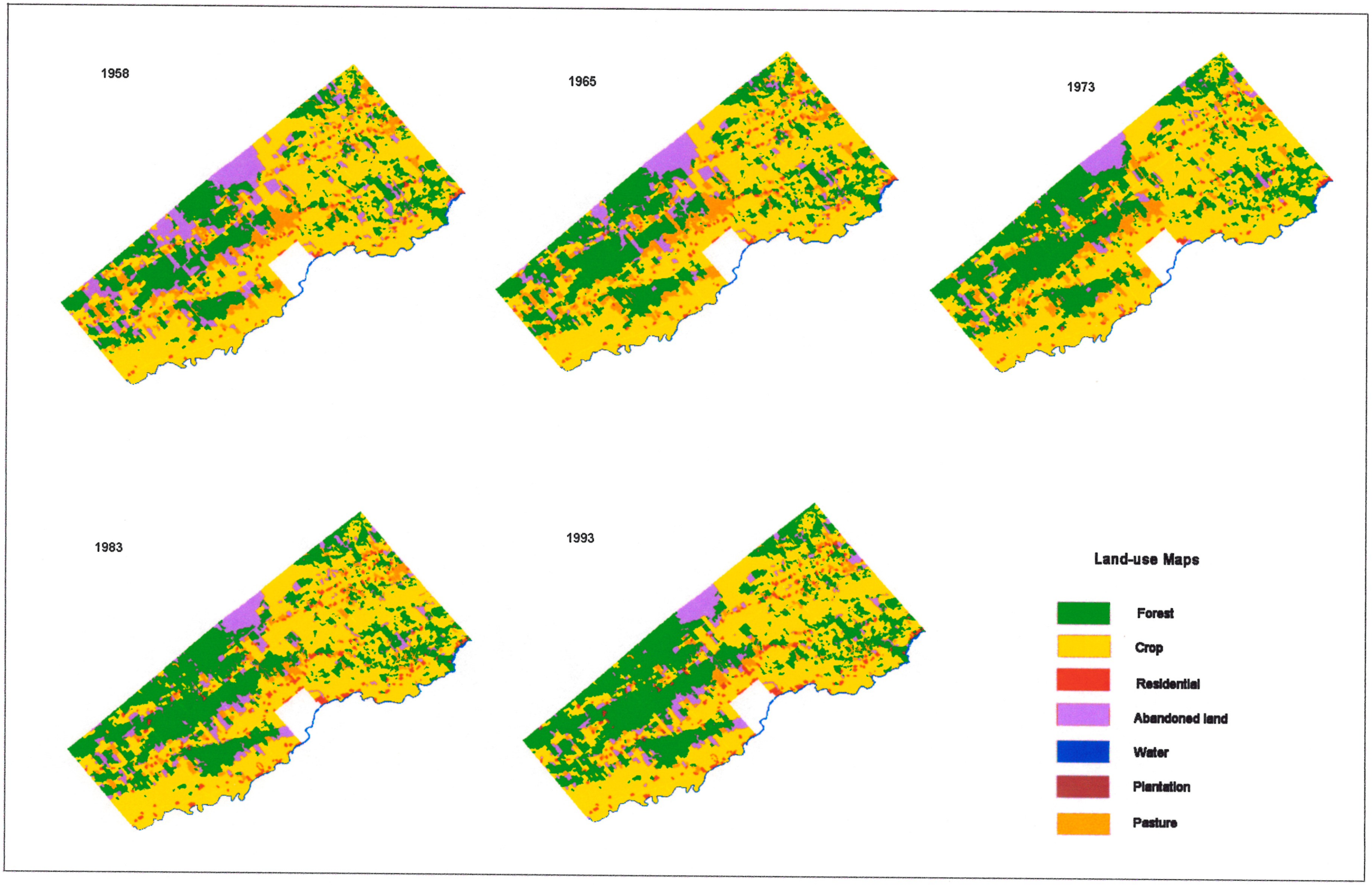



Figure 3-2. Land use maps of the study area in 1958, 1965, 1973, 1983 and 1993.

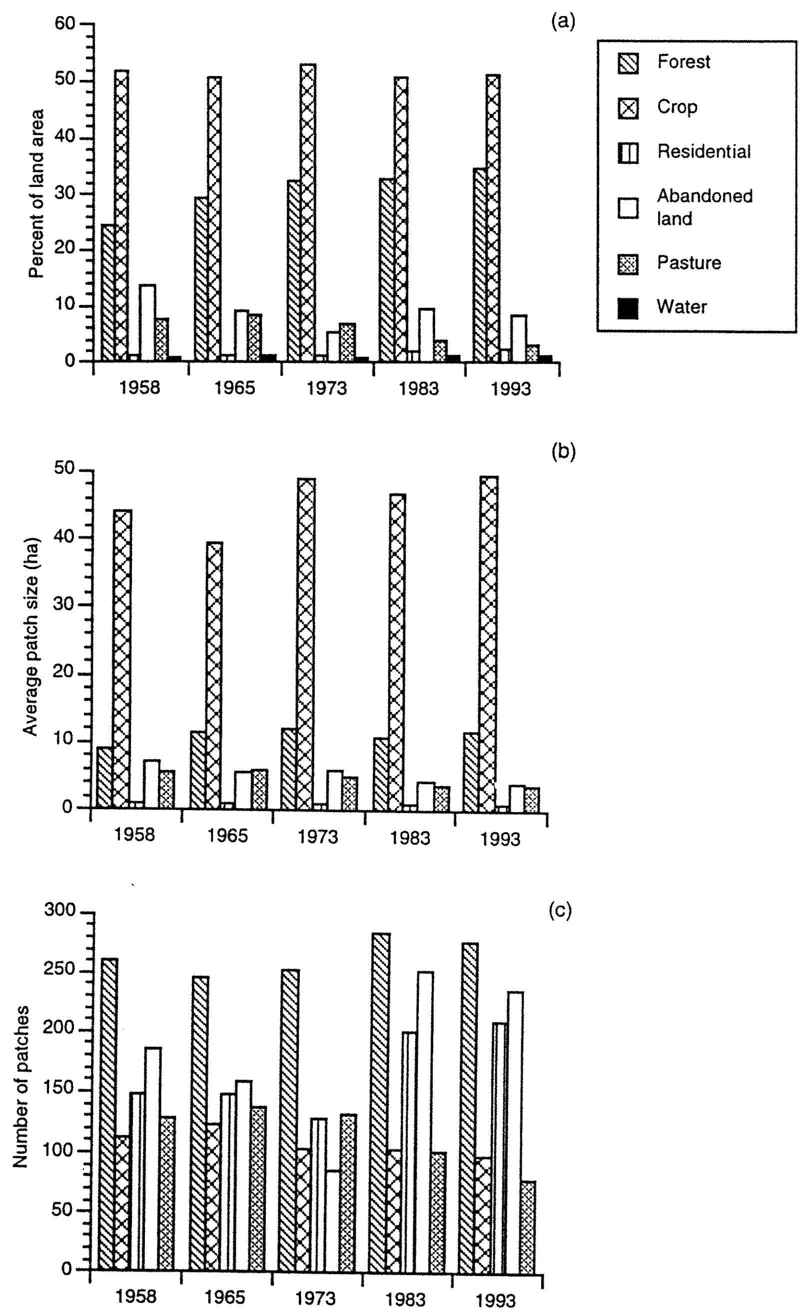



Figure 3-3. Area percentage (a), patch size (b), and patch number (c) for the land use types during the period 1958-1993.

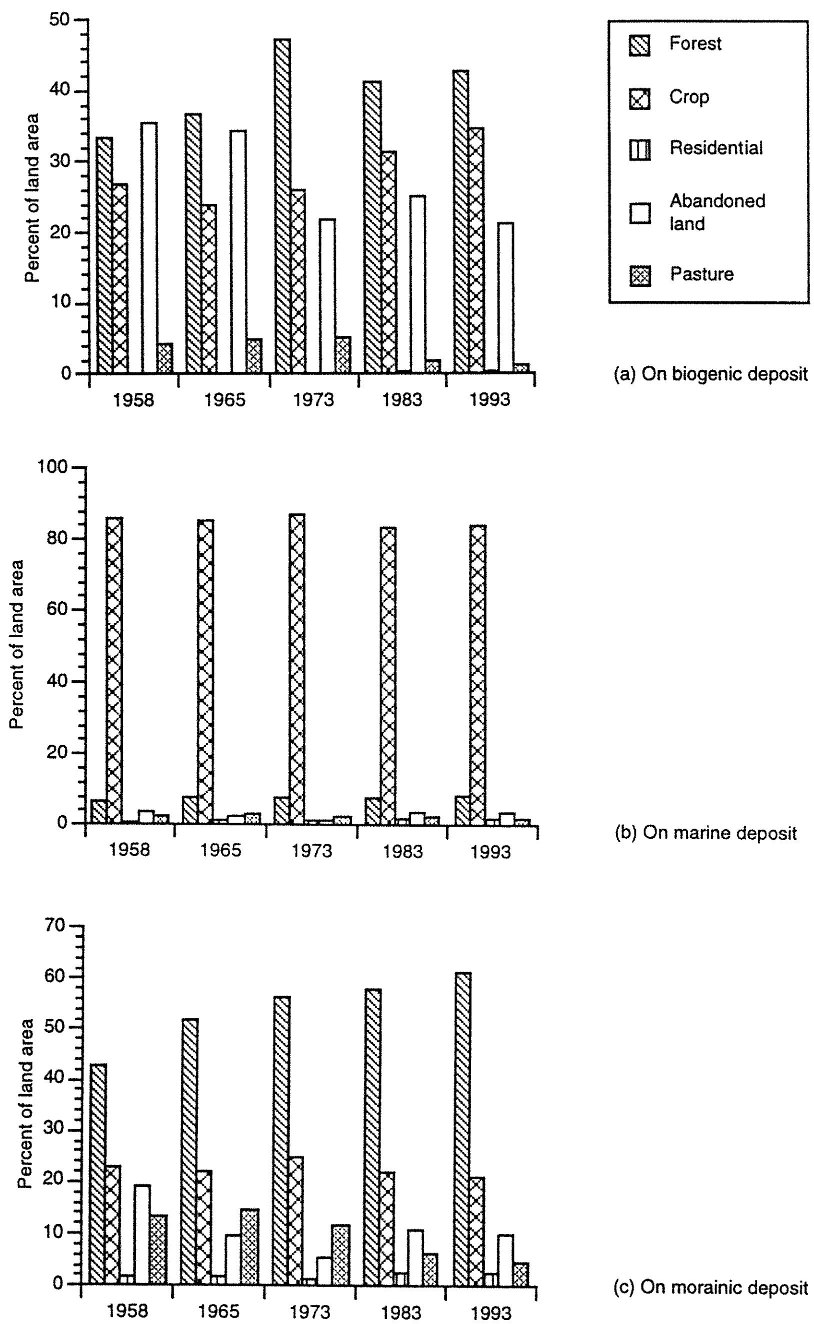



Figure 3-4. Percent of area of different land use types on the three geomorphological deposits during 1958-1993.

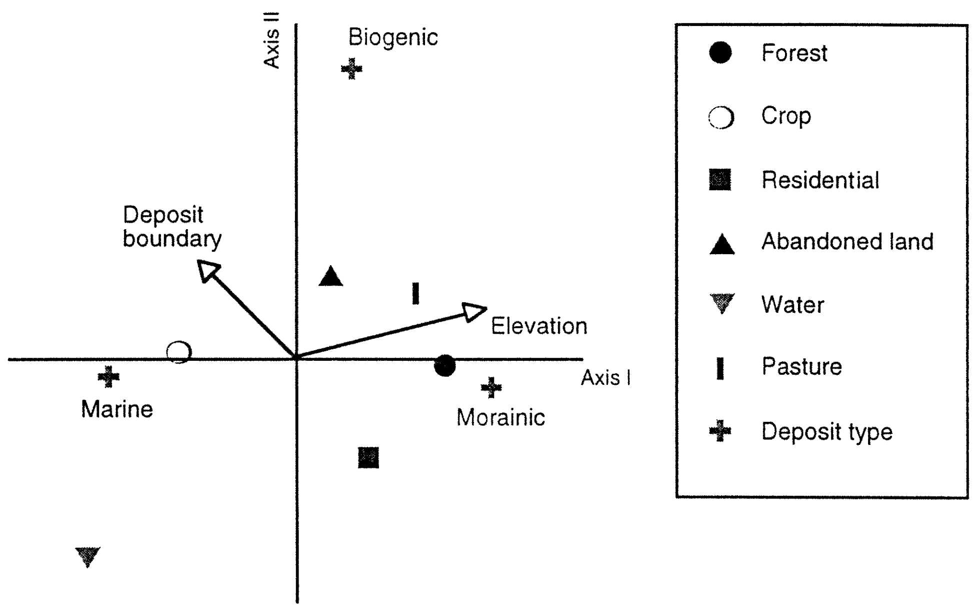
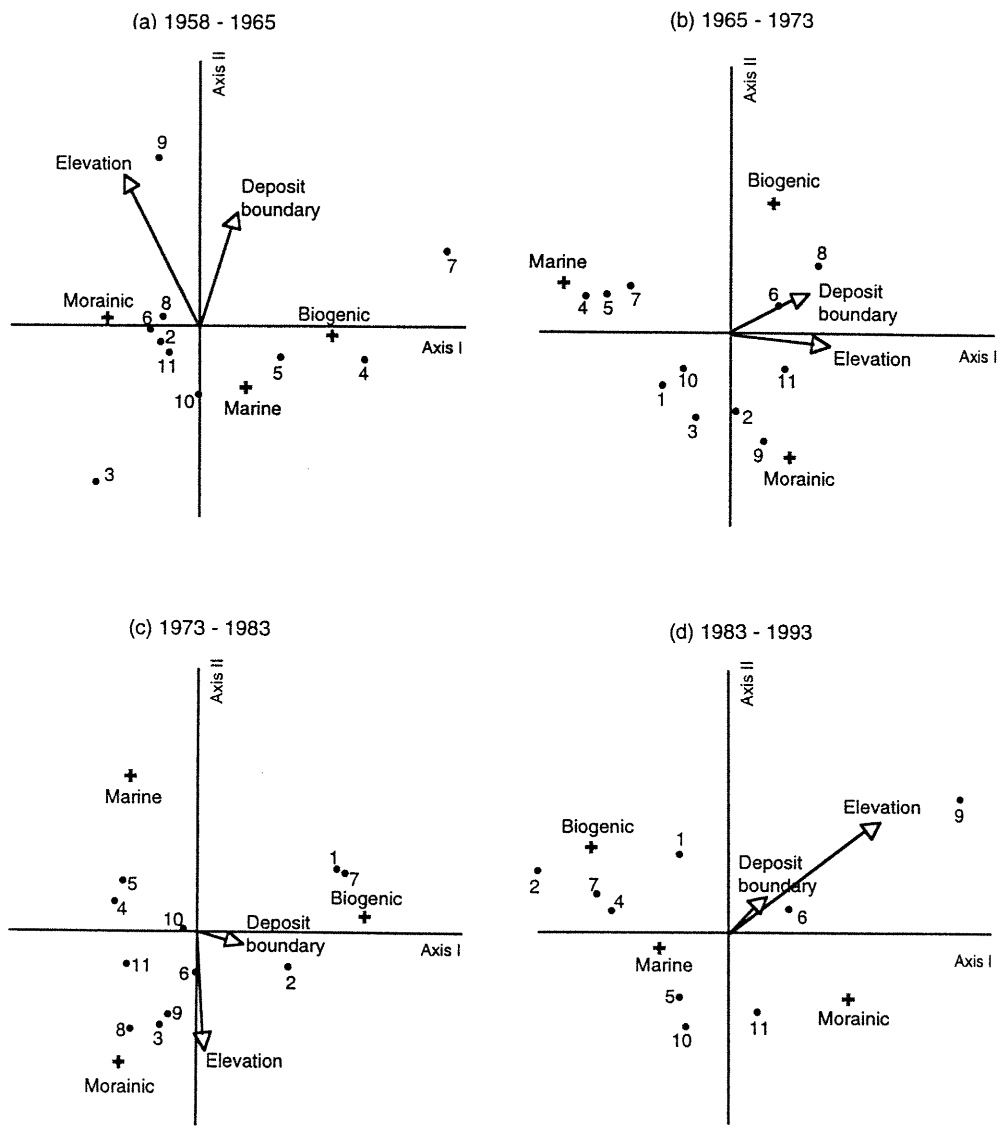



Figure 3-5. CCA ordination of the land use data set in 1993. Quantitative variables are represented as arrows, and geomorphological deposit types are represented as crosses.




1. Forest to crop; 2. Forest to abandoned land; 3. Forest to pasture; 4. Crop to abandoned land; 5. Crop to pasture; 6. Abandoned land to forest; 7. Abandoned land to crop; 8. Abandoned land to pasture; 9. Pasture to forest; 10. Pasture to crop; 11. Pasture to abandoned land.

Figure 3-6. CCA ordination of the four land use transformation data sets. Quantitative variables are represented as arrows, and geomorphological deposit types are represented as crosses.

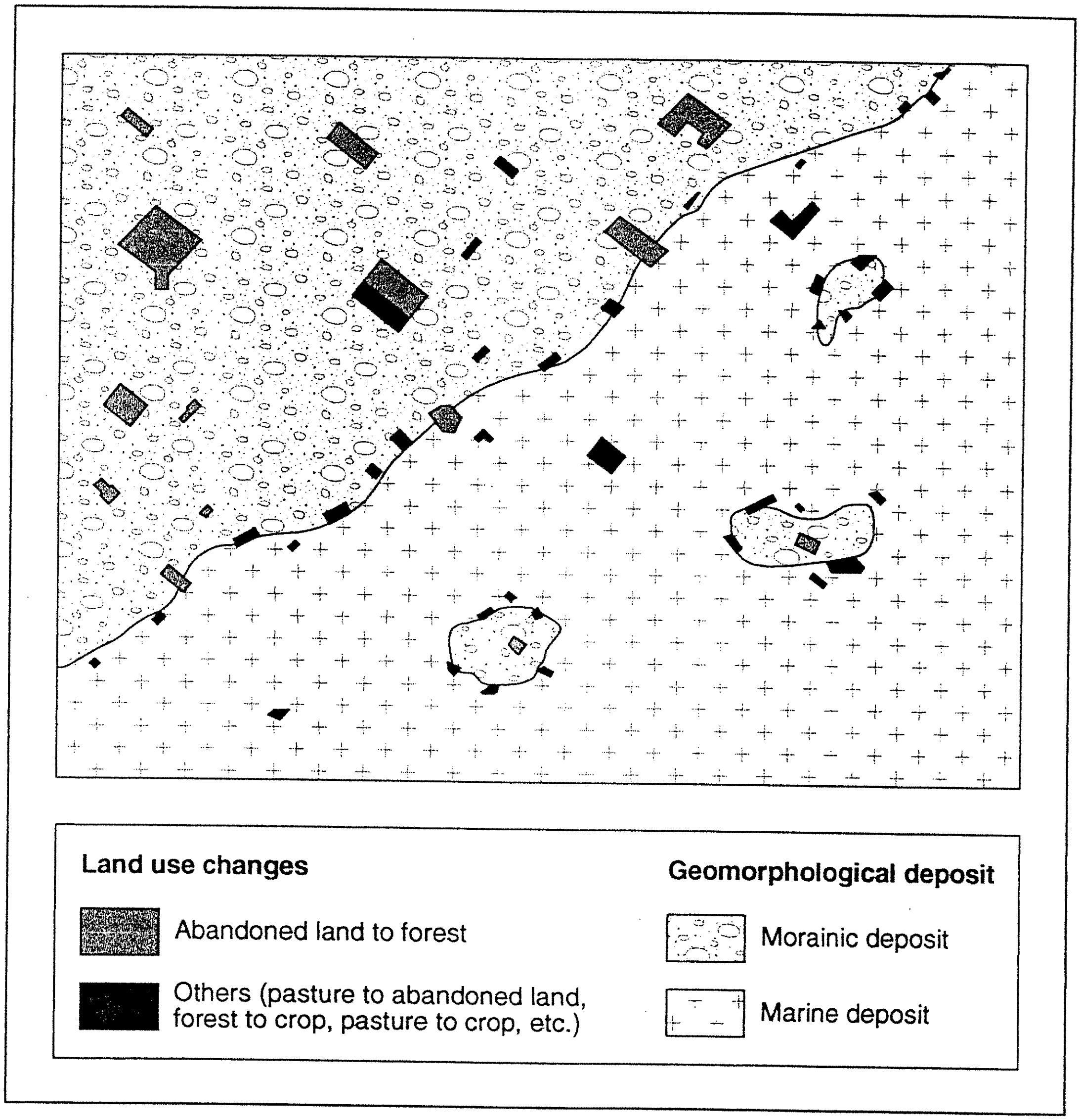



Figure 3-7. Diagram showing the major land use changes during the period 1958-1993 and their relations to the geomorphological deposit type and boundary.

# CHAPTER FOUR

## The influence of edaphic factors on the spatial structure of inland halophytic communities: a case study in Xinjiang, China

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### Abstract

In order to understand the influence of edaphic factors on the spatial structure of inland halophytic plant communities, a 2.6 km$^2$ study site, located on the lower fringe of the alluvial fan of the Hutubi River, in an arid region of China, was intensively sampled and mapped. 105 patches were found to be homogenous in species composition. Plant Species and their coverage were recorded in each patch. 45 patches were randomly selected for the measurement of edaphic variables. The eight selected edaphic factors were: electrical conductivity, pH and hydrolytic alkalinity of the first soil layer; depth to the water table, total salt content and pH of the ground water; and the depth and thickness of the clay layer. The map with quadrat locations and boundaries of patches was digitized into a GIS and related to the vegetation and edaphic data matrices. CCA was used to evaluate the relative importance of edaphic factors in explaining the variation of the species assemblages and to identify the ecological preferences of species. The spatial structure of the communities and of the main edaphic factors was analyzed using correlograms, Mantel correlograms and clustering under constraint of spatial contiguity. Gradient analysis showed that there are two distinct vegetation gradients in the study area, one of which is determined mainly by soil moisture (represented by depth to the water table), and the other by soil salinity (represented by electrical conductivity and hydrolytic alkalinity of the first soil layer). However, spatial analyses showed that at the sampling scale the halophytic communities in the study area are structured along one main spatial gradient determined by the water table level. Similar spatial autocorrelation structure between the factors related to the first soil layer and the communities, given our sampling scale, could not be detected. Our results suggest that the relative importance of the effects of different edaphic factors on the spatial structure of halophytic communities is scale-dependent. The partitioning of species variation showed that nearly half of the variation explained by the spatial matrix is independent of the edaphic factors. This result indicates that other factors, such as biotic interactions, may play an important role in structuring these communities.

*Key words:* CCA, indicator species, Mantel test, soil salinity, spatial autocorrelation, variation partitioning.

*Abbreviations:* CCA = Canonical correspondence analysis; GIS = Geographical information system.

*Nomenclature:* Anon. (1978) and references therein.

## 4.1 Introduction

A major goal of plant community ecology is to test hypotheses concerning the factors that may control the composition and structure of plant communities. It is now recognized that multiple factors must be invoked to explain the structure of communities (e.g. Quinn & Dunham 1983; Dunson & Travis 1991). It has also become apparent that different factors may affect community structure at different spatial and temporal scales (Wiens 1989; Allen & Hoekstra 1991; Levin 1992). One of the challenges of community ecology is to untangle the interactions among these factors.

In inland saline ecosystems, the important role of edaphic factors in structuring plant communities has long been noted in a number of studies throughout the world (e.g. Waisel 1972; Chapman 1974; Ungar 1974; Anon. 1978; Sen & Rajpurohit 1982; Carnevale & Torres 1990; Burchill & Kenkel 1991; and many others). Many studies have revealed that species and plant community distribution follow a salinity gradient which reflects their degree of salt tolerance. However, some studies also showed that many halophytes have a wide amplitude for soil salinity, but a narrow one for soil humidity. Thus, some species with a common range of salinity tolerances are segregated on the basis of their water requirements (see Waisel 1972). No matter which edaphic factor is predominant, the influence of edaphic factors as a whole on the distribution of halophytic species and communities is important. Prior to the 1970's, there has been an emphasis on edaphic factors. Ungar (1974), when reviewing the previous studies on the inland halophytes of the United States, summarized as follows: "The distribution of these inland halophytes appears to be controlled mainly by edaphic conditions. Species appear to be selected out by the highly saline environment in a gradient from the most to least salt tolerance, with climate, topography, soil moisture, and biotic factors playing secondary roles (p.237)". Because of the strong relationships between halophytes and edaphic factors, certain species have been proposed as indicators of saline soil conditions. However, at the same time, researchers also noticed that many of the inland halophytic species can grow and reproduce under non-saline conditions, and that some indicator species were also found to be unreliable (Barbour 1970). Competitive exclusion may explain their elimination from moderate sites (Ungar 1974). Since the 1970's, the influence of competition has been emphasized and investigated. More and more field transplantation and laboratory experiments have suggested that interspecific competition indeed exists in these stressed habitats, and that it is also important in structuring these communities (e.g. Barbour 1978; Ungar et al. 1979; Badger & Ungar 1990; Kenkel et al. 1991). Some species can be limited at low salinity by competition and at high salinity by their physiological tolerance limits (Ungar et al. 1979). However, the upper and lower limits of distribution of some other species along the soil salinity gradient are determined by both stress tolerance and competition. Currently, it is clear that both edaphic factors and biotic factors (e.g. competition, dispersal, herbivory) must be used to explain the structure of inland halophytic communities. However, the relative importance of these factors remains to be explored and tested. Furthermore, among the edaphic factors, factors other than salinity, such as soil moisture and alkalinity (because they often act synergistically with salinity) have received little attention. The use of halophytes and halophytic communities as indicators of soil salinity has received even less attention since the 1960's.

Recently, Borcard, Legendre & Drapeau (1992) proposed a quantitative statistical approach, based on canonical correspondence analysis (CCA) (ter Braak 1986, 1987a; ter

Braak & Prentice 1988), to discriminate between various variables influencing species assemblages, which partitions the variation of species assemblages and allows one to measure the relative contribution of sets of explanatory variables. This method is conceptually linked to the idea that ecological heterogeneity in natural communities is explained by non-mutually exclusive abiotic and biotic factors that overlap in space and time. Geographical information system (GIS) methods and spatial statistical analyses provided powerful means to describe and detect the spatial patterns of communities and environmental factors (Johnson 1993; Legendre & Fortin 1989). The objective of this paper is to examine the influence of edaphic factors as a whole, as well as the influence of specific edaphic factors on the spatial structure of inland halophytic communities using these methods. We will first evaluate the relative importance of the specific edaphic factors in explaining the variation of the species assemblages, and identify the ecological preferences of the species. We will then analyze the spatial patterns of the communities and of the major edaphic factors, and partition the species variation among the different sources of assumed influence. Our research also emphasizes the use of halophytes and halophytic communities as indicators of the soil properties and for soil mapping purposes. This investigation is intended to give some insight on the cause of the spatial structure of inland halophytic communities. This research will also facilitate the identification of soil properties and soil mapping using halophytes and halophytic communities, in order to improve vegetation management in the Xinjiang Autonomous Region of China.

### 4.2 Study site

The study site is located in the Xinjiang Autonomous Region of China (Fig. 4-1), where a long-term ecological monitoring project on the dynamics of vegetation, soil water and salinity is in progress. The annual average temperature is 6.8 °C, the monthly average temperature is -16.9 °C in January and 25.6 °C in July. The annual precipitation is only ca. 170 mm, but the potential evaporation is ca. 2300 mm. Geomorphologically, the study site is located on the lower fringe of the alluvial fan of the Hutubi River, which is part of the Junggar basin whose central portion is occupied by the Gurbantünggüt desert.

The study site lies in the transition zone between the oasis and the desert. Temperate desert vegetation dominated by *Reaumuria soongorica* is distributed on the well drained plain connected to the alluvial fan. On the upper and middle area of the alluvial fan are new or old oases. Due to the large amount of salt in the soil, as well as the relatively high water table, not only salt desert, but also salt marsh vegetation are distributed extensively in this transition zone. It provided an ideal location to analyze the relationships between the spatial structure of halophytic communities and edaphic factors. In addition, because this is the only zone with high potential for agricultural development which remains in this extremely arid region, it has been the object of several research projects in grassland management and soil salinization control in China (Xu 1995).

The study site extends over a 2.6 $km^2$ area (Fig. 4-2). The topography is undulating and elevation varies between 446.0 and 449.5 m above sea level; the southeastern part of the area is at higher altitude than the western part (Fig. 4-2). In the upper part, the water table is between 1.5 and 2.5 m below the soil surface, whereas in the lower part, the water table is between 0.7 and 1.5 m below the soil surface. Salt content in the ground water varies from 2.3 to 38.5 g/L. Soil salinity varies spatially. Electrical conductivity of the first soil layer (0-30 cm) ranges between 0.1 and 0.9 S/m. Salts are generally sodium sulfates or sodium chlorides. In some areas there also exist sodium carbonates, where the pH and alkalinity are relatively high. The pH of the first soil layer varies between 8.2 and 9.9, hydrolytic alkalinity varies from 0.1 to 1.8 meq/100g soil. Soil texture is usually fine sand or light loam with one clay layer occurring at varying depth, ranging from 30 to 120 cm. The thickness of the clay layer varies from 25 to 120 cm. The spatial variation of the plant communities in the study area is notable. The extremely xerohalophytic species such as *Reaumuria soongorica, Nitraria sibirica* and *Suaeda physophora*, occur in the upper parts (micro-elevation), while in the lower parts the communities are dominated by hydrohalophytic species such as *Aeluropus littoralis*, *Limonium gmelinii* and *Tamarix ramosissima.* Between the upper and lower parts, xerohalophytic species such as *Kalidium foliatum* and *Halocnemum strobilaceum* dominate most of the area. Although the study site is located near an oasis, anthropogenic disturbances, such as animal grazing, have not occurred because they were prohibited due to the fact that the site is used for research purposes.

## 4.3 Methods

### *4.3.1 Sampling and mapping*

The study site was intensively sampled and mapped. A 10 m × 10 m grid (x: east-west direction, y: south-north direction) was laid over the entire area in order to record the coordinates of the sampling points and draw the boundaries of homogeneous patches.

Patches which were homogeneous in species composition were determined by surveyors and the boundaries were delineated on a base map. Due to the fact that there are relatively few species in these halophytic communities, and that the boundaries are very sharp in some locations, the homogeneous patches determined by the surveyors are relatively objective. In addition, in some locations where the boundaries are not easy to determine, the homogeneous patches were defined by as small an area as possible, in order to maximize the detail of the spatial structure. In order to record the species present and their coverage in each homogeneous patch, a single quadrat was selected at random in each of the patches. Quadrat size was 1 $m^2$ for herb-dominated patches and 25 $m^2$ for shrub-dominated patches. 105 patches were found to be homogeneous in species composition, and thus 105 quadrats were sampled in the study site (Fig. 4-2). Twenty-nine species were recorded. Among the 105 quadrats, 45 were selected randomly to record the edaphic variables (Fig. 4-2). The eight selected edaphic factors were: electrical conductivity, pH and hydrolytic alkalinity of the first soil layer (0-30 cm); depth to the water table; total salt content and pH of the ground water; and the depth and thickness of the clay layer. The map with quadrat locations and boundaries of patches was digitized into a GIS system and related to the vegetation and edaphic data matrices. The elevation map of the study site was also digitized into this system (Fig. 4-2). By visually comparing the spatial pattern of the species, patches and communities to the topography and spatial patterns of the edaphic factors, the GIS allowed us to check the validity of the relationships uncovered by the following statistical methods. The GIS system was also used to map soil properties by interpolating the edaphic data for the other unsampled quadrats using the data of the 45 quadrats sampled.

### *4.3.2 Statistical methods*

Our analyses were mainly carried out using CANOCO (ter Braak 1986, 1987b) and the R package (Legendre & Vaudor 1991). Rare species (frequency < 2%) were removed before any analysis, because some of the multivariate analyses are sensitive to rare species and deviant sites (ter Braak & Prentice 1988). CCA was used to obtain an ordination of the vegetation data in the 45 quadrats, constrained by the edaphic variables. Partial CCA produced constrained ordinations while controlling for the effect of a number of edaphic variables. Partitioning the variation of the species data between the edaphic and spatial components was obtained by partial CCA (Borcard et al. 1992). The spatial data consisted in the x and y geographic coordinates of the quadrats, as well as the other terms of a third-degree surface trend polynomial equation of the x and y coordinates (Legendre 1990); significant terms of that polynomial were selected using the forward selection procedure available in the CANOCO programme. Although CCA has been proven to be robust to highly skewed species data (Palmer 1993), we still made several runs with different log-transformed species data or log-transformed edaphic data in order to get the appropriate result. Considering the lax convergence criterion in the CANOCO programme, which may cause instability of the results (Oksanen & Minchin 1997), the analysis was repeated using a CCA program written by one of us (P. Legendre), which uses a more strict convergence criterion. Weighted average scores were used to draw the ordination diagram of the quadrats.

CCA is an ordination method that forces species axes to be linear combinations of edaphic variables. It provided an evaluation of the influence of the eight measured edaphic factors on the halophytic communities. Species were plotted as points which represent their optimum in canonical space. Quantitative edaphic factors are represented by arrows from which the direction of influence of the edaphic factors can be deduced. The projection of species scores on the arrows was used to identify the ecological preference of species under the assumptions that species are indeed controlled by edaphic factors in the environment under study and that they have unimodal distributions. The root mean squared deviation of the species was used to identify the realized niche width of the species in the environmental space, as well as to determine the indicator species. Monte Carlo permutation tests were performed to assess the significance of the canonical axes showing the relationships between species and the selected edaphic factors. The variation partitioning yielded four fractions of the species data variation: a) local species variation, explained by the edaphic factors independently of any spatial structure, b) spatial structure in the species data which is shared by the edaphic factors, c) spatial structure in the species data which is not shared by the edaphic factors, and d) unexplained variation (Borcard et al. 1992; Borcard & Legendre 1994). This approach has successfully been used by Jean & Bouchard (1993) in a study of riverine wetland vegetation.

The R package was used to analyze the spatial structure of the communities and edaphic factors. To describe the spatial structure of the edaphic factors, we used the 45 quadrats with edaphic data to compute correlograms (with Moran's I) of each factor. We used proportional-linked agglomerative clustering with spatial contiguity constraint (Legendre & Fortin 1989) and a Mantel correlogram to describe the spatial structure of the communities within the 105 quadrats. The Mantel test was used to test the significance of the relationship between the community similarity matrix and the geographical distance matrix, and to study the niche segregation of the two most widely distributed species, *Kalidium foliatum* and *Halocnemum strobilaceum.* Both of these species are widely distributed between the upper and lower topographic positions. One of the two species, or both, are present in the 39 quadrats of the total 45 quadrats. The differences in their edaphic preferences needed to be determined. A model similarity matrix among quadrats was constructed, containing 1's for pairs of quadrats that were dominant for the same species and 0's for pairs of quadrats differing as to the dominant species. Using the Mantel test, this matrix was compared to a similarity matrix computed from the edaphic variables. A series of *a posteriori* tests were used to determine the significant factors. Steinhaus's coefficient (Legendre & Legendre 1983) was used to compute this similarity matrix.

## 4.4 Results

### *4.4.1 Gradient analysis of species assemblages and edaphic factors*

Examining the results of CCA with different transformations of the data, we found that they gave comparable results. We adopted the data set with log-transformed electrical conductivity and alkalinity of the first soil layer, and log-transformed total salt content of the ground water because it is biologically more reasonable (Palmer 1993). The stability of our results with CANOCO was confirmed by repeating the run with P. Legendre's programme. The results of CCA are shown in Figs. 4-3 and 4-4 and in Tables 4-1 and 4-2. A Monte Carlo permutation test of the trace (i.e. the sum of all canonical eigenvalues; 999 permutations) confirmed the overall significance of the canonical ordination ($p<0.001$). Three main edaphic factors, depth to the water table, electrical conductivity and alkalinity of the first soil layer, are determined by significance tests for partial CCA analyses where the other variables had been placed as covariables in the analyses ($p<0.01$). Variance explained by these three variables represents 70% of the variance explained by all of the eight variables. The first CCA axis is positively correlated with depth to the water table, while the second axis is negatively correlated with electrical conductivity and hydrolytic alkalinity of the first soil layer. Other factors have little effect on the two major vegetation gradients. Monte Carlo permutation tests confirmed the significance of the first two axes

($p<0.001$).

The ordination of quadrats (Fig. 4-3) clearly distinguishes the edaphic conditions of the five main community types pre-defined by the single dominant species. Some community types with few stands and community types dominated by two or more species are unlabelled. Three *Aeluropus littoralis* stands are located on the left of the diagram, where the characteristic edaphic conditions are shallow but saline and alkaline ground water. These stands are distributed locally in the lower part, topographically, of the study sites. The coverage of *A. littoralis* can reach as high as 50%. The *Suaeda physophora* stands are located in the lower right corner of the diagram where the edaphic conditions are high aridity and high salinity. The stands of *S. physophora* are found only in the upper parts of the study site with 2-10% of total coverage. Two *Phragmites communis* stands are located in the upper part of the diagram where the edaphic conditions are characterized by low salinity. They are distributed in between the upper and lower parts of the site, with very high coverage (60%). The stands dominated by *Kalidium foliatum*, *Halocnemum strobilaceum,* or both, are widely distributed between the upper and lower parts of the sites. The CCA results reveal that the stands dominated by *H. strobilaceum* are located in areas with better water conditions (higher water table), than the stands dominated by *K. foliatum.* Segregation of their niches was confirmed by the Mantel test ($p<0.05$). Surprisingly, the significant edaphic factors are salt content and pH of the ground water. The roles of other factors are not significant. Since these two species usually occur in the locations with a relatively shallow water table, they are not normally considered as phreatophyte (deep-rooted plants that obtain a dependable water supply from the "phreatic surface"). However, our results indicating that the salt difference in the ground water plays a significant role, suggest that at some seasons the two species may obtain their water supply directly from the water table.

From the positions of the species in the ordination diagram (Fig. 4-4), the ecological preferences of the species to the main edaphic factors were identified. The four quadrants roughly represent four different combinations of soil aridity and salinity. The fourth quadrant represents the most stressed edaphic condition in the study area. Species in this quadrant can usually tolerate both high salinity and high aridity and reach their maximum coverage in this environment. Species in the upper parts (topographically elevated), such as *Suaeda physophora* (27), *Nitraria sibirica* (21), *Reaumuria soongorica* (23) and *Lycium ruthenicum* (20) all fall in this quadrant. Many species occurring between the upper and lower parts of the site, such as *Kalidium foliatum* (16) and *Halimodendron halodendron* (10) are also located in this quadrant. In the third quadrant, species have better water conditions than those in the fourth quadrant, but the salinity is still as high. Some species frequently occurring in the lower parts, such as *Alhagi sparisifolia* (3) and *Tamarix ramosissim*a (29) fall in this quadrant. Only two species, *Aeluropus littoralis* (2) and *Limonium gmelinii* (19) fall in the lower part of the first quadrant. Their preferences of ecological conditions are characterized by shallow and saline ground water. These two species occur in the lower parts of the topography. The second quadrant represents the lowest salinity conditions of the study site. Four species, *Phragmites communis* (22), *Glycyrrhiza uralensis* (9), *Suaeda glauca* (28) and *Artemisia schrenkiana* (5) fall in this quadrant. *Phragmites communis* (22) is widely distributed in the whole study site. The other three species occur in some locations between the upper and lower parts of the site. Five species, *Aeluropus littoralis* (2), *Alhagi sparisifolia* (3), *Halimodendron halodendron* (10), *Nitraria sibirica* (21) and *Suaeda physophora* (27) were selected as indicators of the different degrees of soil aridity and salinity, because they have the lowest standard deviations of species scores along the first two ordination axes, and were recorded in more than 10 of the 45 quadrats. An alternative method to identify indicator species is the IndVal method of Dufrêne & Legendre (1997). For accurate forecasting of specific edaphic factors, however, further analysis of the selected species should be done using methods of calibration (Jongman et al. 1987; ter Braak 1987b; Birks 1995; ter Braak 1995).

*4.4.2 Spatial structure and variation partitioning*

The result of the variation partitioning shows that 40% of the variation (Table 4-3 and Fig. 4-5. a+b) has been explained by the selected edaphic factors, while 33% of the variation (Table 4-3 and Fig. 4-5. b+c) has been explained by the spatial variables. In the analysis of the relationships between the species and spatial variables, the selected monomials were x, y, xy, $y^2$, $x^2y$, $x^3$ and $y^3$. The high eigenvalues and species to explanatory variable correlations (Table 4-1, step 2) indicate that the community has obvious spatial structure. A Monte Carlo permutation test of the trace statistic confirmed the significance of the canonical relationship between the species and spatial variables ($p<0.001$). Fig. 4-5 shows that fraction b, found by subtracting a from a+b in Table 4-3 (40.20% - 22.24% = 17.96%), represents 18% of the species variation. This fraction represents the spatial variation which has been explained by the edaphic factors. Therefore, nearly half of the variation explained by the spatial matrix is independent of the edaphic factors (compare b and c in Fig. 4-5). On the other hand, 22% of the variation explained by the edaphic factors is local variation (compare a and b in Fig. 4-5). After removing the effect of the spatial structure, the correlation of hydrolytic alkalinity of the first soil layer with the first axis greatly increased (right-hand part of Table 4-2). The importance of hydrolytic alkalinity was confirmed by significance tests ($p<0.01$) for partial CCA, where the spatial and other edaphic variables had been placed as covariables in the analyses. The role of depth to the water table was also significant at the 0.05 level. Variance explained by these two variables occupied 51% of the variance explained by all of the eight variables. This shows that the two variables make an important contribution in determining the local species variation.

The correlograms of the edaphic factors (Fig. 4-6) show that the three ground water factors, depth to the water table, pH and total salt content of the ground water, have obvious gradient structures; at the a=5% level, depth to the water table, in particular, has significant positive autocorrelation within distance classes 2, 3, 4 and 5, and significant negative autocorrelation within the distance classes from 8 to 12. However, the three factors of the first soil layer, electrical conductivity (correlogram not shown), hydrolytic alkalinity and pH, do not have obvious spatial structures. Hydrolytic alkalinity and pH of the first soil layer are only significant for distance class 2 (no quadrat pairs were located within distance class 1) and electrical conductivity is not significant for any distance class. The Mantel correlogram (Fig. 4-6f) shows that the communities had a spatial autocorrelation structure very similar to that of the three ground water factors. The Mantel test also confirmed the overall significant spatial autocorrelation ($p<0.05$) of the plant communities. From these results we see that at the scale at which sampling has been conducted, the spatial structure of the communities is mainly determined by the water table. The result of clustering with spatial contiguity constraint (level 0.54, connectedness 0.5, Fig. 4-7) clearly shows that the communities have a spatial structure that follows relative elevation (compare Fig. 4-2 and 4-7). In the flat locations (east), the clusters of vegetation patches are large, whereas in the undulating portion (west and southeast) the clusters are small, with several patches remaining unclustered at the selected level. Different topographic positions create variation in the water table level and the communities probably respond to this by a similar variation pattern.

### 4.5 Discussion

Our gradient analyses not only confirmed the important role of edaphic factors on the species and community distribution as a whole, but, more importantly, they showed that two distinct vegetation gradients exist, one of which is determined mainly by soil moisture (represented by depth to the water table), and the other by soil salinity (represented by electrical conductivity and hydrolytic alkalinity of the first soil layer). Although salt stress is physiologically difficult to distinguish from water stress (Osmond et al. 1987), at the community level we found that plants and communities reacted to two distinct stresses. In some sites with the basin-shaped topography, water table is highly correlated with salinity, i.e. there is a gradient from dry, less saline areas to moister, more saline areas. That may explain why water table has not been paid much attention to previously. However, in some sites with the undulating topography, spatial variation of salinity is usually not correlated with water table level, and thus a single gradient does not exist. Actually, plants in the salt desert need to develop tolerance mechanisms to both the water stress and the salinity stress. Noticing that most of the laboratory experiments on competition of halophytes have concentrated on one edaphic factor, i.e. salinity, our results suggest that at least two edaphic factors, i.e. soil moisture and salinity, must be included when studying the xerohalophytes.

Although alkalinity is highly correlated with salinity, we included alkalinity in our analysis because, on one hand, we wanted to verify which one best explained species and community distribution; on the other hand, a CCA ordination diagram is not in any way hampered by high correlations between environmental variables (ter Braak 1987b), and such redundancy is probably actually beneficial because some errors in measuring the environmental data may be averaged out (Palmer 1993). At first glance, it seems that alkalinity and salinity are measuring essentially the same thing, ion concentration. Upon further consideration, however, alkalinity usually has deleterious effects on the physical and chemical properties of the soils (Shainberg; 1975). Therefore, alkalinity would appear to be a better integrating and comprehensive index of saline soil properties than salinity. In soil science these two factors are combined to classify the different types of saline soils (Waisel 1972; Shainberg 1975). Our CCA results not only show that both salinity and alkalinity play significant roles and were highly correlated with the second axis of the CCA ordination, but also shown that alkalinity plays a more important role than salinity on the local fraction of variation (fraction a in Fig. 4-5). Waisel (1972) stated that halophytes do not respond only to salinity, but are also more tolerant to the entire complex of physical, chemical, and biological modifications induced in the soil by salt. The important role of alkalinity in the local fraction of variation confirmed his statement to some extent.

Although CCA analysis revealed two gradients, our spatial analyses showed that, at the sampling scale used, the halophytic communities in the study area are structured along one main spatial gradient determined by the water table level. Similar spatial autocorrelation structure between the factors related to the first soil layer and the communities, given our sampling scale, could not be detected. This indicated that factors of the first soil layer influence the community structure at some different spatial scale. In this paper we have clearly shown that alkalinity in the first soil layer played an important role in determining the local fraction of variation. The local fraction of variation usually reflected the finer scale ecological pattern than the sampling scale. Furthermore, the spatial autocorrelations of hydrolytic alkalinity and pH of the first soil layer are significant for distance class 2. These results indicate that the community and the factors of the first soil layer may have a similar spatial autocorrelation structure at some finer scale than the one used in this study. In addition, if we only examine two close-neighbouring species, other factors can also play significant roles. For instance, our analysis on niche segregation of *Kalidium foliatum* and *Halocnemum strobilaceum* showed that salt content and pH of ground water played significant roles. The discrepancy about the importance of soil salinity in opposition to soil water regime could be due to the different spatial scales in which sampling was conducted. Our results suggest that the relative importance of different edaphic factors on spatial structure of halophytic communities is scale-dependent.

While noticing that many of the inland halophytic species can grow and reproduce under non-saline conditions, other researchers tested the hypothesis that salt-tolerant species are excluded from areas of no or low salinity, through competitive exclusion by less salt-tolerant, but faster growing glycophytes. However, the growth of dicotyledonous halophytes is frequently stimulated by salt, that of most monocotyledonous halophytes is not (Flower et al. 1986). In salt deserts, dicot plants usually dominate. Therefore, evaluating the relative importance of edaphic and biotic factors has important implications in the salt desert. In inland saline systems, vegetation discontinuities are often not linked to the environmental discontinuities (e.g. Ungar 1974; Burchill & Kenkel 1991). This feature has been assumed as an evidence for competition. Some simulation or hypothetical models of plant communities have suggested that competitive displacement may result in the development of vegetation discontinuities along continuous environmental gradients (Pielou 1974; Czárán 1989; Smith and Huston 1989; Kenkel et al. 1991). In our study area, we have observed both sharp and diffuse boundaries when we determined homogeneous patches. Some of the sharp boundaries followed topographic undulations, while others did not. With our spatial polynomial, not only the linear gradient patterns in the species data were extracted, but also more complex features like patches or gaps (Legendre 1990). Our results showed that nearly half of the variation explained by the spatial matrix is independent of the edaphic factors (compare b and c in Fig. 4-5). This result indicates that other factors, such as biotic interactions, may play an important role in structuring these communities in our study site, although the influence of other factors such as disturbance may also be reflected in this fraction (fraction c).

While the previous studies (Pan et al. 1995) provided a general overview, the present one showed the halophytic communities as complex mosaics of patches rather than a classical gradient. It made it possible to comprehensively evaluate the relative importance of different sources of assumed influences responsible for the spatial structure of the communities. Further studies of the dynamics of patches and communities, as well as of soil moisture and salinity should be done by generating maps at time intervals. The strong relationships between the distribution of halophyte or halophytic communities and some critical edaphic factors will facilitate the forecasting and mapping of soil properties such as moisture and salinity. This is indeed a rapid and economical way to proceed compared to using instrumental measurements (Tóth et al. 1995). Because the area encompassing the study site has a potential for reclamation for agriculture, the indicator species of different soil salinity levels are of high practical value.

### *4.6 Acknowledgments*

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Table 4-1. Results of Canonical correspondence analysis. Eigenvalues ($\lambda$) and species to explanatory variable correlations ($\gamma$) for the first two axes, as well as significance of trace and of the first two canonical axes (Monte Carlo permutation tests), are shown.

| Analysis* | $\lambda_1$ | $\lambda_2$ | $\gamma_1$ | $\gamma_2$ | p(trace) | p( $\lambda_1$ ) | p( $\lambda_2$ ) |
|---|---|---|---|---|---|---|---|
| 1. CCA (ED) | 0.460 | 0.394 | 0.858 | 0.859 | 0.001 | 0.001 | 0.001 |
| 2. CCA(SPA) | 0.424 | 0.307 | 0.817 | 0.810 | 0.001 | 0.001 | 0.02 |
| 3. CCA(ED)[SPA] | 0.269 | 0.186 | 0.870 | 0.823 | 0.002 | 0.056 | 0.29 |
| 4. CCA(SPA)[ED] | 0.138 | 0.116 | 0.749 | 0.762 | 0.045 | 0.61 | 0.45 |

* ( ) represents the constraint variables, [ ] represents the covariables. ED= edaphic variables, SPA= spatial variables.

Table 4-2. Correlations of edaphic factors with the first and second canonical axes of CCA.

| Edaphic factor | 1. CCA(ED) | | 3. CCA(ED)[SPA]* | |
|---|---|---|---|---|
| | Axis I | Axis II | Axis I | Axis II |
| Electrical conductivity of the first soil layer | -0.178 | -0.711 | -0.321 | 0.516 |
| pH of the first soil layer | 0.312 | -0.048 | -0.438 | 0.111 |
| Hydrolytic alkalinity of the first soil layer | -0.331 | -0.556 | -0.769 | 0.343 |
| Depth to the water table | 0.694 | -0.373 | 0.409 | 0.389 |
| Total salt content of the ground water | -0.423 | 0.098 | -0.213 | -0.319 |
| pH of the ground water | -0.457 | -0.178 | -0.221 | -0.454 |
| Depth of the clay layer | 0.300 | -0.232 | -0.137 | 0.258 |
| Thickness of the clay layer | 0.192 | 0.240 | -0.219 | -0.078 |

* ( ) represents the constraint variables, [ ] represents the covariables. ED= edaphic variables, SPA= spatial variables.

Table 4-3. The sum of canonical eigenvalues of partial CCA and their percentage of the sum of eigenvalues of CA (i.e. total species variation).

| Step and method* | Sum of canonical eigenvalues | Percentage of the sum of eigenvalue of CA | Fractions in Fig4- 5 |
|---|---|---|---|
| 1. CCA ( ED ) | 1.357 | 1.357/3.377 = 40.20 | a+b |
| 2. CCA ( SPA ) | 1.114 | 1.114/3.377 = 32.98 | b+c |
| 3. CCA ( ED ) [SPA] | 0.751 | 0.751/3.377 = 22.24 | a |
| 4. CCA (SPA ) [ED] | 0.507 | 0.507/3.377 = 15.01 | c |

* ( ) represents the constraint variables, [ ] represents the covariables.
ED= edaphic variables, SPA= spatial variables.

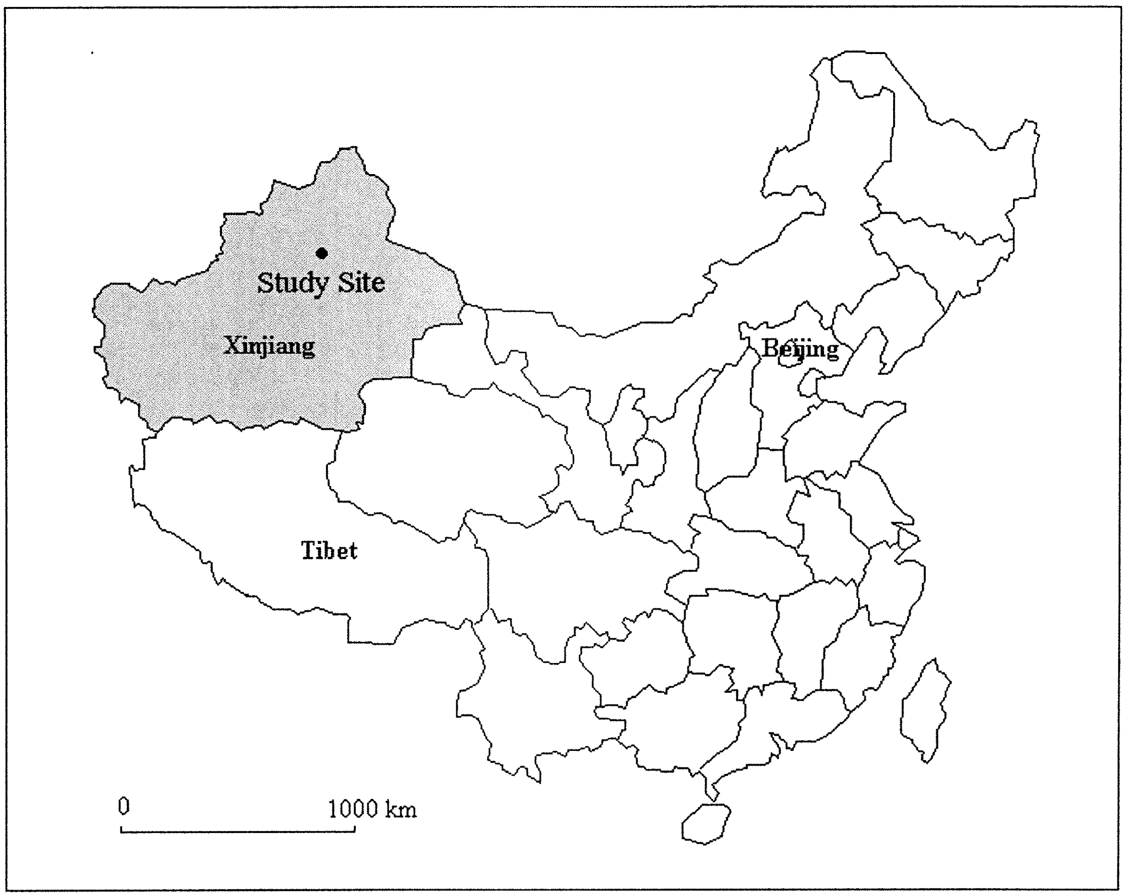



Figure 4-1. Location of the study site

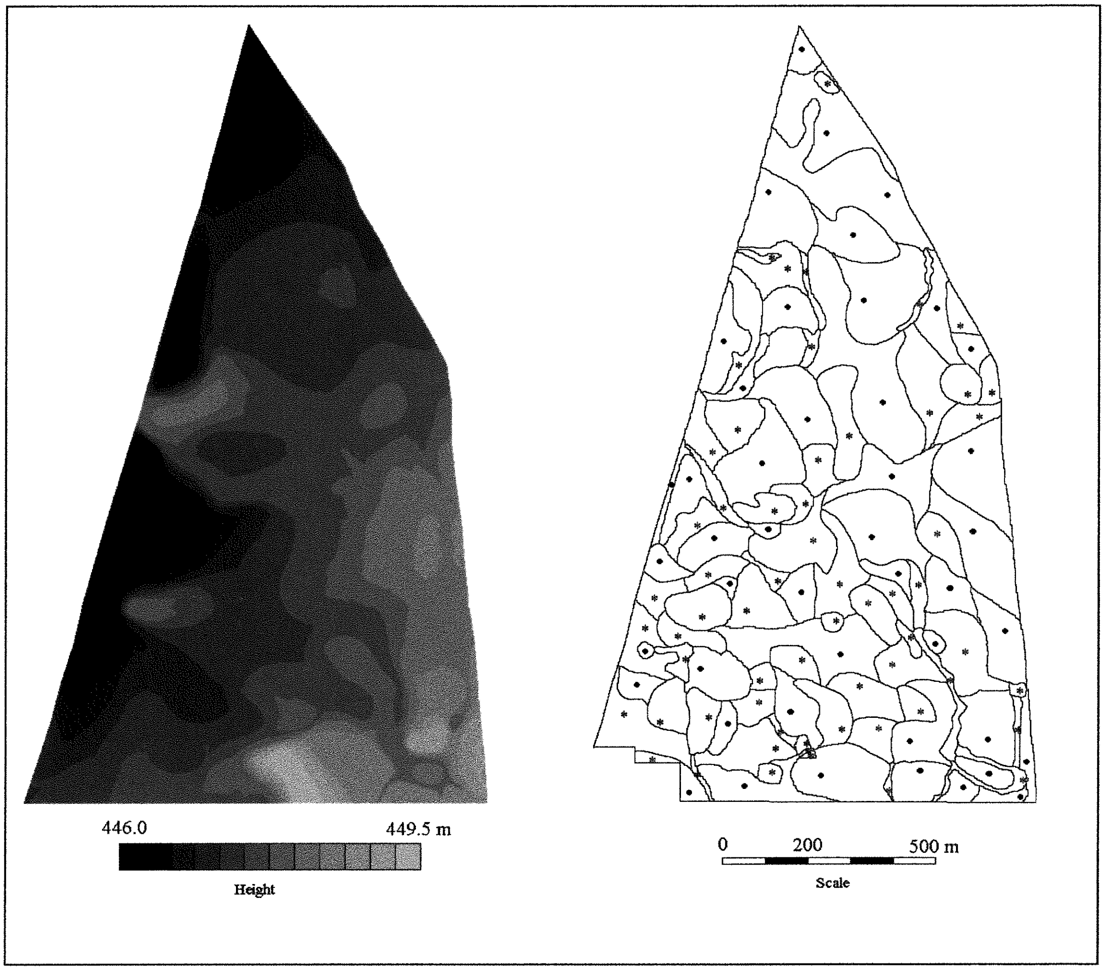



Figure 4-2. Maps showing the elevation of the study site (left) and the locations of the sampled quadrats (points) and homogeneous patches (right); · represents a quadrat with sampled edaphic data and * represents a quadrat without sampled edaphic data.

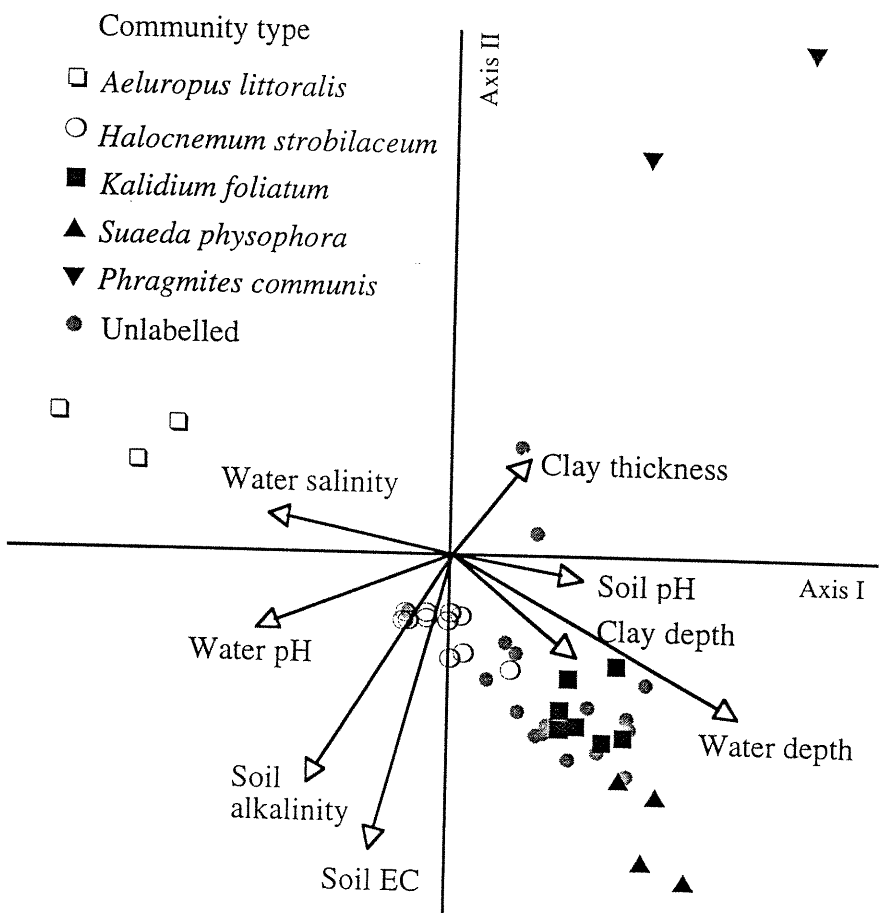
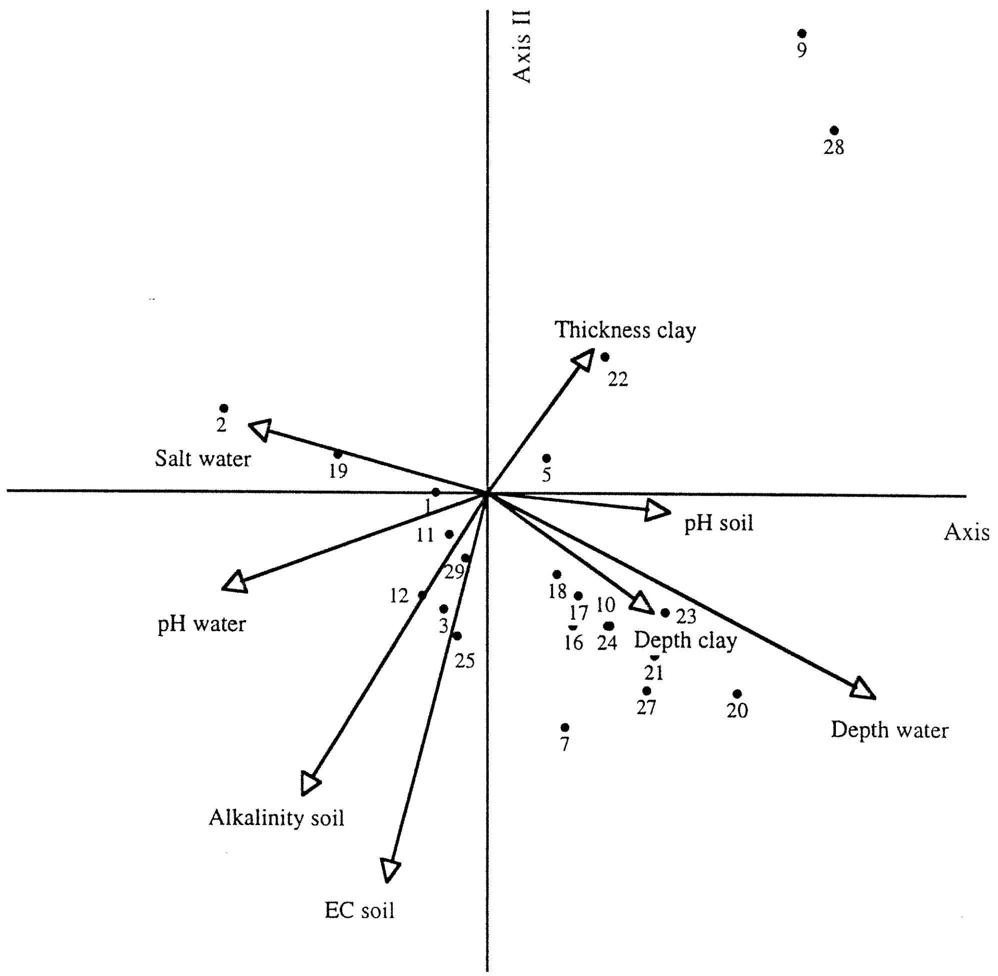



Figure 4-3. Canonical correspondence analysis ordination of the 45 quadrats. The five main community types were predefined by the single dominant species. Some community types with few stands and those dominated by two or more species are unlabelled. Edaphic variables are represented as arrows. Abbreviations: EC soil = Electrical conductivity of the first soil layer, pH soil = pH of the first soil layer, Alkalinity soil = Hydrolytic alkalinity of the first soil layer, Depth water = Depth to the water table, Salt water = Total salt content of the ground water, pH water = pH of the ground water, Depth clay = Depth of the clay layer, Thickness clay = Thickness of the clay layer.




1. *Achnatherum splendens*, 2. *Aeluropus littoralis*, 3. *Alhagi sparisifolia*,
5. *Artemisia schrenkiana*, 7. *Camphrosma lessingii*, 9. *Glycyrrhiza uralensis*,
10. *Halimodendron halodendron*, 11. *Halocnemum strobilaceum*,
12. *Halostachys belangeriana*, 16. *Kalidium foliatum*, 17. *Karelinea caspica*,
18. *Limonium otolepis*, 19. *Limonium gmelinii*, 20. *Lycium ruthenicum*,
21. *Nitraria sibirica*, 22. *Phragmites communis*, 23. *Reaumuria soongorica*,
24. *Salsola sp.*, 25. *Scozonera sp.*, 27. *Suaeda physophora*,
28. *Suaeda glauca*, 29. *Tamarix ramosissima.*

Figure 4-4. Canonical correspondence analysis ordination of the species. Edaphic variables are represented as arrows. Abbreviations of the edaphic variables are listed in Fig. 4-3.

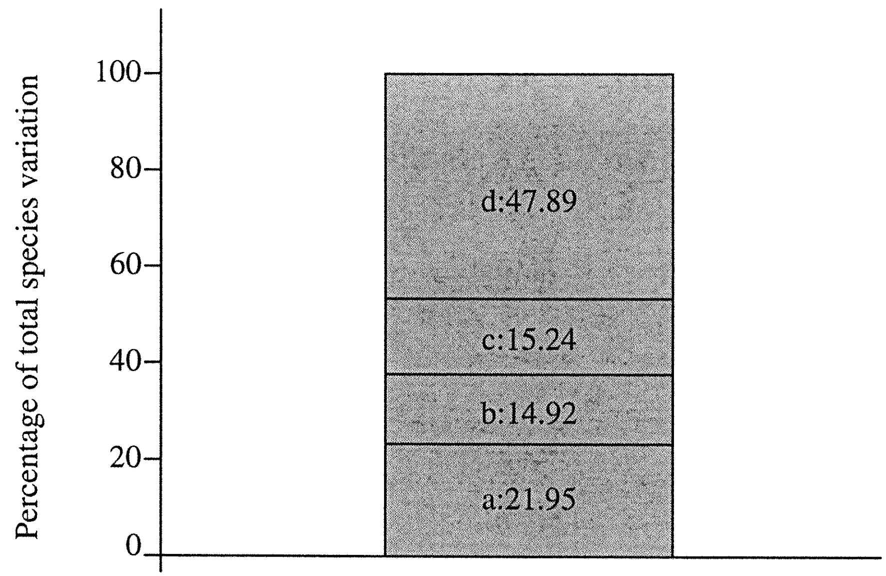



Figure 4-5. Percentage of the variation of the species data matrix explained by different factors. a. local species variation, explained by the edaphic factors independently of any spatial structure, b. spatial structure in the species data which is shared by the edaphic factors, c. spatial structure in the species data which is not shared by the edaphic factors, d. unexplained variation.

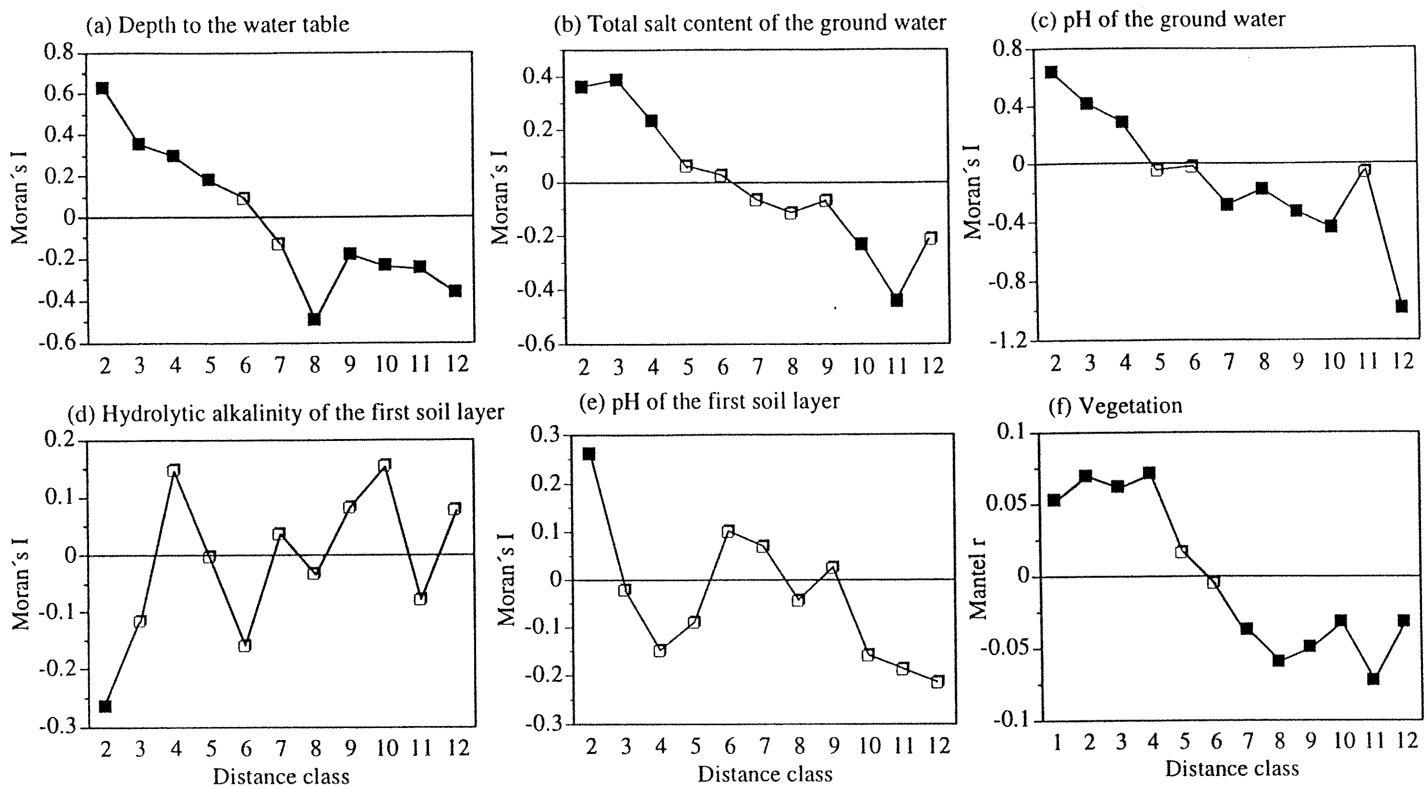



Figure 4-6. All-directional spatial correlogram of some edaphic variables (a-e) and Mantel correlogram for the structure of halophytic communities (f). Abscissa: distance classes, one unit of distance is 98.6 m on average for correlogram (a-e) and 97.2 m on average for the Mantel correlogram (f). Dark squares correspond to significant values of Moran's I ($p<0.05$) (a-e) or of Mantel r ($p<0.05$) (f). Gower's coefficient was used to compute the similarity matrix for the Mantel correlograms.

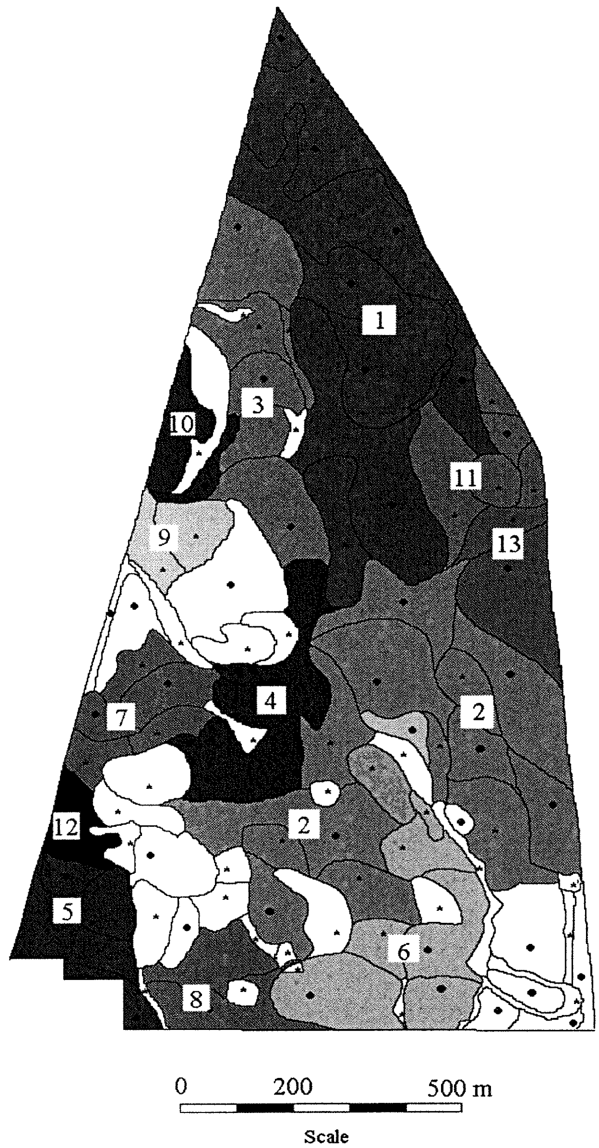



Figure 4-7. Map of the multivariate vegetation structure obtained by spatially constrained proportional-link linkage agglomerative clustering. Group 1 is dominated by *Suaeda physophora* and *Halocnemum strobilaceum*; group 2, 5 and 7 are dominated by *Halocnemum strobilaceum*; group 3 is dominated by *Nitraria sibirica* and *Phragmites communis*; group 4 and 6 are dominated by *Kalidium foliatum*; group 8 is dominated by *Phragmites communis* and *Aeluropus littoralis*; group 9 is dominated by *Nitraria sibirica*; group 10 is dominated by *Achnatherum splendens*; group 11 is dominated by *Artemisia schrenkiana*; group 12 is dominated by *Tamarix ramosissima*; group 13 is dominated by *Suaeda physophora*. Unclustered quadrats (white) are not labelled.

# CHAPTER FIVE

## Conclusions

The three case studies presented in this thesis show how physical factors influence the spatial and dynamic patterns in ecology at different spatial scales and organizational levels. The spatial pattern of coniferous and deciduous forest patches in the agricultural landscape of southern Quebec was first investigated (Chapter 2). The analyses reveal quite different spatial and dynamic forest patch patterns from the ones in a natural landscape. Spatially, coniferous patches are usually located on the margins of the overall forest patches, and they are connected to non-forest land-use types such as crop and pasture. Dynamically, the results reveal that on past abandoned land, conifers expand with increasing stand age, mostly by invasion from neighboring coniferous patches. Results show that the role of landscape physical factors on forest patch pattern has been modified by land use. Coniferous or deciduous patches are not associated with a specific surface deposit. In addition, physical factors explain a small proportion of the abundance of conifers on past abandoned land, when compared with land-use factors. Physical factors only indirectly influence the forest pattern because they strongly influence the land-use practices.

The role of physical factors on land-use patterns in the same study area was then further investigated (Chapter 3). Results show that there are clear relationships between land-use types and surface deposit types during the period of time studied. At the landscape level, crops are dominant on marine deposits, while forests are the dominant land use on moraine. In addition, the area of changes is larger on moraine than on any other deposit for the period of time studied, and some of the transition types have a explicit deposit tendency. However, at the patch level, the analyses reveal very dynamic patterns. Results show that small size dynamic patches are mainly distributed on moraine and marine deposits, whereas large patches are mainly distributed on moraine and biogenic deposits. Also, more land-use changes occur at the boundaries between surface deposit types than in any other location. The results at the patch level, in contrast to the results at the landscape level, highlight the fact that the role of surface deposit is different at the different levels.

In case study three (Chapter 4), the analyses not only further confirm the important role of physical factors at the species and community level, they also allow an in-depth analysis of the role of individual edaphic factors on the spatial structure of halophytic communities. Results show that there are two distinct vegetation gradients, one of which is determined by soil moisture, and the other by soil salinity, although salt stress is physiologically difficult to distinguish from water stress. In addition, the analyses show that the relative importance of the two factors on the spatial structure of halophytic communities is scale-dependent. The results suggest that the role of soil salinity is at a relatively fine scale in contrast to the role of soil moisture. This study also revealed that soil alkalinity would appear to be a better integrating and comprehensive index of saline soil properties than soil salinity.

From these three case studies, it can be concluded that physical factors play a role in determining ecological spatial patterns in rather diversified ways, at different levels, across different scales, and for different patch types. First, case study two clearly shows that the same physical factor has different roles at different levels. At the landscape level, land-use types have a clear relationship with surface deposit types. However, at the patch level, instead of surface deposit types, the boundaries of surface deposits play an important role on determining land-use dynamics. Secondly, case study three identifies that the relative importance of the physical factors changes with scale. The results show that at a relatively fine scale, soil salinity is important, while at relatively broad scale, soil moisture becomes more important. Finally, in comparing case study one and two, it can be concluded that the role of physical factors changes with the patch types. From case study two, it can be concluded that there are clear relationships between land-use types and surface deposit types. However, for the forest patches (case study one), coniferous or deciduous patches are not associated with specific surface deposits. Surface deposit only indirectly influences the forest pattern.

The three case studies showed that the role of physical factors could be analysed from three aspects: manner, intensity and frequency. First, manner considers if the role is direct or indirect. For example, in case study two and three, direct relationships between the role of physical factors and spatial patterns have been identified. However, in case study one, physical factors only indirectly influence the pattern of deciduous and coniferous forest since they have strong influence to the land use. Secondly, the intensity of the role of physical factors could be classified qualitatively or quantitatively. Qualitatively, the intensity varies from 'constrain' (such as the surface deposit on land use in case study two) to 'control' (such as soil salinity and ground water level on the pattern of plant community in case study three). Quantitatively, the relative intensity to other factors can be identified with a percentage using some multivariate analyses. Finally, comparing with biological processes, some physical processes are slow and the factors could be thought as constants (such as the surface deposit in case study one and two), whereas other processes are variable (such as soil salinity and ground water level in case study three). The three case studies together demonstrated the role of physical factors from a direct, strong and variant form (soil salinity and ground water level in case study three) to an indirect, weak and constant form (surface deposit in case study one).

From all three case studies, it can be concluded that no matter the location on the earth surface, the organisational level or the spatial scale, the ecological patterns have a physical basis. In addition, the relative importance of physical factors changes with scale, level and patch type. Obviously, biotic interactions or human and social-economic factors may be dominant at some scales and at some levels. However, knowledge of the inherent variability of the physical factors at different scales and levels provides a framework on which patterns and dynamics of landscapes and plant communities can be based.

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(Introduction and Conclusion)

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