DECISION RULES FOR RIPARIAN VEGETATION: PREDICTING THE DISTRIBUTION OF PLANT FUNCTIONAL GROUPS FROM TRAIT-ENVIRONMENT RELATIONSHIPS

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ABSTRACT

The conservation of biological diversity requires simple, predictive models that yield quantitative guidelines for management. This is illustrated by contemporary problems in managing wetlands. Riparian wetlands, in particular, are under heavy pressure from the hydrological changes produced by dam construction and water diversion projects. There has been ample documentation of the significance of substrate and hydrologic variables on the composition of shoreline plant communities, yet we have few models that yield quantitative predictions for conservation management. My goal has been to provide quantitative decision rules that predict the composition of wetland plant communities.

A principal obstacle to generating predictions for wetland vegetation is the large species pool. One solution is the assignment of species to functional groups that are recognizable by a few, simple traits. The distribution of these functional groups could then be described by trait-environment relationships. I have investigated the relationship between the distribution of functional groups and a set of hydrological and substrate variables, using the wetlands of the Ottawa River as my study system. I first identified two fundamental functional groups of wetland species, woody and herbaceous. The model with the highest accuracy was composed of two hydrologic variables, the last day of the first flood and the time of the second flood. The combination of these two variables correctly identified which group was the cover type for over 80% of the original data points.

I then investigated the relationships between functional groups defined by the presence or absence of floating leaves and/or flexuous stems and the environmental variables. The duration of flooding best described the distribution of this group, again with an accuracy of over 80%, using the original data points.

Finally I compared the merits of five classifications of emergent species in identifying functional groups that can be predicted from hydrological and substrate variables. The traits used in these classifications included leaf shape, area or arrangement; stem characteristics; ramet biomass; ramet height; and the number and length of rhizomes. The most accurate models (based on the original data) related the distribution of the functional groups that were defined by leaf shape, leaf area and stem diameter to hydrology and the sand fraction in the soil.

I generated and tested quantitative predictions from the 11 models with the highest accuracy (using the original data) from the above work. Four models performed well when tested with data from other regions or from Ottawa River sites not previously included in the analysis. The corresponding functional groups were woody plants, floating leaved/flexuous stemmed plants, plants with leaf area equal to zero and plants with lanceolate, elliptical or compound emergent leaves. Using the model parameters I formulated inclusion and exclusion rules to predict the presence or absence of these functional groups at various ranges of the significant environmental variables. These decision rules provide valuable tools for the conservation management of the vegetation of riverine wetlands.

RÉSUMÉ

La conservation de la diversité biologique requiert l'utilisation de modèles de prédiction. Ces modèles permettent généralement d'intégrer des paramètres quantitatifs au sein des stratégies de gestion. Le besoin d'utiliser des paramètres quantitatifs est particulièrement apparent lorsqu'il s'agit de préserver les différents milieux humides. Les terres humides riveraines sont particulièrement sensibles aux pressions exercées suite à la construction de barrages ou de tous autres aménagements susceptibles d'altérer le cours normal des eaux. Plusieurs études ont documenté l'influence du substrat et des variables hydrologiques sur la composition des communautés de plantes riveraines. Cependant, très peu de ces études ont réussi à quantifier ces phénomènes afin de pouvoir en tirer des prédictions. Cette étude cherche à définir des critères de décision quantifiables qui pourront être utilisés afin de prédire la composition des communautés de plantes au sein des différentes terres humides.

Les habitats humides présentent une très grande variété d'espèces végétales. Cette diversité rend la génération de prédictions particulèrement difficile. L'utilisation de groupes fonctionnels, à traits simples, permet cependant de minimiser le nombre de caractères et par conséquent de simplifier la génération de prédictions. La distribution de ces différents groupes fonctionnels peut être caractérisée par des relations à caractère environnemental. Au cours de cette étude, les relations qui existent entre les caractéristiques du substrat, les différentes variables hydrologiques et les divers groupes fonctionnels ont été étudiées au sein des différents écosystèmes humides de la vallée de la rivière Outaouais. Deux groupes fonctionnels particuliers caractérisent l'ensemble de la végétation présente aux abords des milieux humides: 1) les espèces ligneuses et 2) les espèces herbacées. La distribution de ces groupes fonctionnels est largement influencée (80%) par la date de la dernière journée de la première période d'inondation ainsi que par la durée de la seconde période d'inondation.

Dans un second temps, deux nouveaux groupes fonctionnels ont été étudiés: la présence ou l'absence de feuilles flottantes et la flexibilité de la tige. La distribution de ces groupes est de nouveau largement influencé (80%) par la durée des périodes d'inondation.

Finalement, certains traits représentatifs des espèces émergentes ont été étudiés afin d'être reliés aux caractéristiques du substrat et aux conditions hydrologiques. Les traits étudiés comptent parmis eux la forme, la surface et l'arrangement des feuilles, les caractères de la tige, la biomasse et la hauteur des rameux ainsi que le nombre et la taille des rhizomes. Le modèle le plus adéquat relie la distribution des groupes fonctionnels, soient la forme et la surface des feuilles et le diamètre de la tige à l'hydrologie et à la fraction sablonneuse des sols.

Des prédictions quantitatives ont été générées et testées pour un total de 11 modèles. Quatre de ces modèles s'avèrent adéquats pour les différents milieux humides

de la vallée de la rivière Outaouais. Les meilleurs prédicteurs fonctionnels associés à ces modèles sont les espèces ligneuses, les espèces herbacées, la présence ou l'absence de feuilles flottantes, la flexibilité de la tige et la forme des feuilles des espèces émergentes. Certaines règles d'inclusion ou d'exclusion ont été formulées afin de prédire la distribution de ces groupes fonctionnels selon différents gradients environnementaux. Ces nouvelles règles de décision sont précieuses et elles pourront désormais être intégrées aux différentes stratégies de gestion visant à préserver les différentes terres humides riveraines.

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CHAPTER 1

TRAIT-ENVIRONMENT RELATIONSHIPS AND THE POTENTIAL FOR PREDICTIVE RULES FOR WETLAND VEGETATION.

Introduction: problem and goals

The conservation of biological diversity requires simple, predictive models that yield quantitative guidelines for management strategies. The need for such quantitative models is especially apparent in the case of wetland conservation and restoration. Human impact on these systems has been widespread and, in many cases, severe. For example, in the United States, between 35% and 50% of inland wetlands have been drained, or otherwise altered, since presettlement times (Mitsch and Gosselink 1986). In particular, the effect of river regulation on shoreline vegetation has emerged as a pressing problem due to (1) the major effects of hydrology upon wetland vegetation, (2) the geographical extent of regulation, and (3) the biological diversity of riparian corridors.

The importance of hydrology is suggested in the zonation of wetland vegetation; that is, the formation of distinguishable bands of vegetation (e.g., floating-leafed plants, reeds, woody plants) at different vertical positions on the shore (Sculthorpe 1967). Yet, the hydrology of most of our major river systems has been severely altered by dam construction and water diversion projects (Dynesius and Nilsson 1994). These vast areas of regulated shorelines include assemblages that are characterized by structural diversity and high species numbers (Nilsson 1992). The structural diversity of riparian vegetation refers to the change in dominant life form (e.g., tree, shrub, herbaceous plant), often over relatively short distances (Nilsson 1992). High species numbers have been recorded from several sites covering a wide geographic range. In Sweden, 131 species of vascular plants were recorded for 200 m segment of river bank (Nilsson 1992), and in southwestern France, 428 plant species were recorded from a 2 km stretch of shoreline (Tabacchi 1995).

Ironically, the diversity of riparian systems makes quantitative modelling a difficult task. One course of action is to divide the species pool into subsets, then describe the relationships between these groups and environmental variables. Not only would this simplify the task of producing wetland models, a wise selection of these groups could reflect the fundamental elements of wetland diversity. Thus, models at the level of the functional group could provide effective tools for protecting the diversity of wetland vegetation.

The goal of my study was to describe quantitative decision rules for the conservation management of the riverine wetlands of Canada's eastern temperate region (as defined by the National Wetlands Working Group 1988). Specifically, I sought :

1) to identify functional groups that are likely to be predictable from environmental variables.

2) to identify the strongest relationship between these functional groups and environmental variables.

3) to quantify these relationships in the form of "if-then" predictions or decision rules.

4) to test the decision rules generated from these relationships.

I have used the term "functional group" throughout my thesis for any non-phylogenetic group that can be identified by traits. As such it includes vegetation types (e.g., wooded or herbaceous), life-forms (e.g., saggitarid, isoetid), canopy types (e.g., multilayer, monolayer), functional guilds (e.g., matrix, dominant), and groups described by single quantitative traits (e.g. plant height, leaf area).

The idea that the composition of wetland vegetation is predictable is not new. There has been a rich history of research relating wetland community composition to environmental variables (e.g., Pearsall 1920, Spence 1967, Hutchinson 1975). Moreover, two important environmental factors have been described, hydrology (Hutchinson 1975, van der Valk 1981, Day et al. 1988) and substrate, where the latter incorporates the effects of disturbance (Day et al. 1988), resource levels (Gaudet 1993) and successional stage (Pearsall 1920). In short, we have a largely qualitative understanding of the role of hydrology and other variables in maintaining the diversity of the system. The next logical step is to ask which elements of the vegetation can be most accurately predicted (Rigler 1982) and which of the possible hydrological and substrate variables are the best predictors. We should then be able to generate accurate, quantitative models.

Approach: creation of functional groups

I identified a wide array of functional groups in order to determine which could be most accurately predicted from environmental variables, where accuracy is the percentage of occurrences of a functional group that are correctly predicted for a given site. My division of vegetation into groups may be represented in an hierarchical fashion (Figure 1.1), starting with the basic separation of woody and herbaceous plants.

The next division of wetland species was based on the presence or absence of a flexuous stem or floating leaves among the herbaceous species. This separated the aquatic and emergent functional groups.

At the finest level of division I compared the strength of trait-environment relationships for five classifications of the emergent species. The classifications included (1) Hutchinson (1975), (2) Shipley et al. (1989), (3) Boutin and Keddy's (1993) functional guilds, (4) functional groups based on single quantitative traits (e.g. plant height, stem diameter) and (5) phylogenetic groups. The phylogenetic groups were included as a control, to test whether "ecologically meaningful" groups would yield more accurate models than groups defined by floristic criteria. I expected to be able to identify three or four strong trait-environment relationships that would allow me to map the distribution of the corresponding functional groups with respect to a few key predictors.

My thesis can therefore be divided into two parts: 1) my protocol for idenfying accurate models and generating quantitative predictions (Chapters 2 and 3) and 2) the tests of these predictions (Chapters 4 and 5). It should be noted that the distribution of the woody and herbaceous groups were studied in depth (Chapters 2 and 4) for two reasons: 1) they represent fundamental elements of shoreline vegetation and

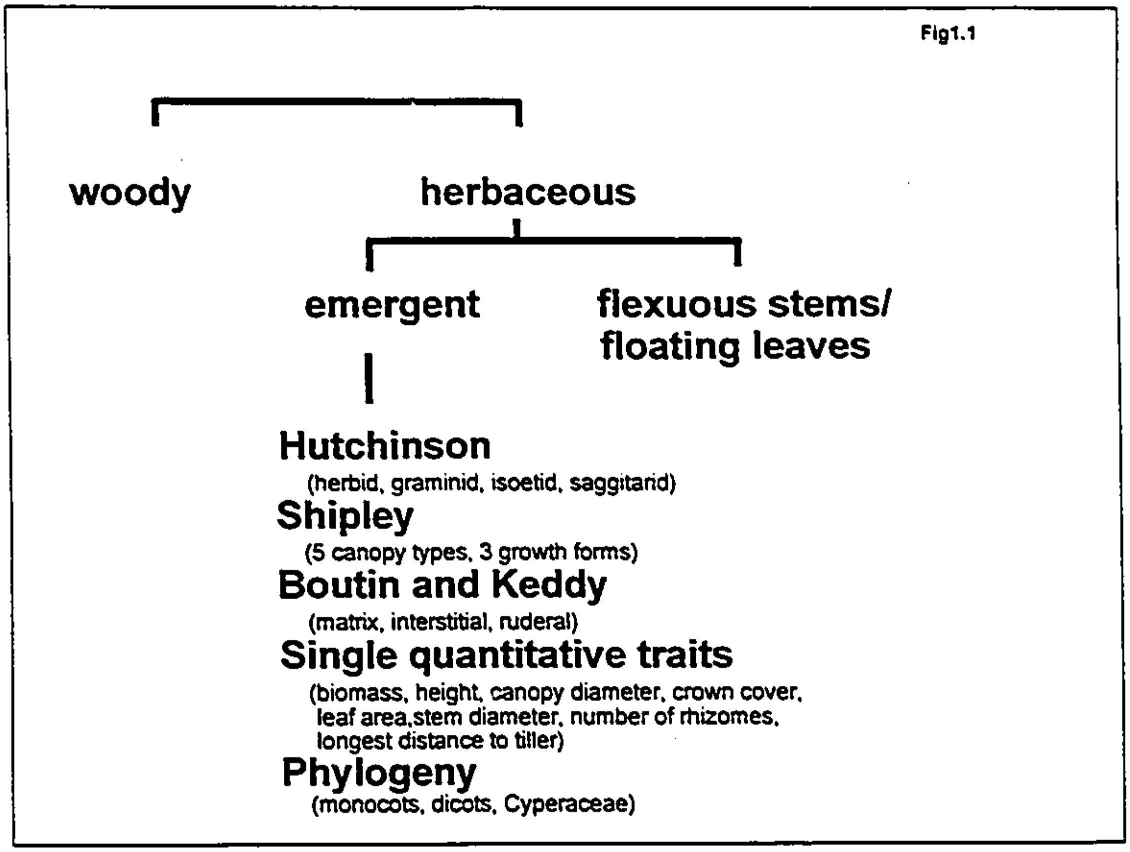


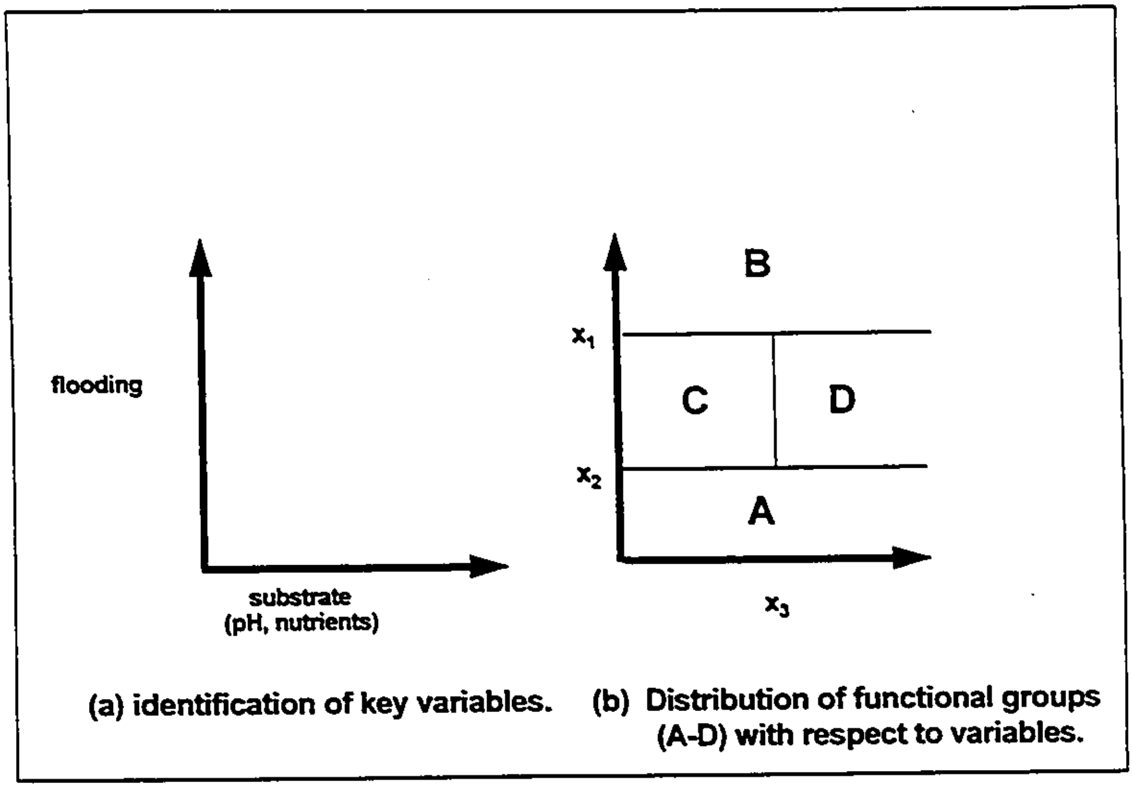
FIGURE 1.1. Successive divisions of wetland plant species into functional groups. The first two levels are dichotomous divisions. At the third level the same set of species are divided according to separate applications of five different classifications.

2) their treatment in the literature suggests that they might be accurately predicted (e.g. Hall and Smith 1955).

Output: decision rules

The translation of the quantitative models into predictions or decision rules is an important aspect of my project. I have applied the term "decision rule" to the predictions of the presence or absence of a functional group, as determined from specific values of the variables of the model. For example, functional group *x* could be related to the mean depth of flooding. Using the equation that describes this relationship, I could generate decision rules of the form, "Functional group *x* will not be present if the mean depth of flooding is greater than *y*" or "Functional group *x* will be present if the mean depth of flooding is less than *y*." These two options, presence or absence, give rise to two forms of rules, inclusion and exclusion. Inclusion rules predict the presence of a functional group, while exclusion rules predict the absence.

Figure 1.2 provides an illustration of the approach. Assuming that flooding and substrate are important environmental gradients, I sought functional groups (A - D) with a limited distribution with respect to specific measures of flooding or substrate conditions. For the sake of this example, let the flood variable be duration of flooding (measured as fraction of the growing season flooded) and let the substrate variable be phosphorous (in ppm). All four functional groups (A- D) have a restricted range with respect to at least



(a) identification of key variables.

(b) Distribution of functional groups (A-D) with respect to variables.

FIGURE 1.2 An application of trait-environment relationships to wetland vegetation. (a) potential gradients. (b) distribution of functional groups A-D with respect to gradients.

one of these variables. Therefore, we could generate inclusion or exclusion rules for all the groups. An example of an inclusion rule for C is, "Functional group C will be present if the duration of flooding is between x_1 and x_2 and if the level of phosphorous in the soil is less than x_3." An exclusion rule would be, "Functional group C will be absent if the duration of flooding is less than x_2."

There have been at least two discussions of ecological rules that are closely related to my approach. The first is the combination of insertion and deletion rules in an algorithm that was designed to predict species composition in a given habitat (Haefner 1975, 1981) Insertion of a species would occur if all its resource requirements were met. Deletion would be the result of competition. Haefner's (1981) algorithm was accurate in predicting the species composition of small numbers of closely related animal species, such as the foliage-gleaning guild of birds on islands off the coast of Maine. The decision rules that I have described differ from Haefner's rules in that they do not distinguish between the effects of competition and resource levels.

The second pertinent discussion is the definition of capacity and allocation rules (Brown 1987). Capacity rules are the "extrinsic patterns and processes" that describe the capacity of the environment to support a given group of organisms. These patterns and processes include both physical constraints and the biological interactions between the members of the group and organisms outside the group. Allocation rules describe "the resolution of interactions" among group members. These interactions are affected by the external patterns and processes. My inclusion and exclusion rules are, in effect, two types of capacity rules. However, I have not used the term "capacity rule" because it fails to distinguish between predicting the presence and predicting the absence of a group. Moreover, it has the connotation of "carrying capacity," which is not strictly appropriate in the case of wetland vegetation.

Significance: moving from description to prediction

It should come as no surprise to find relationships between wetland vegetation and environmental variables. The role of hydrology and substrate in the distribution of wetland species has been inferred or described in many studies (e.g., Pearsall 1920, Spence 1967, Hutchinson 1975). The significance of my work lies in the quantification, comparison, and testing of trait-environment relationships. Although we know which variables are likely to be important in a given wetland, there have been few comparisons of their relative importance in predicting the distribution of plant groups. It has also been rare to quantify the range of a variable at which one trait or functional group is likely to be present or absent. Most of this work has been restricted to the distribution of woody plants, as predicted by duration of flooding (e.g., Hall and Smith 1955, Bedinger 1971). Quantitative decision rules are essential to accurate environmental assessment and to the restoration of altered systems.

The second significant aspect of the project is the comparison of the performance of models based on different ecological classifications or functional groups already described for wetland vegetation. Although some groupings seem intuitively obvious (woody, herbaceous), there has been little testing of the accuracy of the predictions based on these groups.

In addition to comparing classifications of wetland vegetation, I have compared the accuracy that can be achieved using different combinations of a set of environmental variables. It is more common to reduce the number of these predictors through multivariate techniques (PCA, DCA, CCA). I have resisted this temptation because my objective has been to provide much needed tools for conservation management and real variables lend themselves more easily to real management guidelines.

Finally, the output has been translated into testable predictions or decision rules. Although a thorough test is beyond the scope of the study, I have provided a short list of potentially accurate guidelines for wetland conservation. In brief, the investigation of trait-environment relationships has generally revolved around two questions, "What traits?" and "What environmental variables?" There is an obvious need to add "At what range of the environmental variables?" and "With what accuracy?" (Peters 1991). My work is an attempt to address these last two questions.

Theoretical considerations: functional groups and trait-environment relationships.

Ecological classifications: origin of the term "functional group"

The concept of an ecological classification of species can be traced to Theophrastus (ca. 300 BC) or earlier (Gitay and Noble 1994). Over its lengthy history ecological classification has assumed a variety of forms and labels : vegetation types or associations (von Humbolt 1807-1834 in Barbour et al. 1980), guilds (Root 1967), functional groups (Cummings 1974), modules (Paine 1980) and cliques (Yodzis 1982). In the 1960's and 1970's, guilds and functional groups emerged as prominent concepts in ecological discussion (Gitay and Noble 1994). The description of a foliage-gleaning guild of birds in the arid Southwest (Root 1967) generated numerous applications of this term, although seldom with clear definition and often in a manner other than Root's original combination of resource and function (Simberloff and Dayan 1991).

In a similar way, the first use of the term functional group was followed by much discussion and a confusing array of applications. The term was originally applied to stream microbiota and invertebrates in order to group species performing the same function in a community (Cummins 1974). In the case of vegetation, functional groups were first defined according to the rate of a physiological process, such as photosynthesis. Proposed functional groups separated C_3 and C_4 species, and shade- tolerant and shade-intolerant species (Botkin 1974). The definition has been broadened to apply (1) to species responding in a uniform way to a given disturbance or an environmental change and (2) to species sharing a set of traits assumed to be related to environmental factors. Examples of the first application are the response of rangeland plant species to fire or grazing (Friedel et al. 1988) and differences in bird assemblages between grazed and ungrazed habitats (Verner 1984). An example of the second application is the investigation of above- and below-ground biomass allocation as an indicator of plant foraging strategy (Tilman 1988, Boutin and Keddy 1993).

Despite the confusion over terminology, ecological classifications continue to be the avenue of choice for three cases: (1) where specific traits of an organism are linked to its response to an environmental condition, (2) where the number of species is unwieldy or (3) where models are designed for large geographic areas. An example of the first case is the identification of potential plant invaders by traits suited for rapid colonization. Richardson et al. (1990) described the post-fire invasion window in South African mountain fynbos and related dispersability and fire-resistance to successful invasion. The functional group with the highest number of successful invaders was characterized by short juvenile periods, poor fire tolerance, small seeds and a high degree of serotiny (accumulation of seed bank in the canopy). Ellison and Bedford (1995) provide an illustration of the second case. They used life history traits to divide the 169 species recorded from a Wisconsin wetland into 4 functional groups. They were then able to relate the response of the functional groups to changes in hydrology, through a cellular automata model. The third case involves the modeling of vegetation on a global scale. For example, Box (1981) used six sets of traits (plant structural type, plant size, leaf form, leaf size, leaf structure, seasonal photosynthetic habit) to divide global vegetation into 77 physiognomic groups. The distribution of the groups was then modeled as a function of 8 climatic variables which reflected global variation in temperature and precipitation. When tested with data from sites not included in the original analysis, the model identified all groups present at the sites with an accuracy of 92%. Box's approach demonstrates the relevance of ecological classifications to the study of climate change, and this area of research has engendered much discussion of the definition (Gitay and

Noble 1994) and delineation (Grime et al. 1994) of functional groups. My application of the term incorporates the first two cases, the identification of specific traits (e.g. leaf area and arrangement) and the problem of a large number of species (200 to 300 in my sample area).

Trait-environment relationships in plant ecology

One of the central themes in plant ecology has been the identification of traits that lead to ecologically meaningful groupings (e.g., Raunkiaer 1934, Hutchinson 1975, Grime 1977). Among the most commonly cited examples is Raunkiaer's (1934) classification of plant species into five major life forms according to the position of the perennating organ (e.g., tips of branches, underground). Raunkiaer (1934) related the distribution of these life forms to global climate by comparing the proportion of the species pool represented by each life form in different regions of the world.

The investigation of trait- environment relationships, however, predates Raunkiaer by nearly a century. The recognition of distinct vegetation belts on a global scale and the association of these belts with specific climatic conditions was the first, and perhaps most thoroughly studied, example of trait-environment relationships in plant ecology. These early efforts involved the description and cataloguing of information on vegetation from different parts of the world by von Humbolt, Warming , Schimper and others (Barbour et al. 1980). The first descriptions of trait-environment relationships covered themes and concepts that are still pertinent: the description of vegetation types or associations, the emphasis on physiognomy and the recognition of vegetation patterns involving climate (temperature and moisture), latitude, elevation and soil (Barbour et al. 1980). Advances in information gathering and computer technology have provided the possibility for sophisticated global models based on elaborations and refinements of these early directions. The precision and complexity (e.g., 77 physiognomic groups) of Box's (1981) model is a case in point. Functional groups and trait-environment relationships will necessarily continue to provide the basis for modelling the response of vegetation to climate change (Grime et al. 1994).

On a finer scale, trait- environment relationships have been used (1) to monitor spatial and temporal changes in vegetation (e.g., Jaworski et al. 1979), (2) to develop models of successional patterns in forests (Botkin et al. 1972, Connell and Slatyer 1977), (3) to explain general patterns of plant distribution (Grime 1977, Tilman 1988), and (4) to predict the response to variables or events such as fire (Noble and Slatyer 1980) and flooding (van der Valk 1981, Ellison and Bedford 1995). The use of trait-environment relationships has been common in monitoring changes in temperate zone wetlands. Jaworski et al. (1979) related the changes in area occupied by 5 vegetation types (wooded, meadow, sedge marsh, emergent and submersed/floating-leafed) to long term water level fluctuations in the Great Lakes. A similar approach has been used in studies of wetlands along the St. Lawrence River, Quebec (Jean et al. 1992), of the Peace-Athabaska Delta (Townsend 1986) and in New England (Golet and Parkhurst 1981).

The applications of trait-environment relationships in successional models have usually been with respect to life history and degree of shade-tolerance. For example, in the "facilitation model" of succession, the success of pioneer species is attributed to their shade-intolerance, large number of propagules and seed dormancy (Connell and Slatyer 1977). According to the "tolerance" model, the late successional species must be shade-tolerant, and in the "inhibition" model they must be both shade-tolerant and long-lived (Connell and Slatyer 1977). In application, the forest dynamics simulated in the computer model, JABOWA (Botkin et al. 1972), have been simplified by categorizing species as shade-tolerant or shade-intolerant.

Two prominent models of the general patterns of plant distribution incorporate trait-environment relationships. Grime's (1977) model describes selection for competitive ability, stress tolerance and ruderal traits (C-S-R model). Each "strategy" is defined by a series of traits that correspond with the position of a species along gradients of stress and disturbance. The distinction between groups is based on differences in traits such as plant height, leaf form and frequency of flowering. Tilman (1986) described plant morphology in terms of allocation patterns to stem, root and leaf. Through a series of computer simulations he demonstrated that allocation patterns can be related to the differences in levels of light intensity and soil nutrients between habitats.

Finally, in systems where there are obvious and recurring disturbances (fire, hurricane), trait-environment relationships provide a potential basis for prediction. The traits that determine the response to these events (fire resistance, time to reproductive maturity) have been used to model the functional group that is likely to be present at different time intervals following the event. Noble and Slatyer (1980) call these traits "vital attributes." They have identified three sets of traits that determine the replacement sequence of dominant vegetation following disturbance: the method of arrival or persistence of a species, the ability to establish and grow to maturity, and the time needed to reach critical life stages. They illustrate their approach by generating a post-fire replacement sequence for the dominant vegetation of an aspen community in Montana and for the wet sclerophyll and rain forests of Tasmania.

Summary

From this review of trait-environment relationships, three conclusions may be drawn. First, trait-environment relationships have been successful as predictive models most often in systems with obvious and steep abiotic gradients. The examples discussed above include the range of temperature and precipitation on a global scale (Box 1981) and the light gradient across the open and closed canopies of early and late successional communities (Botkin et al. 1972, Connell and Slatyer 1977).

Second, the identification of ecologically meaningful traits and therefore ecologically meaningful functional groups has generally proceeded from the researcher's knowledge of the natural history of the study system (Gitay and Noble 1994). Hutchinson's (1975) classic summary and revision of the classification of wetland life forms is a case in point. These functional groups have often been based on obvious structural differences (tree, shrub, herb) or morphological differences (needle-leafed, broad-leaved). Although this subjective assignment of species to functional groups is not ideal, adherence to a clearly defined protocol can make arbitrary classifications acceptable (Simberloff and Dayan 1991). Indeed, there may be systems for which an intuitive proposal of functional groups is preferable to the alternative, multivariate techniques, as the latter do not always yield repeatable results (Gitay and Noble 1994). In short, many of the most robust, and potentially predictable, functional groups have been intuitively obvious and have been based on qualitative traits.

Finally, many of the trait environment relationships have been described only qualitatively (e.g., "more" flooding, "robust" emergents, "thick" bark). There may well be instances, perhaps successional models, where a qualitative description of the sequence of community development is adequate. If so, these are the exceptions. We need models that allow us to predict the outcome of different management scenarios, and in most cases the quantification of the predictor variables is essential.

CHAPTER TWO

PREDICTING THE LOWER LIMIT OF WOODED WETLAND FROM RIVER HYDROLOGY

Introduction

The structure (dominant life-form) and species composition of riparian vegetation constitute fundamental elements of the diversity of riparian ecosystems. The uniqueness of shoreline vegetation is especially evident in arid and semi-arid regions where corridors of riparian forest rise above a landscape "barren of large woody plants" (Rood and Mahoney 1990). However, even in the forested watersheds of the humid temperate and boreal regions, riparian vegetation incorporates plant assemblages that differ markedly from the surrounding vegetation (Nilsson 1992, Malanson 1993). These assemblages are generally high in species numbers (Nilsson et al. 1988 and Nilsson 1992) and encompass structurally distinguishable vegetation types, from trees through shrubs and herbaceous vegetation (Nilsson 1984, 1992).

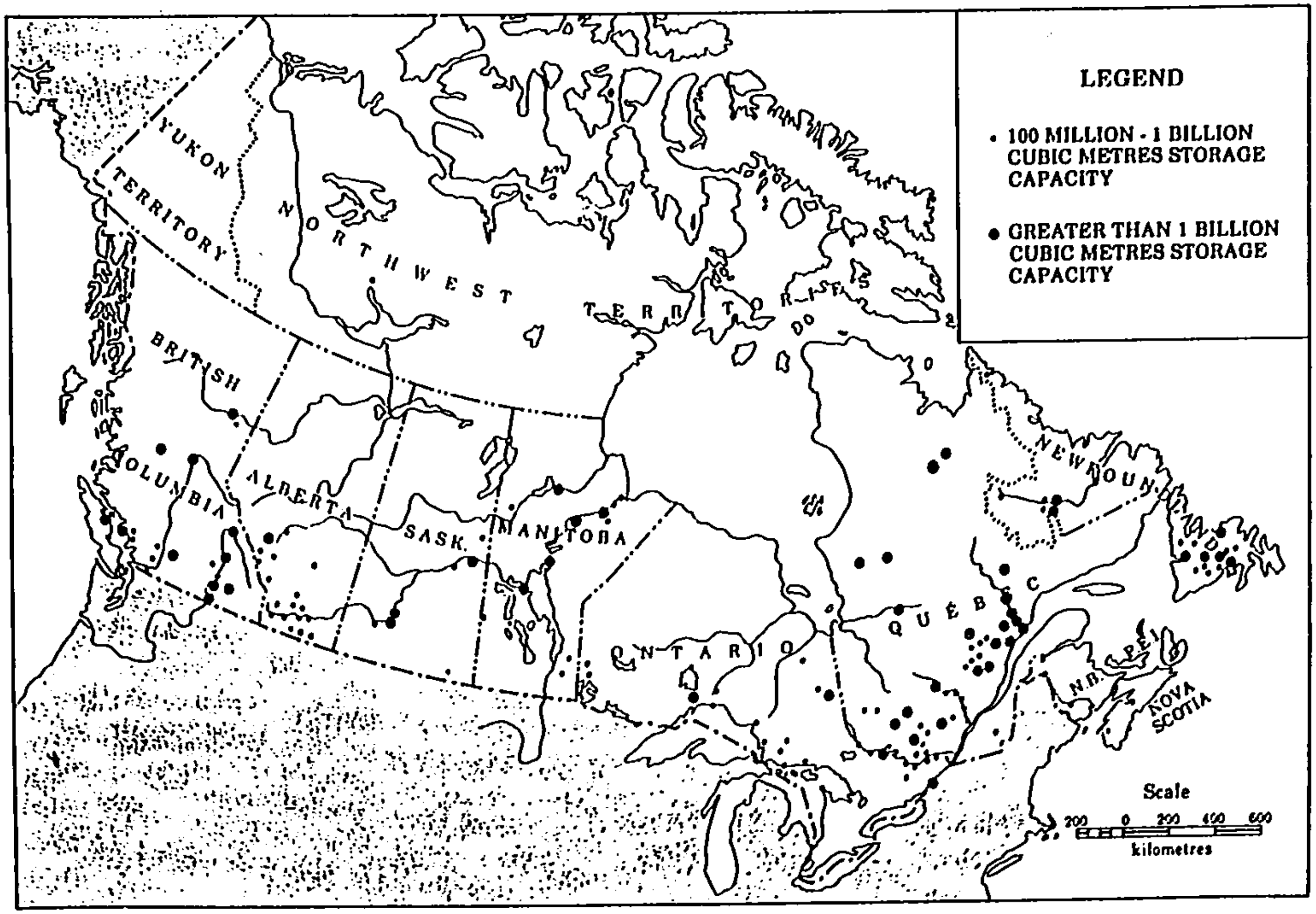
Much of the research on the riparian vegetation of North America has revolved around woody species. The bottomland forests of the southeastern United States (e.g., Hall and Smith 1955) and the poplar stands of the semi-arid regions (e.g., Rood and Mahoney 1990) are cases in point. However, in the boreal and northern temperate regions, herbaceous marshes are significant elements of riverine wetlands in terms of their area, species composition and structural diversity. The extent and biological importance of these marshes have been documented for the river shores of northern Sweden (Nilsson 1984, 1992) and Canada's eastern temperate zone (National Wetlands Working Group 1988), as well as the river deltas of Canada's boreal region (National Wetlands Working Group 1988). For example, the area of the Peace-Athabaska Delta is

3 775 km^2 (National Wetlands Working Group 1988) of which 300 000 to 400 000 acres is herbaceous marsh or exposed mudflats (Townsend 1986). Although the value of herbaceous wetlands has often been measured in terms of animal habitat (Dirschl 1971, National Wetlands Working Group 1988, Townsend 1986), the flora merits attention for its high species numbers and rare plant component. Cases in point include the marshes along the Ottawa River, where 2 to 24 species have been recorded per .25m^2 (Shipley et al. 1991) and the narrow herbaceous wetlands in the Tusket and Medway River systems, which support concentrations of Canada's threatened coastal plain flora (Keddy and Wisheu 1989, Wisheu et al. 1994)

The threat of river regulation to riparian vegetation has been well documented (Dirschl 1971, Johnson et al. 1976, Nilsson 1984 and 1992, Bradley and Smith 1986, Rood and Heinze-Milne 1989, Rood and Mahoney 1990, Johnson 1994). Dam construction and diversion projects have altered the hydrology of the majority of the drainage basins of the Northern Hemisphere (Dynesius and Nilsson 1994). Figure 2.1 indicates the thoroughness of our exploitation of Canadian rivers alone. A major concern is the loss of wetlands and shoreline plant assemblages along these vast lengths of regulated shoreline (e.g., Johnson et al. 1976, Rood and Mahoney 1990, Stromberg and Patten 1990, Dynesius and Nilsson 1994).

Some work has been done in modeling the dynamics of single dominant or threatened species, particularly in semi-arid regions of western North America (Baker 1990, Rood and Mahoney 1990, Stromberg et al. 1993). In the forested drainage basins of more humid climates, however, river regulation poses the specific threat of changing the distribution of two major vegetation types or functional groups. The area dominated by the herbaceous functional group risks being reduced by the invasion of the woody plants. This is due to the nature of river regulation in these regions. The alteration of hydrological regimes often results in a damping of seasonal fluctuation, with a reduced spring flood and an augmentation of the low, late summer flows. These trends are evident in the water level records available from Environment Canada. The reduced water level fluctuations are often followed by the succession of dominance by the herbaceous functional group to dominance by the woody functional group (Keddy and Reznicek 1986). As early as 1945, Hall et al. (1945) described the disappearance of the emergent/wet meadow zone following water stabilization in the Tennessee Valley. A reduction in spring floods on the Peace-Athabaska Delta was followed by "unchecked succession" of herbaceous to woody dominance (Dirschl 1971). Jaworski et al. (1979) described an extension of the area dominated by the woody functional group into areas formerly dominated by the herbaceous functional group, during years of low water levels in the Great Lakes system. A similar phenomenon has been associated with water diversions in Sweden (Grelsson and Nilsson 1980, Nilsson 1984). Conserving the diversity of the riparian wetlands of the boreal and humid, temperate regions thus requires that we be able to predict which flood regimes will foster and which will prevent incursion by woody plants.

FIGURE 2.1. An illustration of the scale of alteration of riparian hydrology in Canada. Location of large dams; large circle indicates a storage capacity exceeding 10^9 m^3, small circles indicate a storage capacity exceeding 10^8 m^3. (Source: Pearse et al. 1985. Currents of Change, Final Report: Inquiry on Federal Water Policy , Environment Canada, Ottawa, Canada. Reproduced with permission of the Minister of Supply and Services Canada, 1994).


LEGEND
• 100 MILLION - 1 BILLION CUBIC METRES STORAGE CAPACITY
● GREATER THAN 1 BILLION CUBIC METRES STORAGE CAPACITY
YUKON TERRITORY
NORTHWEST TERRITORIES
BRITISH COLUMBIA
ALBERTA
SASK.
MANITOBA
ONTARIO
QUEBEC
NEWFOUNDLAND
N.B.
P.E.I.
NOVA SCOTIA
Scale
200 0 200 400 600
kilometres

We need a simple model of the distribution of the woody functional group, based on a small number of easily calculated variables that capture the impact of flooding. A number of varibles are suggested by the literature. First, there is ample evidence that the time (Karr 1989, Johnson 1994) and duration (Yeager 1949, Hall and Smith 1955, Bedinger 1971) of flooding are important factors in the distribution of woody cover. They have been identified as paramount in reviews of research on the flood tolerance of woody plants (Gill 1970, Teskey and Hinkley 1977). Water depth (Yeager 1949, Harris and Marshall 1963, Harms et al. 1980, Nilsson and Keddy 1988, Karr 1989) and the frequency of flooding (Bedinger 1971, Nilsson and Keddy 1988) have also been identified as potential predictors.

In terms of the quantification of these predictors, several authors have designed measures of the duration of flooding from the data available for their study systems (Hall and Smith 1955, Bedinger 1971, Bell 1974, Nilsson and Keddy 1988, Auble et al. 1994, Johnson 1994). There has been less effort, however, to quantify the time of flooding and few comparisons of the predictive ability of the different hydrological variables one could imagine to be important, two exceptions being Nilsson and Keddy (1988) and Johnson (1994). I have therefore selected a set of hydrological variables, including several measures of the time of flooding. I have averaged these variables over four time intervals, as it is not clear what length of time would be required for a given flood regime to have an impact on vegetation or for the response of the vegetation to be evident. My goals were (a) to identify the best predictors of the lower boundary of the area where the woody functional group would be dominant, (b) to identify the range of these predictors where there is a low probability of woody cover and (c) to identify the period of time over which these variables would be effective.

Methods

Study sites

The Ottawa River (mean annual discharge > 1000 m^3/s) appears to be typical of large rivers in the eastern temperate region in both the extent of regulation (10 major dams (Ottawa Board of Engineers 1965)) and the occurrence of herbaceous wetlands (Day et al. 1988). Some shoreline marshes are as wide as 200 m. The first dam projects, in the early 1900's, were primarily flood control measures (Legget 1975). Subsequent hydro-electric projects have reduced the natural fluctuation in water levels by as much as half (Legget 1975), while leaving the general pattern of spring flood and lower late summer flows intact.

I examined a two hundred-kilometer portion of the Ottawa River between Westmeath, Ontario (45° 46' N, 76° 55' W) and Cumberland, Ontario (45°31' N, 75°25' W), locating wetlands that were near water gauges (Figure 2.2). Six such sites were found, four of which (Fitzroy Provincial Park, Westmeath Provincial Park, Andrew Hayden Park and Masson) were judged to be sufficiently close (1- 5 km) to gauging stations for direct use of gauge records.

A fifth site (Breckenridge Marsh) was 15 km from the nearest gauge. A small set of rapids separated a sixth site (Lucerne Boulevard) from a gauging station, although the actual distance was less than 2 km. Calibration curves ($R^2 = .98$ and $R^2 = .96$, n = 10) indicated that there were only small differences between fluctuations in water levels measured on regular visits to these sites and fluctuations recorded nearby at the Brittania gauge; thus, the gauge records were adjusted accordingly.

I was aware of the importance of disturbance on the distribution of shoreline vegetation (Sculthorpe 1967, Keddy 1983) and included subjective classifications of the slope as gentle or steep (> 15°) and of the degree of exposure to wave and channel action as protected, moderate or strong. The degree of exposure was based on the orientation of the shoreline with respect to the direction of the current.

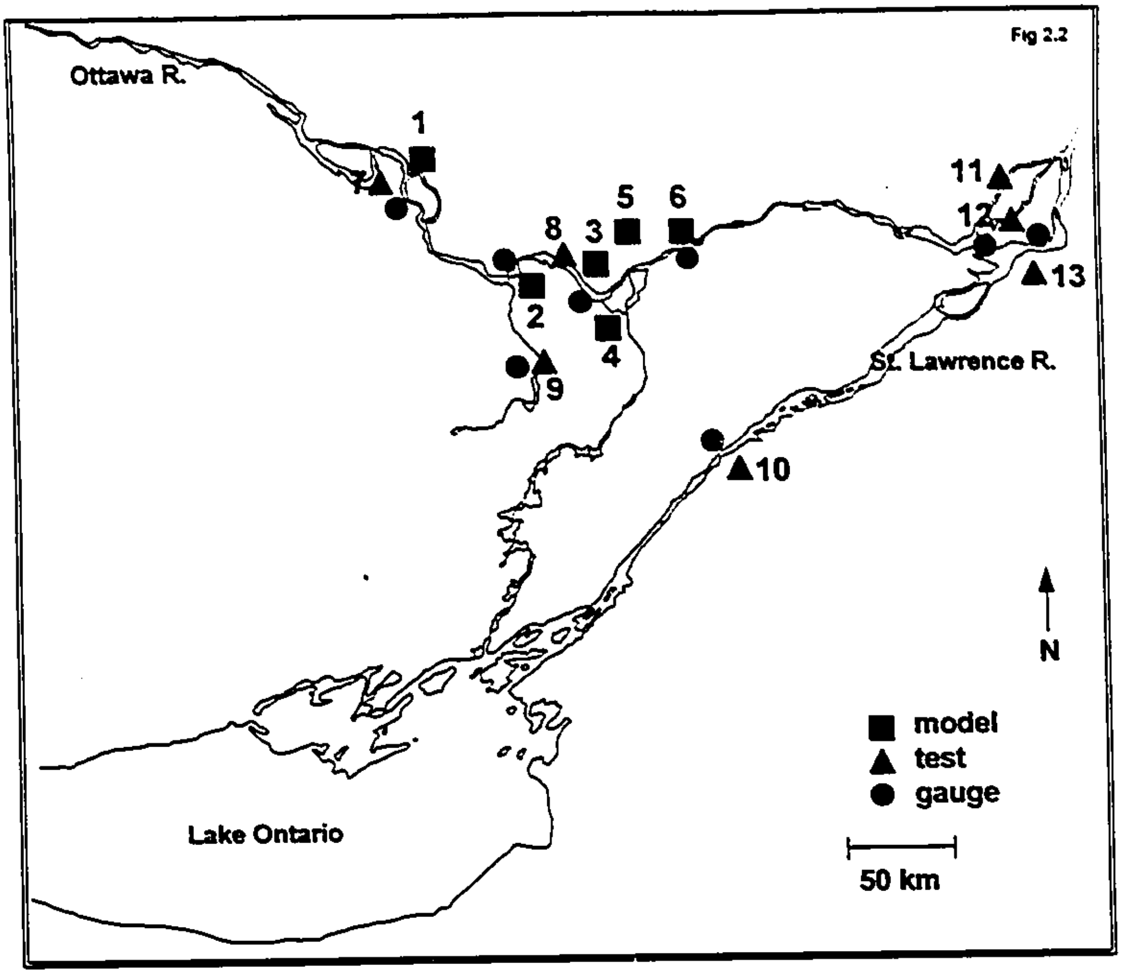


FIGURE 2.2. Map of study sites. Location of sites of data collection for developing the model (squares) and for testing the model (triangles). The locations of water gauges (circles) are also included. Sites are: 1: Westmeath Provincial Park; 2: Fitzroy Provincial Park; 3: Breckenridge Marsh; 4: Andrew Hayden Park; 5: Lucerne Boulevard; 6: Masson; 7: Westmeath Provincial Park, site b; 8: Luskville; 9: Appleton; 10: Waddington, NY; 11: Lac des Deux Montagnes; 12: Cape St. Jacques; 13: Iles de la Paix.

Dependent variable

The dependent variable was simply the presence or absence of woody cover. The cover type, or dominant functional group, was described for points above and below the lower boundary of woody cover, at 21 random points (5-7 points per 80m) at each site. This boundary was defined as the base of the woody plants at the lowest limit of continuous cover by woody species. I sought to minimize the confounding role of disturbance by restricting the study to portions of shorelines where there was 100% cover by vegetation and where there were no signs of erosion near the lower boundary of continuous woody cover. Data were collected during the growing season of 1993. The sample size was smaller at some sites due to the size of the wetland or to local disturbance, such as footpaths.

At each point, the lower limit of woody cover was identified, the species noted and the elevation of the point measured with respect to the water level. Water level readings for the time of sampling (within the hour) were either provided or calculated for the gauges mentioned above. At one site it was necessary to refer to a daily mean. Monitoring of the stage at this site indicated that there was little fluctuation throughout the day of sampling.

These measurements of the elevation of the boundary were used to generate the new pairs of elevation measurements, above and below the boundary, with known cover. The first datum would be a point where the cover, or dominant functional group, was woody (original elevation plus 5 cm), the second, a point where the dominant group was herbaceous (original point minus 5 cm). The independent variables were therefore descriptors of flooding at each of these new points, where flooding was defined as water level greater than 0. The horizontal distance associated with an elevation change of 5 cm varied from less than 1 m to greater than 10 m.

Independent variables (hydrological)

Records of the daily mean water level for the period from 1974 to 1992 were obtained from the Water Survey Division of Environment Canada and from Ontario Hydro. There were missing data, amounting to less than 2%, from two gauges. These values were inferred from calibration curves ($R^2 = .99$ and $R^2 = .96$, N = 222) based on records from gauges located upstream.

A set of seven hydrological variables (Table 1.1) were calculated for each of the data points. The variables were selected to reflect the depth, duration, time, and frequency of flooding. The fraction of the growing season flooded was an obvious choice given its straightforward calculation and prominence in the literature (Hall and Smith 1955, Bell 1974, Malecki et al. 1983, Nilsson and Keddy 1988). The only potential for ambiguity lies in the arbitrary definition of the growing season (Hall and Smith 1955, Malecki et al. 1983, Nilsson and Keddy 1988). I addressed this by using the 5.5 degree rule (Grandtner 1966), an accepted practice for forests of Quebec and Ontario (Ontario

Ministry of Natural Resources and Environment Canada 1984, Le Groupe Dryade 1985) (see below). The growing season was therefore defined by number of days, with the beginning of the growing season set as day one.

The mean depth of flooding (Yeager 1949, Harmes et al. 1980) and the number of floods per season (Phipps 1979, Nilsson and Keddy 1988) were selected as the most straightforward measures of the depth and frequency of flooding.

Finally, I wanted to test for the impact of the time of flooding and of a possible second and/or midseason flood, so included the end of the first flood, the beginning and end of the second flood and the duration of the drawdown preceding the first midseason flood. The midseason was defined as the period from day 90 to day 120 of the growing season (day 85 to day 115 in the case of Westmeath Provincial Park). An eighth variable, the beginning of the first flood (Nilsson and Keddy 1988), was omitted as there was little variation in its value; points were generally flooded on the first day of the growing season. Calculations were based on daily averages of water levels. Drawdowns of only one day were thus considered questionable events and were ignored in assessing the duration of flooding.

TABLE 2.1. Hydrological variables with abbreviations.

Abbreviation	Variable (unit)
gs	fraction of the growing season during which flooding occurred. (no unit)
eff	end of the first flood. (day of growing season)
lsec	length of the second flood. (days)
md	mean depth of flooding. (m)
nf	number of floods per growing season. (number per season)
tbf	number of days without flooding preceding floods that began in the midseason, defined as day 90-120 of the growing season. (days)
bsec	beginning of the second flood. (day of the growing season)

The values for the variables were averaged over four intervals- the 3, 7, 12 and 18 growing seasons previous to the collection of data. The shortest interval is the time between onset of high water levels and dieback of woody plants (Jaworski et al. 1979). The longest interval is the period identified as the requirement for succession of herbaceous wetland to wooded wetland in the Great Lakes system (Painter and Keddy 1992) and close to the 17- year interval for succession from sedge meadow to low shrub in the Peace-Athabasca Delta (Peace-Athabasca Delta Project Group 1973).

According to conventional interpretation of the 5.5 degree rule, the start of the growing season occurs when the mean daily temperature surpasses 5.5° C for five of seven days, and ends when the mean daily temperature fails to surpass 5.5° C for five of seven days. A climatic map of Canada (Canada Centre for Mapping 1990) indicated that all but the Westmeath site were in the same zone. Temperature records from the Ottawa International Airport (45°19' N, 75°40'W) were used to calculate the growing season for these five sites (Andrew Hayden Park, Breckenridge, Fitzroy Provincial Park, Lucerne Blvd. and Masson). The beginnings and endings of the growing season were averaged over the 18 - year interval. Records from the Petawawa weather station (45°57' N, 76°14' W) were used to determine the growing season at Westmeath. In this case, data were averaged over only 16 years due to gaps in the records. I used the mean rather than the yearly estimates of the growing season in my calculation of hydrological variables, as an average offered the advantage of a broader interpretation and application of the results.

Independent variables (site variables)

Although site selection was designed to minimize the effect of disturbance, I decided to test for effects of exposure to waves or destructive floods by calculating three additional variables for each of the study sites: (1) effective fetch (Keddy 1984), (2) effective fetch multiplied by average wind speeds and frequencies (Keddy 1984) and (3) peak flow. A fourth variable, soil drainage, was included in the analysis as I was concerned about differences in the impact of duration of flooding depending on substrate. The methods for calculating these variables are described in Appendix 2.1.

Analyses

Analyses were conducted separately for each of the four time intervals: 3 growing seasons (1990-1992), 7 growing seasons (1986-1992), 12 growing seasons (1981-1992) and 18 growing seasons (1975-1992).

(a) Pearson product moment correlations for pairs of flood variables were obtained using Sigmastat for DOS (Jandel Scientific 1992).

(b) Logistic regressions (logit function) performed by SAS (SAS Institute 1987) were used to model (i) each hydrological variable in combination with the four site variables (fetch, fetch adjusted for wind speed and frequency, discharge, soil drainage) and (ii) all possible combinations of hydrological variables. The presence or absence of woody cover was the dependent variable.

Logistic regresssion is a statistical technique that describes the relationship between a binary dependent variable and one or more independent variables (continuous or discrete). The model has the form of a logistic function:

$$p(x) = [e \exp (B_0 + B_1 x)] / [1 + (e \exp (B_0 + B_1 x))]$$

where p (x) is the probability of occurrence of one of the two possible levels of the dependent variable for a given value of the independent variables. Thus, logistic regression differs from a classical linear regression in at least two respects: 1) the model is a logistic function and 2) the output is a probability of occurrence of one of two responses rather than a predicted value of a continuous response. I selected ranges of these probabilities to generate testable predictions or decision rules. I predicted that woody cover would occur at a point if the probability of its occurrence was greater than or equal to .7. I am not aware of any convention for determining such a range. I considered .7 to be an acceptable level of confidence if I were making management decsions. Moreover, I believed that it was a realistic level of confidence for an ecological model. For similar reasons I selected the range of probabilites of less than or equal to .3 to predict that woody cover would not occur (1 - .7 = .3). By identifying the range of independent variables that would yield these probabilites, I was able to formulate a set of predictions.

Four criteria were selected for evaluating the models. First, models were compared by examining the amount of deviance remaining. The best model had to have one of the lowest Akaike Information Criteria (AIC), a statistic that is analogous to the Residual Mean Square of linear regression models (Hosmer and Lemeshow 1989) (Appendix 2.2). Second, I compared the accuracy of models, where accuracy is defined as the percentage of the original data correctly identified by the model as having woody or herbaceous cover. Third, I favored models that were consistently among the better models over the four time intervals. Finally, I chose the simplest model (fewest number of independent variables) in cases where there were only small differences in the measures of the first three criteria.

The results of the best model were used to plot the probability of woody cover at various combinations of the component variables, to form a set of testable predictions.

(c) After selection of the best models, dummy variables (Kleinbaum et al. 1988) were introduced to test for site differences, for the time intervals where prediction was accurate. This had not been done earlier because my emphasis was on identifying the best hydrological predictors. In evaluating all possible combinations of hydrological variables, I was at the limit of a manageable number of independent variables.

In addition, a separate series of logistic regressions, with hydrological variables only, was carried out for each site, for the time interval with the best results. The number of variables in the site-specific models was limited to one or two, as the calculation of a logistic regression requires a large number of data and the site data represented only small subsets (n= 32-42) of the total data (n = 222). Results were compared for consistency between sites and with the best model from the combined data.

(d) Finally, the diagnostic procedures available in SAS were used to identify (1) data which were not well explained by the model (Pearson residual), (2) data that had the greatest impact on the disagreement between the model and original data.(DIFCHISQ), (3) data which had the greatest effect on the parameter coefficients (DFBETAs) and (4) data which had the largest effect on the Maximum Likelihood Estimates (C and CBAR). A large portion of such data from one site would signal a problem with grouping points from different sites. In addition, the standardized deviance residuals were plotted as a function of the predicted values to check the goodness of fit of the logistic function. This was done for the best model only. A curved pattern would indicate a poor fit.

Results

I found ten woody species at the lower boundary of woody cover: Acer saccharinum L., Myrica gale L., Salix discolor Muhl., Salix nigra Marsh, Salix rigida Muhl., Fraxinus pennsylvanica Marsh, Cornus stolonifera Michx, Cephalanthus occidentalis L., Alnus rugosa (DuRoi) Spreng. and Spirea alba DuRoi. Acer, Myrica and Salix were by far the most common genera. Alnus rugosa and Spirea alba were seen only rarely.

The only steep slopes encountered were portions of the shoreline at Fitzroy Provincial Park. This site included the most exposed shores and portions of shoreline had to be excluded due to disturbance or removal of vegetative cover by wave action and human activity. The greatest range in exposure, from protected to exposed, was found at Masson and Lucerne Boulevard.

Significant correlations.

The average values for variables were calculated for growing seasons of 194 days (April 16 to October 26) for five of the sites and 184 days (April 19 to October 19) for Westmeath Provincial Park. As there were few mid-season floods, my measure of the lag before the mid-season flood (tbf) was zero for most of the points when measured over intervals of 3 or 7 growing seasons. The mean and standard deviation for the variables are included in Table 2.2.

The hydrological variables were strongly correlated (Table 2.3), with similar patterns over the four intervals (Appendix 2.6). The highest correlation, $r = .83$ ($p < .001$), occurred for the relationship between the end of the first flood (eff) and the fraction of the growing season flooded (gs). The nonsignificant correlations usually involved the mean depth of flooding (md).

TABLE 2.2. Mean and standard deviation (in parenthesis) for hydrological variables, as averaged over the 12-year interval. Cover types are woody (w) and herbaceous (h).

Site	Cover	Variables						
		gs	eff	lsec	md	nf	tbf	bsec
Andrew Hayden	w	0.29	44. 6	6.53	0.51	3.17	0.00	94.4
		(0.03)	(3.95)	(2.11)	(0.00)	(0.34)	(0.00)	(2.02)
	h	0.34	47.9	8.38	0.52	3.28	0.79	93.1
		(0.04)	(3.26)	(1.22)	(0.01)	(0.32)	(1.96)	(3.22)
Breckenridge	w	0.29	42.7	8.07	0.46	3.13	0.29	92.0
		(0.04)	(5.80)	(2.87)	(0.00)	(0.50)	(1.31)	(5.27)
	h	0.35	49.8	8.88	0.47	3.32	1.24	89. 9
		(0.05)	(3.97)	(4.76)	(0.01)	(0.57)	(2.62)	(6.53)
Fitzroy	w	0.16	29.6	8.76	0.48	1.88	0.00	51.3
		(0.05)	(5.26)	(3.31)	(0.05)	(0.53)	(0.00)	(29.7)
	h	0.19	32.3	10.4	0.50	2.24	0.00	41.5
		(0.06)	(6.73)	(3.20)	(0.03)	(0.72)	(0.00)	(33.4)
Lucerne Blvd	w	0.34	48.5	8.03	0.44	3.19	1.95	92.9
		(0.08)	(11.3)	(3.60)	(0.01)	(0.49)	(8.49)	(10.6)
	h	0.42	58.9	10.1	0.45	3.19	4.63	94.6
		(0.11)	(15.8)	(6.95)	(0.01)	(0.68)	(10.2)	(23.3)
Masson	w	0.17	29.6	5.69	0.27	2.19	0.00	79.4
		(0.03)	(3.72)	(2.34)	(0.01)	(0.71)	(0.00)	(25.1)
	h	0.24	35.7	6.69	0.28	3.14	0.00	66.3
		(0.05)	(6.22)	(4.54)	(0.00)	(0.59)	(0.00)	(17.1)
Westmeath	w	0.13	23.2	7.79	0.58	1.73	0.00	71.7
		(0.02)	(1.58)	(1.52)	(0.03)	(0.49)	(0.00)	(31.5)
	h	0.17	25.3	8.00	0.55	2.62	0.00	48.8
		(0.04)	(2.30)	(1.36)	(0.04)	(1.03)	(0.00)	(22.6)

TABLE 2.3. Correlation of variables. Matrix of Pearson product moment correlation coefficients for hydrological variables. Probability values are in parenthesis, unless <.001 (***) or <.01 (**). N=222.

Variable		Pearson product moment coefficients						
		gs	eff	lsec	md	nf	tbf	bsec
fraction of the growing season flooded	gs	1.00						
end of first flood	eff	.83 ***	1.00					
length of second flood	lsec	-.35 ***	-.52 ***	1.00				
mean depth of flooding	md	.13 (.053)	.30 ***	-.060 (.38)	1.00			
number of floods	nf	.64 ***	.52 ***	-.33 ***	.019 (.78)	1.00		
lag to midseason flood	tbf	-.60 ***	-.67 ***	.34 ***	-.21 **	-.57 ***	1.00	
beginning of second flood	bsec	.62 ***	.73 ***	-.54 ***	.075 (.27)	.22 ***	-.48 ***	1.00

Site variables

The fetch, effective fetch, drainage, and discharge were not significant in any of my regression models and will not be discussed further.

Best model.

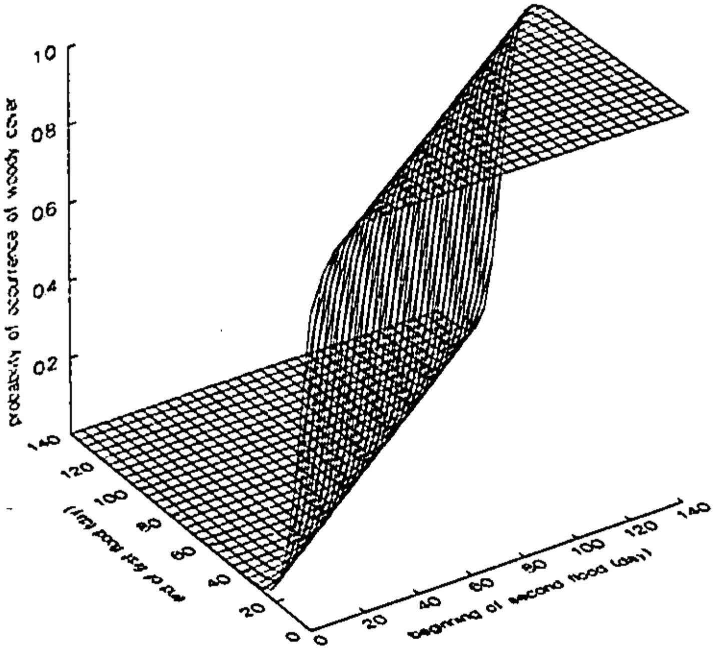
The best model combined two hydrological variables, the end of the first flood (eff) and the beginning of the second flood (bsec) (Figure 2.3). This choice is based on criteria described in the methods section: 1) its AIC score was the lowest or close to the lowest among the models; 2) it was consistently accurate (> 80%) over all but the three-year interval (Table 2.4, Column 2); and 3) it comprised only two variables.

The probability of woody cover was calculated for different values of eff and bsec (Figure 2.4) using the regression equations from the model for the twelve-year interval [$\ln(p/(1-p)) = .16(\text{bsec}) - .23(\text{eff}) + 1.42$]. (The equations and figures for the 7 and 18-year intervals are included in Appendix 4.2). As described above, a probability of greater than .7 was considered high while a probability of less than .3 or less was considered low. Using these criteria, all but 17 of the 222 points were correctly classified. Of these, the 9 points which were erroneously assigned to areas with woody cover were from Masson and 4 of the points which were incorrectly assigned to areas with herbaceous cover were from Lucerne Boulevard. As mentioned above, both these sites included the extremes of protected and exposed shoreline in my sampling.

TABLE 2.4. Best one, two and three-variable models (columns 1 to 3) for each of the four time intervals. The variables included in each model are followed by the AIC scores and the accuracy (in parenthesis) expressed as a percentage. The last column includes the results for fraction of the growing season flooded (gs) and beginning of the second flood (bsec), for the intervals where it was the second best 2-variable model. Abbreviations for other variables as per Table 2.1.

Interval (yrs)	Number of variables			
	1	2	3	2
18	nf 279 (69.4)	eff.bsec 214 (81.1)	eff,gs,bsec 212 (81.1)	gs.bsec 258 (73.0)
12	nf 287 (64.4)	eff,bsec 156 (86.0)	eff,bsec,lsec 157 (86.5)	gs,bsec 219 (77.0)
7	bsec 287 (61.3)	eff,bsec 172 (81.1)	eff,bsec.lsec 164 (83.3)	gs,bsec 222 (75.7)
3	bsec 279 (66.2)	gs,bsec 276 (56.8)	eff,gs,bsec 267 (67.6)	

FIGURE 2.3. The probability of occurrence of woody cover as a function of end of the first flood and beginning of the second flood (both calculated as days from the first day of the growing season. Model equation is $[\ln(p/(1-p)) = .16(\text{bsec}) - .23(\text{eff}) + 1.42\ ]$.


probability of occurrence of woody cover
10
08
06
0.4
02
140
120
100
80
60
40
20
0
end of first flood (day)
0
20
40
60
80
100
120
140
beginning of second flood (day)

The second best model, also composed of two variables, combined the fraction of the growing season flooded (gs) and beginning of the second flood (bsec) (Table 2.4). This model was the best model for the three-year interval and always among the best for the other intervals. I have included its AIC scores and percent accuracy in the last column of Table 2.4 to allow comparisons with the model composed of eff and bsec, as eff and gs are highly correlated.

Two other trends emerged from the analysis. First, the better models were all combinations of two variables. No single hydrological variable yielded a model with an accuracy greater than 70% or an AIC less than 250 (Table 2.4, Column 1). Further, models based on three or more hydrological variables had AIC scores that were only slightly lower than the value for the best model and were only one or two percentage points more accurate, with the exception of the three-year interval (Table 2.4, Column 3).

Second, no model based on the three-year interval performed well. The accuracy never surpassed 70% and the AIC scores were all greater than 250. Best results were obtained using the twelve-year interval, though they did not differ greatly from the seven- and eighteen-year intervals.

Site differences.

Three intervals (7, 12 and 18 years) had led to accurate models and were thus chosen for further analysis; dummy variables were used for sites in a series of logistic regressions. The number of site differences for the best model (eff, bsec) increased with the length of the interval considered. One site, Lucerne Boulevard ($X^2 = 3.88$, $P = .049$), was slightly aberrant for the seven-year interval. For the twelve-year interval two sites were found to be significantly different, Lucerne Boulevard ($X^2 = 6.21$, $P = .013$) and Fitzroy Provincial Park ($X^2 = 6.72$, $P = .0095$). There were four site differences for the eighteen-year interval; Lucerne Boulevard had the highest Chi-square value ($X^2 = 14.18$, $P < .001$). The Chi-square values for bsec ranged from 43.97 to 49.81 ($P < .001$) and for eff, from 39.44 to 46.76 ($P < .001$).

In combinations of gs and bsec, only Fitzroy Provincial Park was found to be significantly different for the seven-year interval ($X^2 = 24.08$, $P < .001$) and the twelve-year interval ($X^2 = 29.76$, $P < .001$). Both Fitzroy Provincial Park ($X^2 = 30.08$, $P < .001$) and Lucerne Boulevard ($X^2 = 5.98$, $P = .014$) were significant site variables for the eighteen-year interval.

Logistic regressions were performed by site, using data from the 12-year interval. The beginning of the second flood was the best single variable for four of the sites. Two-variable models always had greater accuracy and lower AIC scores, and the best model at every site included the beginning of the second flood (bsec). The end of the first flood (eff) and the fraction of the growing season flooded (gs) were the second components of the best models for three and two sites, respectively. The mean depth of flooding (md) was the second component at one site.

Diagnostics.

The points identified by the SAS diagnostics (Pearson residual, DIFCHISQ, DFBetas, C and CBAR) did not indicate that any single site was problematic. A set of 10 data points were identified as extreme values by one or more of the diagnostic tests. These points came from three sites, Fitzroy Provincial Park, Masson and Lucerne Boulevard and represented less than 5% of the total data.

The standardized deviance residuals formed two lines which were only slightly curved at the ends. The curvature was not sufficient to dismiss the model.

Discussion

General trends.

One model emerged as the best model, the combination of the end of the first flood (eff) and the beginning of the second flood (bsec). Here we have a simple, testable model from which we can potentially generate decision rules for the protection of wetland area and diversity.

The parameters from the logistic equation [$\ln (p/(1-p)) = .16(bsec) - .23(eff) + 1.42$] indicate the direction of the effect of each of the two variables. The negative coefficient for eff indicates that the longer the first flood, the lower the probability of dominance by the woody plants. Conversely, the later the beginning of the second flood, the greater the probability of woody cover. As I indicated in my introduction, I have chosen probability ranges of greater than .7 and less than .3 to generate predictions. Figure 2.4. illustrates the application to the prediction of where the woody functional group will or will not be dominant. From this figure, we see that we do not expect woody cover if the first flood lasts longer than 70 days. If the first flood is shorter, then woody plants may or may not be dominant (p > .7), depending on the beginning of the second flood. The probability of dominance of the woody functional group will increase with shorter first floods and later second floods.

Beginning of the second flood.

The beginning of the second flood is a prominent variable in the most accurate of the multivariate models and is one of the best single predictors. It is not surprising that the time of flooding is significant, as it is a standard entry in lists of factors affecting the survival of woody plants (Gill 1970, Teskey and Hinckley 1977). However, flood events are commonly separated on a coarse time scale; that is, they are classified as occurring either during the growing season or during the dormant season (Hall and Smith 1955, Gill 1970, Teskey and Hinckley 1977, Karr 1989). The impact of the second flood within the growing season is striking, in part because it has received so little attention. Although the mechanism behind the role of later floods is not clear, some pertinent trends have been described for seedlings of floodplain tree species. Streng et al. (1989) found that species

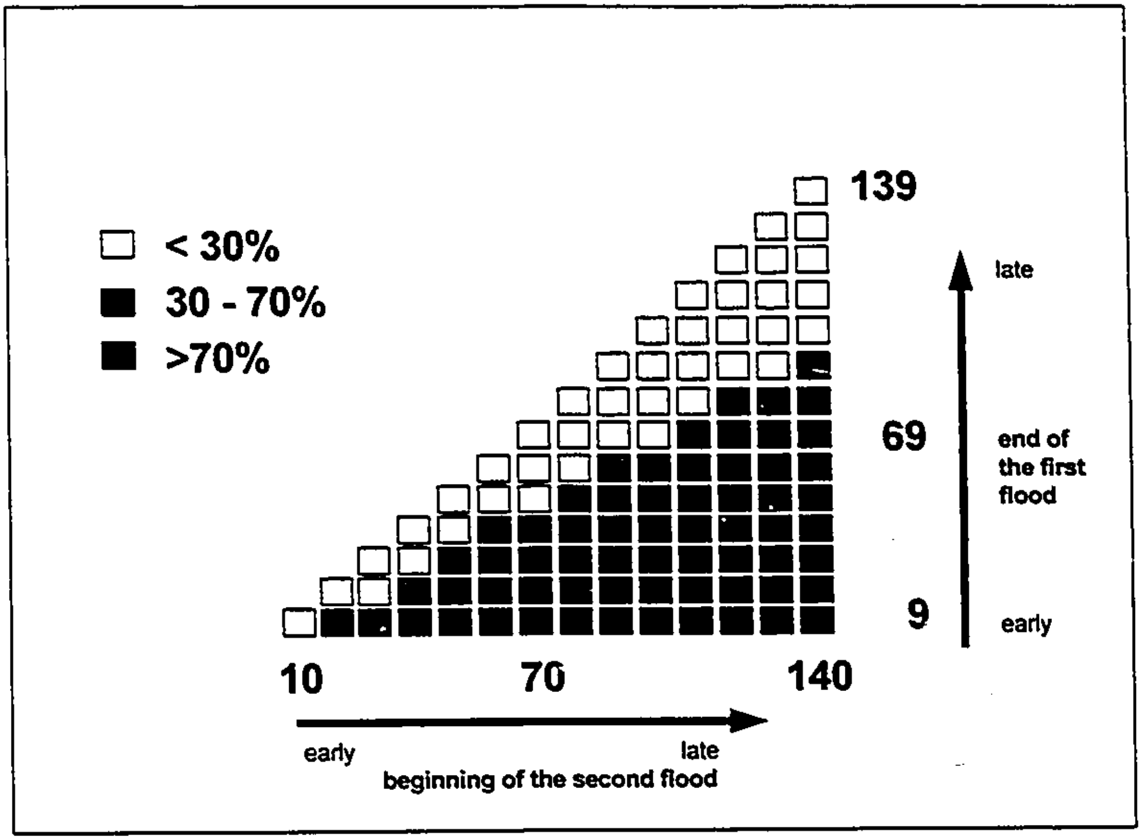


FIGURE 2.4. Model scenarios for dominance of the woody functional group. The probability of dominance of the woody functional group as calculated with respect to the end of the first flood and the beginning of the second flood (measured as day of the growing season, where day 1 is the first day of the season). Parameters are taken from the 12-year interval.

with light seeds generally emerge early in the season, and the earlier the time of emergence, the higher the probability of survival. The higher survival rates were attributed to canopy conditions and better light availability, hence, greater opportunity for photosynthesis. Higher rates of photosynthesis lead to larger plants, thereby improving the probability of surviving adverse conditions.

A similar line of reasoning offers an explanation for the effect of the second flood at our sites. It is generally accepted that flooding during the growing season adversely affects the growth of most tree species (Kozlowski 1984). If a second flood occurs early in the growing season there is little time for the plants to recover, less if the first flood has lasted long. In fact, if the second flood begins shortly after the end of the first flood, it represents simply an extension of adverse conditions. If the combined flood periods are long enough, they may surpass the tolerance of seedlings, or even mature trees. It seems reasonable to assume that this combined period would have to be longer than the critical period represented by a single flood, due to the interruption of the flood event. If, on the other hand, the first flood ends early and the second begins late in the season then there is a period of more favorable conditions. The longer the interval, the greater the chance that the plant will have recovered sufficiently to survive a second adverse period. Thus, the greater the period between the end of the first flood and the onset of the second flood, the higher the probability of occurrence of wooded wetland.

Effect of first flood.

The end of the first flood is strongly correlated with the fraction of the growing season flooded and is therefore consistent with the importance assigned to duration of flooding in the literature (e.g., Yeager 1949, Hall and Smith 1955, Bell 1974). In fact, replacing the end of the first flood with the fraction of the growing season still yields a reasonably accurate model.

The critical period of 70 days of flooding represents 36% to 38% of the average growing season. This range is consistent with the results of Hall and Smith (1955), who found that floods surpassing 40% to 45% of the growing season (April 1 to October 1) prevented healthy growth of the most tolerant species in their study (Planera aquatica, Salix nigra and Quercus lyrata). Their study site, in Tennessee, did not include the remarkably flood tolerant Taxodium distichum. Bedinger (1971) also mentions a maximum of 40% in his study of the White River floodplain in Arkansas. However, comparisons with my results are difficult, as he used the year and not the growing season as his study period.

Despite the agreement of my results with studies of the flood limits for mature trees, the range that I have identified is more likely a threshold for seedling establishment, as I rarely saw unhealthy adult trees. My interpretation is supported by Gill (1970), who suggests that flooding that lasts longer than 40% of the growing season prevents colonization by woody plants. While 36 to 38 % of the growing season is a reasonable range to suggest for the flood tolerance of woody plants in our region, my field observations indicate that I have modeled the barrier to establishment of seedlings rather than the survival of adult trees.

The high correlation between eff and gs points not only to the importance of flood duration, but it indicates that the first flood accounts for most of the flooding that occurs during the growing season on the Ottawa River. The pre-regulation cycle of spring floods followed by lower summer levels is intact, though dampened. This cycle may be essential to the regeneration of many of the woody species of riparian zones, hence to the maintenance of the area dominated by the woody functional group. I have described the problem of conversion of herbaceous to woody cover. However, flood regimes can be altered in a manner which threatens populations of woody species. For example, the seeds of both Acer saccharinum and Salix nigra are released in spring and lose viability quickly under dry conditions (Fowells 1975). The moist substrate that is exposed as spring floods recede is a requirement for germination. River regulation can eliminate the conditions necessary for regeneration and thus threaten the persistence of dominant species or entire functional groups in our landscape. Cases in point include the reduction in habitat area for pioneer species in the Missouri River system (Johnson et al. 1976) and the decline in populations of Populus species along rivers in western North America following dam construction (Rood and Mahoney 1990). My model is based on the assumptions that the conditions required for the regeneration of woody plants are present and that it is the herbaceous wetland that is threatened.

Implications for conservation management

My findings have at least four implications for conservation management. First, I have identified three key predictors, eff, gs and bsec that can be used in two combinations (eff and bsec or gs and bsec) to predict where the woody functional group will be dominant. I have also identified the ranges of these predictors where this group is likely to be dominant (Figure 2.4). My model has not yet been tested on other rivers and the results should therefore be treated with some caution.

Second, I have demonstrated the importance of the beginning of the second flood. This was consistently identified as a key predictor, yet has received little attention in the modeling of riparian vegetation to this point. A cursory examination of the 1990 hydrological records for eight Ontario Rivers revealed that a second flood is a common event on our rivers (Table 2.5). The rivers were identified by selecting every twentieth entry from a list of water gauges for the province. For each site I noted if there was a second flood during the growing season and I compared its magnitude with that of the peak flood. There were second floods, of varying magnitude, on five of the eight rivers. Further, these floods are unlikely to attain the magnitude of the first flood, which is usually associated with snowmelt. They therefore offer the advantage of being biologically meaningful and potentially more manageable flood events.

TABLE 2.5. Nature of second flood. Mean annual discharge, management, and time and approximate magnitude of second flood for eight Ontario rivers, based on 1990 hydrological records (Environment Canada). The magnitude of the second flood is based on discharge; where only water levels were provided the magnitude was not estimated.

River	Discharge (m^3/s)	Management	Time of second flood
Holland	1.7	regulated	late May
Bighead	5.1	regulated	late June, early July, 6/7 of first peak
Mississippi	30.7	regulated	continual decrease in discharge over the growing season
Pic	39.1	natural	late June, 1/3 of first peak
Magnetawan	50.4	regulated	late May
English	58.1	natural	continual decrease in discharge over the growing season
St. Clair	175.94	regulated	no fluctuation in discharge
North	——	———	small second peak in late June, early July

Third, the accuracy of the two-variable model suggests that a small number of predictors can provide guidelines for conservation management of major functional groups. Moreover, I was able to formulate quantitative guidelines with definable margins of confidence (Figure 2.4) by using regression equations to assign probabilities for different management scenarios.

A fourth outcome of my study is the emergence of a potential, quantitative criterion for application of the model, the strong correlation between eff and gs. I may find that my model is more accurate, or only accurate, where the first flood represents a large percentage of the total flooding. I believe that most rivers in the eastern temperate and boreal regions would meet this criterion, due to the major role of snowmelt. However, it might point to problematic applications. Quantitative criteria are seldom identified in riparian models: work is often based on one site (Franz and Bazzaz 1977, Phipps 1979, Poiana and Johnson 1993, Ellison and Bedford 1995) or one river system (Auble et al. 1994, Johnson 1994) with the assumption that the results may be applied to qualitatively similar sites. It is likely that there is a small number of categories of rivers (2 to 4), identifiable by simple, but quantifiable, hydrological variables, which would cover most rivers within a climatic zone. A corresponding number of modeling methods and key predictors could be identified and, at the very least, managers would have a starting point for addressing conservation problems.

Model limits.

I have intentionally restricted my study to wetlands with low or intermediate disturbance. I have unintentionally constrained my study to the hydrological conditions represented by 18 years of water level records of the Ottawa River. I could therefore infer that there are other hydrological conditions, not represented by the data from the Ottawa River, where variables other than eff and bsec would be paramount. For example, at extreme values, the mean depth of flooding may become the over-riding predictor of the distribution of the woody functional group. There are most certainly flood events, not described by my data, which would limit the distribution of this group. My model is designed to address a specific problem, the incursion of woody plants in herbaceous wetlands, within the range of variables that is likely to be encountered under current management practices.

One of the weaknesses of my work is the problem of site differences. However, the best predictors were consistently bsec in combination with either eff or gs. The two sites that differed significantly, Lucerne Boulevard and Fitzroy Provincial Park, included the extremes of exposed and protected shoreline. This suggests that the model is most accurately applied to intermediately disturbed wetlands. However, when the probabilities of .7 and .3 were used to identify areas where the woody functional group was dominant, only 17 of the 222 points were incorrectly identified. In short, the general trends are consistent and the accuracy of the model is greater than 70% at its worst site.

Conclusion.

My approach has been an application of trait-environment relationships to predict the distribution of plant functional groups. One trait was used to distinguish two major functional groups of wetland species, the woody and herbaceous functional groups. The relationship between these groups and hydrology has been demonstrated or inferred in many studies. However, this is one of the few comparisons of the strength of the relationship between the distribution of the functional groups and a set of hydrological variables. Moreover, it is one of the very few studies of wetland plants to generate testable rules that can be applied to conservation problems.

CHAPTER 3

DECISION RULES FOR HERBACEOUS WETLANDS: PREDICTING THE DISTRIBUTION OF PLANT FUNCTIONAL GROUPS

Introduction

I have demonstrated that the distribution of the woody and herbaceous functional groups can be described as a trait-environment relationship. The trait used to assign species to these two functional groups is whether or not they are woody, and the distribution of the groups can be predicted from hydrology (see Chapter 2). Having described the distribution of these two rather general groups, I then examined the distribution of functional groups that represented subsets of the herbaceous plants (Figure 1.1, p. 6).

My first goal was to identify the strongest relationships betweeen selected environmental variables and the distribution of these herbaceous functional groups. I then sought to define the ranges of these variables where there were high probabilities of occurrence of the functional group. The results were presented in a series of decision rules for wetland management, the ultimate goal of my thesis. I have illustrated how these rules can be applied to predict the distribution of the corresponding functional groups in a given wetland (Figures 3.6 and 3.7).

TABLE 3.1. Classifications and nature of the traits that define functional groups, and functional groups with representation in data set. In the case of classifications derived from single quantitative traits the name of the classification and the nature of the trait are identical.

Classification	Traits	Functional groups
Life-forms (Hutchinson 1975)	rooting habit and morphology of photosynthetic organ	herbids, graminids, sagittarids, isoetids
Functional guilds (Boutin and Keddy 1993)	life history, height, number of rhizomes, longest distance to tiller or shoot	matrix, interstitial, ruderal
Canopy types & growth forms (Shipley et al. 1989)	presence/absence or arrangement of leaves, stem habit	graminoid, multilayer, monolayer, single stems, tussocks upright, creeping, rosette
Taxonomy	botanical traits	dicot, monocots, Cyperaceae
Quantitative traits	biomass (g)	<.01, .1 - .99, 1.0 - 1.99, 2.0 - 4.99, 5.0 - 9.99, ≥10.0
	canopy diameter (cm)	<10, 10 - 19.99, 20 - 29.99...≥ 60
	crown cover (cm^2)	< 50, 50 - 99, 100 -199, 200 - 299 300 - 399, 400 - 499, ≥500
	height (cm)	<10, 10 - 19.9, 20 - 29.9...≥ 140
	leaf area (cm^2)	0, <1, 1 - 9.9, 10 - 99, ≥100
	longest distance to an attached tiller (cm)	0, < 10, 10 - 99.9, ≥100
	rhizome number	0, < 1, 1 - 1.9, 2 - 2.9, 3 - 3.9, ≥ 4
	stem diameter (mm)	.1 - .9, 1.0 - 1.9, 2.0 - 4.9, 5.0 - 9.9, 10.0 - 19.9, 20.0 - 29.9, ≥30

Methods

A note on the selection of functional groups and classifications

I first divided the herbaceous species into aquatic and emergent functional groups. Assignment of species was based on the presence or absence of floating leaves and/or flexuous stems. I then divided the emergent species into functional groups according to five different classifications: (1) Hutchinson (1975), (2) Shipley et al. (1989), (3) Boutin and Keddy (1993), (4) functional groups based on single quantitative traits and (5) phylogenetic groups.

The division between emergent and aquatic functional groups is well established in both classic texts on wetland plants (e.g., Sculthorpe 1967) and in surveys of wetland vegetation (e.g., Walker 1968, Groupe Dryade 1985). The defining traits reflect the degree to which a plant is dependent on water to support its photosynthetic tissue (floating leaves or flexuous stems versus lignified stems or emergent leaves). It should not be surprising, therefore, to find that the distribution of these two groups is related to hydrology. It is also reasonable to assume that plants that rely on water for mechanical support will be affected by disturbances such as wave action and strong currents. Disturbance is difficult to measure directly, but it may be reflected in organic matter accumulation (Keddy 1985) or in soil particle size if soils are derived from the same parent material (Folk 1974). I have therefore included both substrate and hydrological variables in this analysis. It may seem trivial to find significant relationships between these functional groups and the hydrological or substrate variables. However, there has been little effort to identify a best predictor of their distribution and less to quantify the significant relationships.

Relatively few wetland studies have described functional groups for emergent species. Some exceptions include Hutchinson (1975), Boutin and Keddy (1993), Auble et al. (1994), and Ellison and Bedford (1995). A few additional studies have related traits of herbaceous species to environmental variables, without addressing functional groups per se (van der Valk 1981, Shipley et al. 1989). In most cases the emphasis has been on the significance of hydrology (e.g., van der Valk 1981, Auble et al. 1994). However, studies at the species level (e.g., Day et al. 1988, Gaudet 1993) have demonstrated the importance of substrate variables, as well. I have therefore included both kinds of variables in my analysis of the functional groups defined at this level.

The rationale for including the five classifications is as follows.

(1) Hutchinson (1975) summarized and refined the classification systems described by Thunmark (1952 in Hutchinson 1975) and Hogeweg and Brenkert (1969 in Hutchinson 1975). It has been included because it is a classical synthesis of traits that separate functional groups according to hydrology and sedimentation. There are two drawbacks to using his classification, and both may be easily addressed. First, I have emphasized groups of emergent species, while the classification proposed by Hutchinson was designed with aquatic species in mind. The two main emergent groups, herbid and graminid, were judged by Hutchinson (1975) himself to be an inadequate treatment of emergent species. However, at least two other groups, the sagittarids and the isoetids,

include species that I have classified as emergent. Moreover, Hutchinson's classification is supplemented by the one proposed by Shipley et al. (1989), which deals exclusively with emergent species. Second, Hutchinson's classification was derived from the study of lacustrine wetlands and my focus is on riverine wetlands. This should not be a serious problem as many of the traits that allow functional groups to colonize and persist along lake shores should also characterize the functional groups of river shores.

(2) The canopy types and growth forms proposed by Shipley et al. (1989) represent a refinement of the classification of herbaceous species. As such, it can be considered an extension of Hutchinson's work.

(3) Boutin and Keddy's (1993) functional guilds are one of the few classifications based on quantitative traits. I have included it as a test of the efficacy of this approach compared with the use of qualitative traits.

(4) It seems reasonable to test for relationships between single quantitative traits and environmental variables before examining relationships involving groups of traits. Most of the work on single traits has described relationships between the trait and the type of habitat. For example, Grime and Hunt (1975) related the maximum potential growth rate of 132 species to the major inland habitats of the Sheffield region, UK. Admittedly, between and within habitat variation represent two different scales. Nonetheless, the simplicity of predictions based on a single trait is attractive. I have therefore included an analysis of the distribution of functional groups that are defined by ranges of individual quantitative traits. Because my emphasis has been on general relationships, hence many

species, I have restricted my study to a few, easily measured traits that are suggested by the literature.

(5) Phylogenetic groups were included to test whether functional groups do, in fact, yield more accurate models.

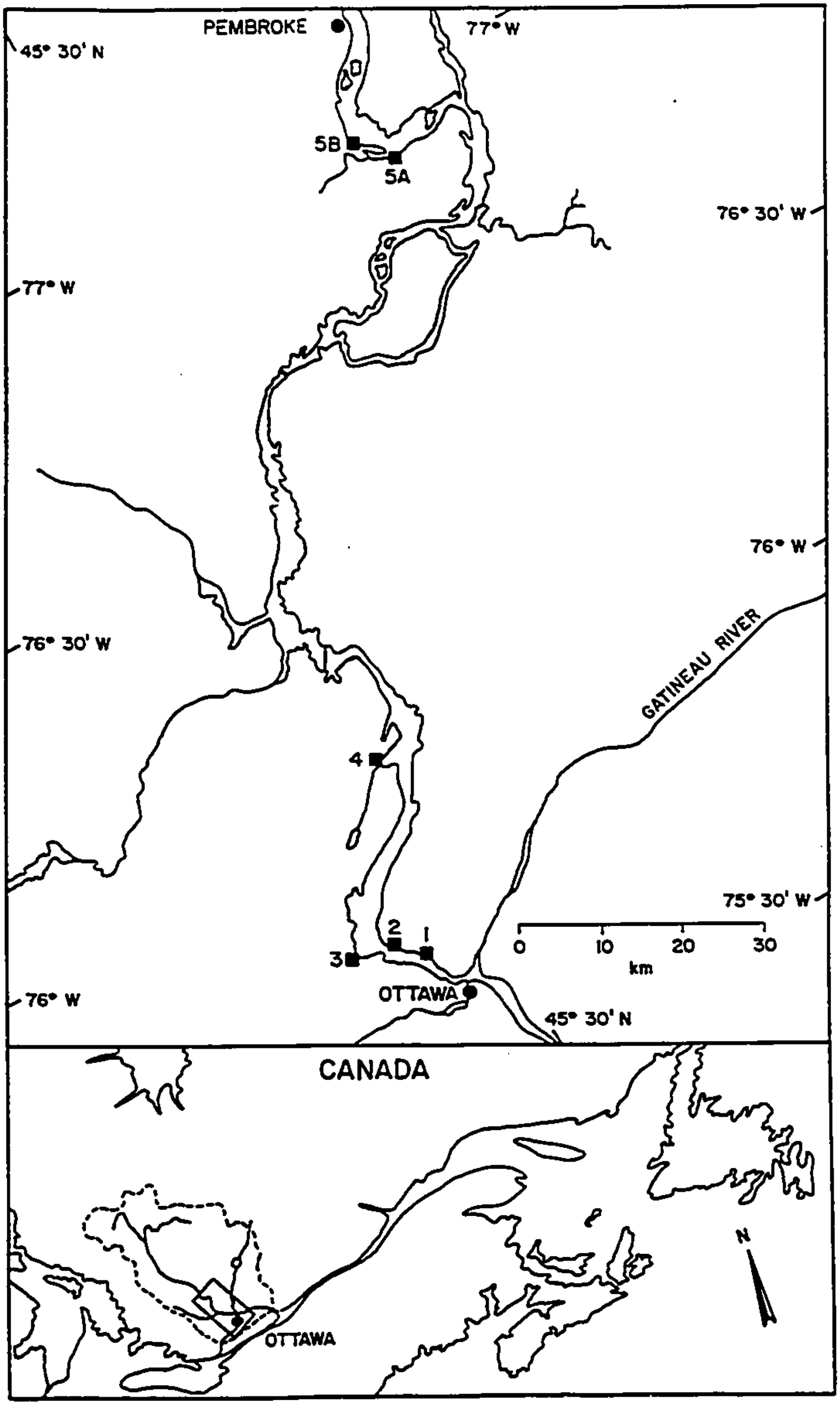
Data Sets

The analysis was based two data sets: 1) a set of quadrat samples collected by Day et al. (1988) between July 27 and September 3, 1983 and 2) trait data which I collected through fieldwork in the fall of 1994.

Day's data. Day et al (1988) collected 94 quadrat samples at five wetlands along the Ottawa River. They examined a 200- km portion of the Ottawa River (between Ottawa at 49° 19' N, 75° 40' W and Westmeath at 45° 57' N, 76° 14' W) in order to describe the regional vegetation types that are characteristic of river shoreline. The quadrats were random samples from each of the vegetation types. Five sites were surveyed, covering a gradient from low to high biomass wetlands. The sites were Lucerne Boulevard, Constance Bay, Andrew Hayden Park, Mousette Boulevard and Westmeath Provincial Park (Figure 3.1). I omitted two quadrats because of missing data.

For each of the .25 x .25 m quadrats, the species were listed and the above-ground biomass was clipped, dried at 60° C for 12 hours in a forced-air oven, and weighed. The biomass of each species of each quadrat was then measured. These data were organized

FIGURE 3.1. Study sites. Top map: location of study sites selected by Day et al. (1988). (1) Mousette Park; (2) Lucerne Boulevard; (3) Andrew Hayden Park; (4) Constance Bay; (5) Westmeath area. Bottom map: eastern Canada showing Ottawa River drainage basin (---) with a rectangular inset of the study region. (Adapted from Day et al., 1988).


PEMBROKE
77° W
45° 30' N
5B
5A
76° 30' W
77° W
76° W
GATINEAU RIVER
76° 30' W
4
75° 30' W
0
10
20
30
km
2
1
3
OTTAWA
76° W
45° 30' N
CANADA
OTTAWA
N

into a quadrat x species matrix (92 quadrats x 69 species) where each entry was the biomass of the species found in a given quadrat.

Environmental data were also included in the data set. Soil samples had been collected for each quadrat and had been analyzed for pH, P, Mg, K, loss of mass on ignition, and particle size (sand, gravel, silt/clay). In addition, the elevation of each quadrat had been measured with respect to a known water level. I was therefore able to calculate values for a set of hydrological variables.

Data from my fieldwork. Traits were measured on plants in the field betweeen August 15 and September 30, 1994. Replicates of each species were sought in high and low biomass wetlands and at high, low and medium elevations of the shore. A population of each species was located and the traits measured on one of the larger plants from this stand. In this way, I targeted the principle ramet for clonal plants. The data therefore approximates the average and standard deviation of the optimum growth of each species under the various substrate and hydrological conditions throughout the riverine wetlands of the region. The traits that were measured and the rationale for their selection are as follows.

(1) Height is an obvious trait to choose as it has been related to water depth (Menges and Waller 1983), is considered to be an indication of competitive ability (Shipley et al. 1989) or survival strategy (Grime 1973, Hill et al. 1994) and is easily measured. I measured the maximum height of photosynthetic tissue (Shipley et al. 1989), taking care not to disturb the position of the plant in the canopy.

(2) Biomass has been related to indirect gradients of nutrient levels (Shipley et al. 1989) and to competitive ability (Gaudet and Keddy 1988). Biomass was recorded as the above-ground biomass of a single ramet following drying in a forced air oven at 60° C for 24 hours.

(3) Maximum canopy diameter (Shipley et al. 1989) and (4) crown area (Gaudet and Keddy 1988) were included as indicators of above ground spread and light capture. Canopy diameter was measured as the longest horizontal axes through the photosynthetic tissue, usually the distance from the tips of the two leaves that were furthest from each other. The width of photosynthetic tissue was measured at right angles to this axis. Crown cover was calculated as a quarter of the sum of the square of these two distances. Care was taken not to disturb the canopy during these measurements.

(5) Leaf area has been used to separate life forms (Raunkaier 1934) and has obvious implications for light capture and plant performance (Givinish 1982). I measured the area of a single leaf, chosen subjectively as the largest leaf of the plant in question.

(6) Stem diameter (Boutin and Keddy 1993) was measured as the diameter of the shoot at ground level. It was included as a potential indicator of aerenchyma and a quantifier of life form.

(7) The number of rhizomes and (8) the distance to the furthest tiller or shoot that was attached to the ramet in question (Shipley et al. 1989, Boutin and Keddy 1993) were included as measures of the capacity for clonal spread. Both measurements were straightforward, but labour -intensive. Therefore the number of replicates per species was lower. Clonal spread is associated with competitive dominance (Grime 1977).

Four traits that had originally been included in the collection of field data were omitted when their measurement was found to be inaccurate or unmanageable. The biomass and volume of the below-ground system were omitted as it was impossible to excavate the underground parts in a consistent manner. The depth to below-ground system was abandoned because of possible confusion and inconsistency in protocol (e.g. does this depth include the depth from the surface of the litter or the surface of the soil?). Finally, the accuracy of the volume of the above-ground system was questionable and the protocol time-consuming.

Dependent variables

Present/absent or dominant/not dominant.

I conducted two separate sets of analysis. In the first, the dependent variable was the presence or absence of a given functional group as defined by traits. In the second, the dependent variable was the dominance or non dominance of a functional group, where a functional group was considered to be dominant if it represented at least 25 % of the above-ground biomass of a quadrat. This differs from the definition of dominance used in Chapter 2, where continuous cover was required in order for woody plants to be considered dominant. I chose the lower criterion because 1) plants with low biomass can still have a high cover score and 2) I did not expect to find continuous cover by single functional groups within quadrats of herbaceous vagetation. I expected to find stronger trait-environment relationships for dominant vegetation than for the presence or absence of a given trait.

Pretreatment of data for analysis.

The matrices used in the analysis were generated through three steps. First, I converted Day et al.'s (1988) quadrat x species matrix by changing the cell entries to 1's and 0's to indicate the presence or absence of a species in a given quadrat. The cell entries had previously been the biomass of the species.

Second, species *x* functional group matrices were assembled for the 69 species listed in the raw data from Day et al. (69 species *x* 19 functional groups defined by qualitative and 9 sets of functional groups defined by quantitative traits). The cell entries were 1's or 0's, denoting the inclusion or exclusion of a species in each functional group. The assignment of species to the aquatic or emergent functional groups is presented in Appendix 3.1. Assignments according to the classifications described by Hutchinson (1975), Shipley et al. (1989) and Boutin and Keddy (1993) are presented in Appendices 3.1 to 3.5. The mean and standard deviation of the quantitative traits for each species are listed in Appendix 3.6.

Finally, these matrices were used in conjunction with the quadrat x species matrix to generate the quadrat x functional group matrix for each functional group (each matrix

= 92 quadrats *x* 1 functional group). As there were two kinds of dependent variables (presence/absence and dominance/nondominance) two matrices were created for each functional group, according to the two following rules. A functional group was present if it was represented by at least one species in a given quadrat. A functional group was dominant if it was represented by at least 25% of the biomass in a given quadrat.

Quadrats were omitted if traits could not be defined for one of the species present. The number of quadrats used for presence/absence was only 89 or 90, depending on whether functional groups were based on quantitative or qualitative traits. There were no missing data for the dominant species, thus no quadrats were omitted for this part of the analysis.

Assignment of species by traits

The distinction between aquatic and emergent functional groups was straightforward, as were the assignments of species according to the classifications of Hutchinson (1975) and Shipley et al. (1989).

In the case of the phylogenetic groups, two references were consulted. Day et al. (1988) had used Fernald (1950) for species and genera nomenclature. I used Scagel et al. (1990) to assign species and genera to higher taxa (family, order, class, superclass). In order to avoid generating a large number of groups with only a few members, I restricted the analysis to taxa with at least five species representing at least two genera. This restriction eliminated all but three taxa: the family Cyperaceae and the monocot and dicot superclasses (Liliidae and Magnoliidae).

Boutin and Keddy's classification was based on discriminant analysis involving 27 traits measured on plants both in the garden and in the field. It was not practical to collect data for these traits for all the species encountered in my study. Therefore, I approximated the assignment in the following manner.

The species from Day et al. (1988) and Boutin and Keddy (1993) were listed in two separate matrices. Data were gathered for each species for life history (obligate annual, facultative annual, perennial), average height, average number of rhizomes and average distance to the furthest attached tiller or shoot. The information on life history was taken from Gleason (1952) and was missing for many species. The three quantitative traits were measured according to the protocol described in the section on fieldwork (p. 68).

The ranges of the traits that defined each of the principle functional groups of Boutin and Keddy (ruderal, matrix, interstitial) were determined from the matrix listing the species from their study. These ranges were then used to assign the species from Day et al. (1988) to the appropriate functional group. Boutin and Keddy's (1993) first division separated the ruderals from the other functional groups and was based on life history traits, above-ground biomass and the capacity for lateral spread. Ruderals were distinguished by their short time to reproductive maturity (facultative or obligate annual), high above-ground biomass and lack of lateral spread. A species from Day et al. (1988) was assigned to this functional group if it was classified as an annual by Gleason (1952) or if its average number of rhizomes and average distance to the furthest attached shoot were both less than unity.

The second division of Boutin and Keddy (1993) separated the matrix and interstitial functional groups and was based on the nature of clonal spread and rooting depth. A species from Day et al. (1988) was assigned to the matrix functional group if it met at least two of the following criteria: average height greater than 100 cm, longest distance to a tiller or shoot greater than 10 cm, or average number of rhizomes greater than 2. The remaining species were assigned to the interstitial guild. Seventeen of the species from Day et al. (1988) had been included in Boutin and Keddy's (1993) data set and their assignment to functional groups was according to Boutin and Keddy (1993). While this is only an approximation of the divisions proposed by Boutin and Keddy, it is at least a classification that is consistent with the logic and intent of the original guilds.

Finally, quantitative traits were used to identify 8 series of functional groups defined by single traits (Table 3.1). Each functional group was defined by an interval in the range of the trait. Thus, there were 4 to 15 functional groups per trait depending on the range of the trait and the distribution of the species along that range. A species was assigned to a functional group if the range of values represented by its mean and standard deviation overlapped with the range of the functional group (Figure 3.2). In this way, species could be assigned to more than one group per trait. For the few species with less than 3 replicates the standard deviation was arbitrarily set at one or two intervals from the mean, depending on the average standard deviation per species for that trait. The range of each trait was divided into intervals (and thus functional groups) by examining the frequency distribution of the species across the range of the trait and then identifying which intervals would lead to reasonably even numbers of species per functional group.

Leaf area was measured on only one or two replicates per species, thus, the calculation of the standard deviation was often impossible. Therefore, the range of leaf area was divided according to a logarithmic scale and species were assigned to only one of these functional groups. Some species had inconspicuous leaves, as in the very small leaves of Equisetum or the bladeless sheathes of Scirpus acutus. These species were designated as leafless, although this is not strictly accurate.

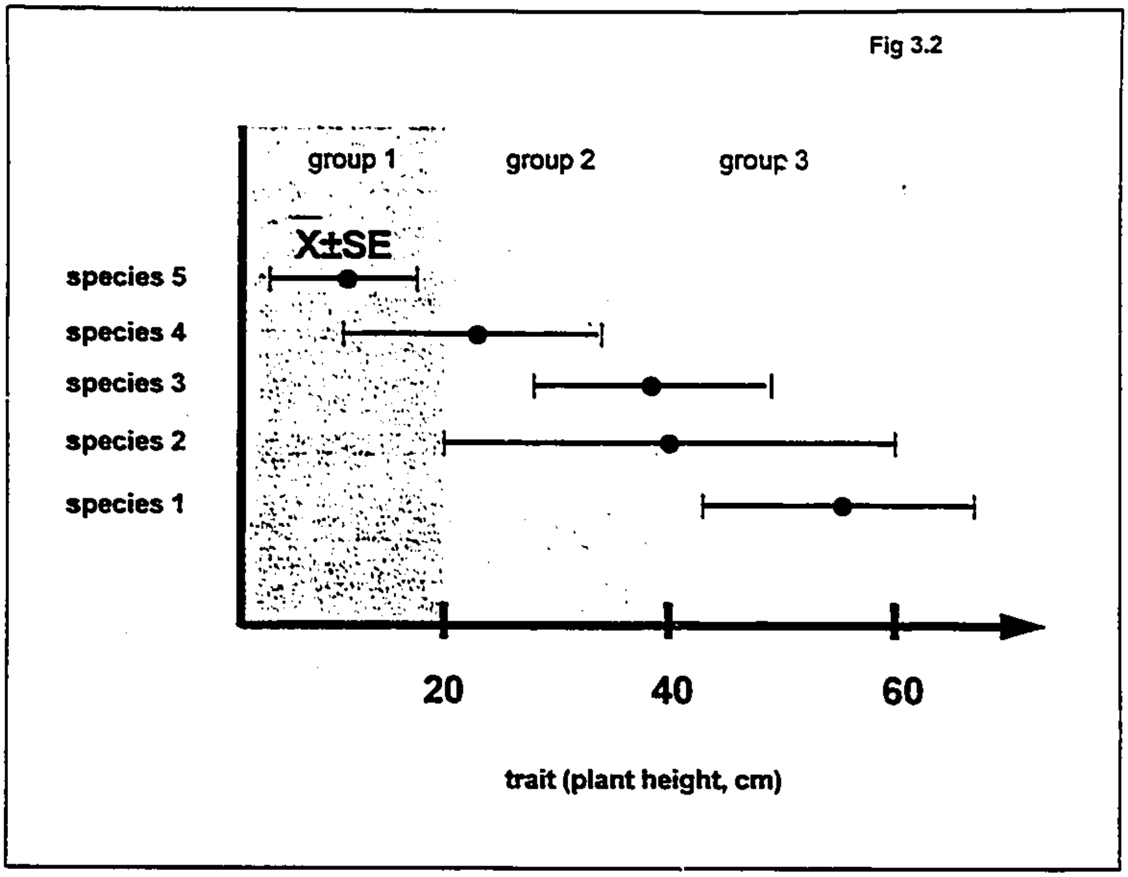


FIGURE 3.2. Assignment of species to functional groups defined by the range of a single quantitative trait. The range of the trait is divided into regions representing a functional group. For example, group 1 includes species 4 an 5, group 3 includes species 1 to 3. A species is assigned to all functional groups that coincide with its mean and standard deviation for that trait.

Independent variables

Ten environmental variables were selected to reflect important aspects of substrate conditions and hydrology (Table 3.2). Substrate variables were available from soil analysis and hydrological variables were calculated from the elevation data recorded for each quadrat. I selected variables that were either cited as important in other studies or easy to measure. Because I wanted to find the best predictors, I included variables that were correlated if they met either of these two criteria. These data were organized in a quadrat x independent variable matrix (92 quadrats x 10 variables).

Substrate variables

The following substrate variables were selected: pH, phosphorous (ppm), loss on ignition (%), and the percentage composition of gravel, sand and silt or clay after ignition of organic matter. These data were taken from Day et al. (1988). Some micronutrients were not included as it was important to have a manageable number of variables. In particular, K and Mg were omitted because they are generally correlated with P.

Ranges of pH are fundamental criteria for distinguishing among wetland classes such as bog, fen, swamp, and marsh (National Wetlands Working Group 1988). Moreover, the results of Gaudet (1993) suggest that pH is unique in its low correlation with the nutrient variables that are normally included in soil analysis (P, NO_3, K, Mg).

TABLE 3.2. Environmental variables used in analysis of trait-environment relationships. Based on the data set assembled by Day et al. (1988).

Variable	Abbreviation	Mean	Standard deviation	Range
Phosphorous (ppm)	P	6.2	4.3	1 - 24
Loss on ignition (%)	org	6.64	6.95	.4 - 30
pH	pH	6.8	.68	5.4-7.8
Sand (%)	sa	78	16	25-99
Silt/clay (%)	scl	17	12	.57-43
Gravel (%)	gra	4.8	13	0 - 73
Fraction of the growing season flooded (12- yr average)	gs	.64	.26	.20 - 1.00
Mean depth of flooding (12- yr average)	md	.59	.10	.45 - 1.03
End of the first flood (12- yr average)	eff	106	52.9	32 - 194
Beginning of the second flood (12- yr average)	bsec	88	42	0 - 140

Phosphorous is one of the two major nutrient gradients that separate low and high productivity habitats (Grime 1981). Twolan-Strutt and Keddy (1996) have demonstrated that the high and low biomass wetlands of the Ottawa Valley can be distinguished by phosphorous concentrations in the soil.

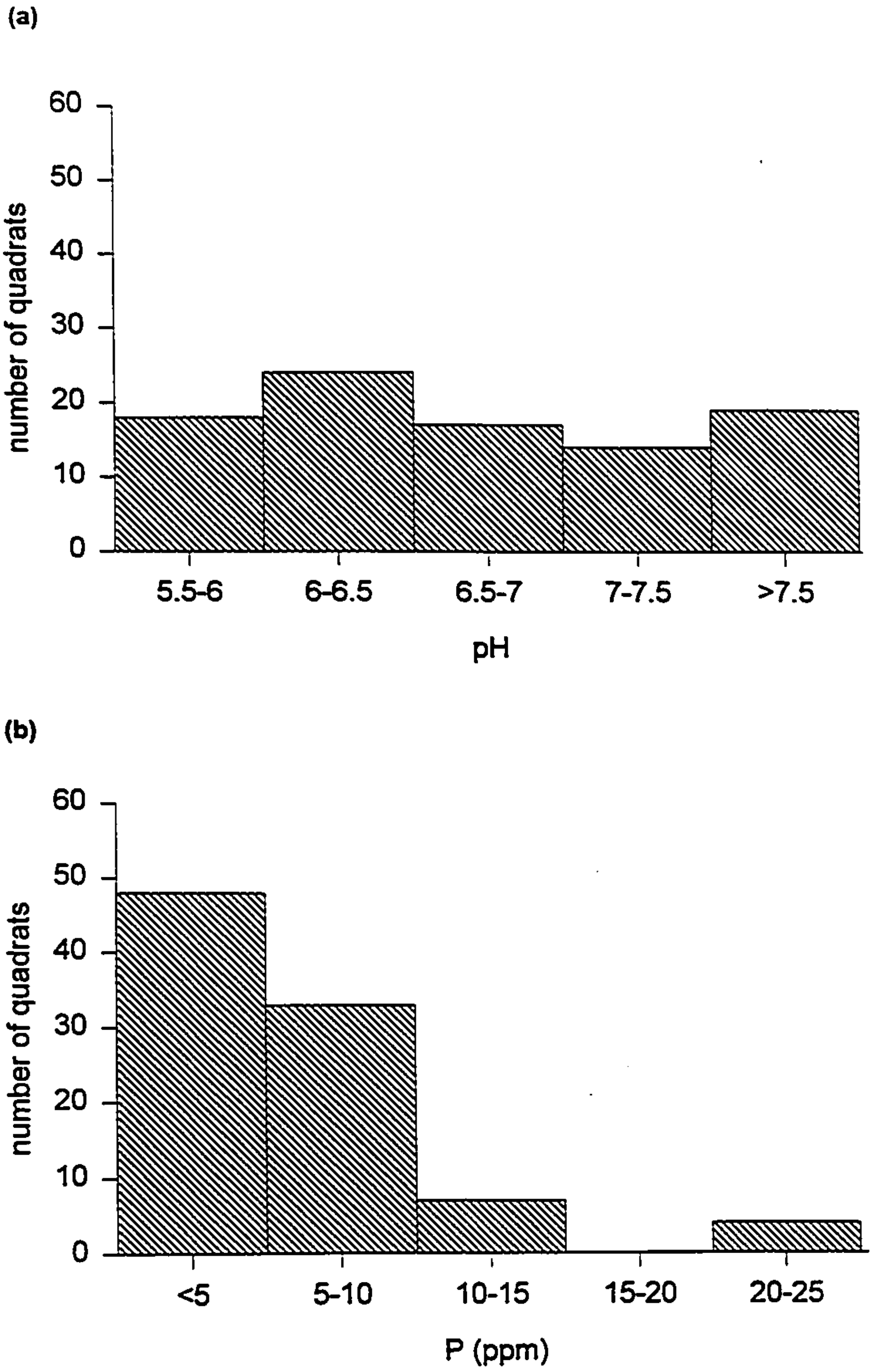
Loss of mass on ignition is a measure of the organic content in the soil and is one of the easiest substrate variables to measure. It may be interpreted as an indicator of disturbance (Keddy 1985) or of the stage of succession (Pearsall 1920), in addition to its role in soil chemistry (Ponnamperuma, 1972).

Soil particle size may also reflect the extent of disturbance, though the results are difficult to interpret and are dependent on the nature of the parent material (Folk 1974). This variable was included because the wetlands were all from the same region (and therefore possibly the same parent material) and particle size could therefore serve as a comparative index of mechanical disturbance and sedimentation.

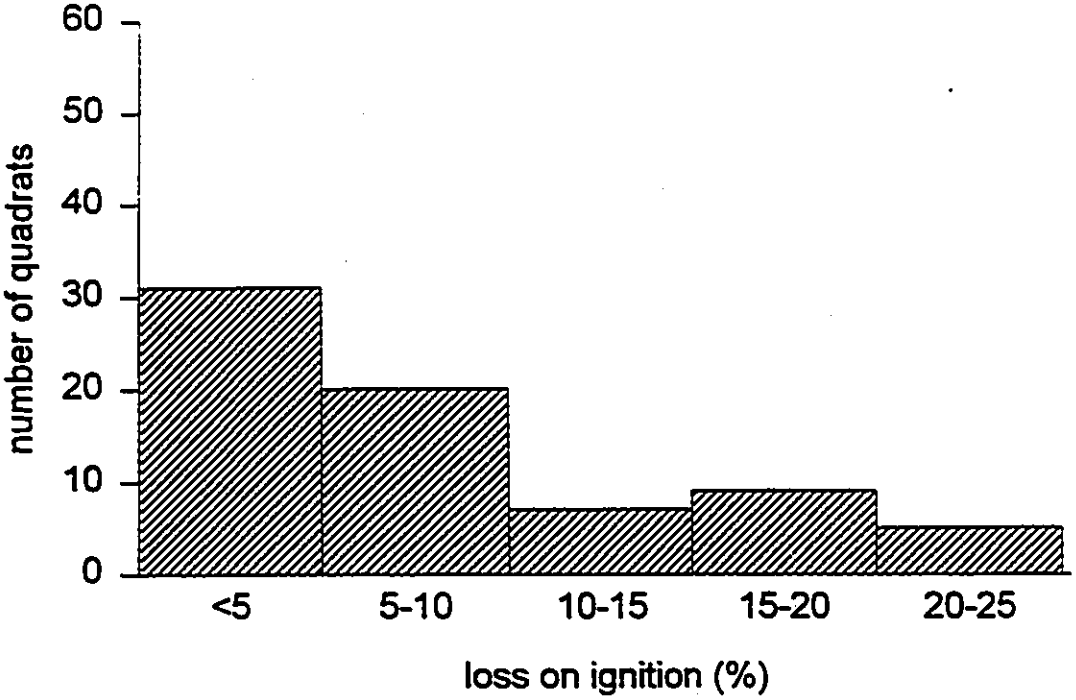
Soil subsamples had been analysed for pH (saturated soil-paste method) and P (sodium bicarbonate extractable P method) at the Department of Land Resource Science, University of Guelph, Ontario.

Another set of subsamples had been used to describe soil structure. Percent organic content had been estimated as loss on ignition at 500° C for 12 hours. The remaining soil had been separated into gravel (>2 mm) and sand (53 μm to 2 mm) by dry-sieving. The fraction of silt and clay had been estimated from 40 1- ml subsamples of the sand fraction through a wet-sieving and pipette technique without dispersants.

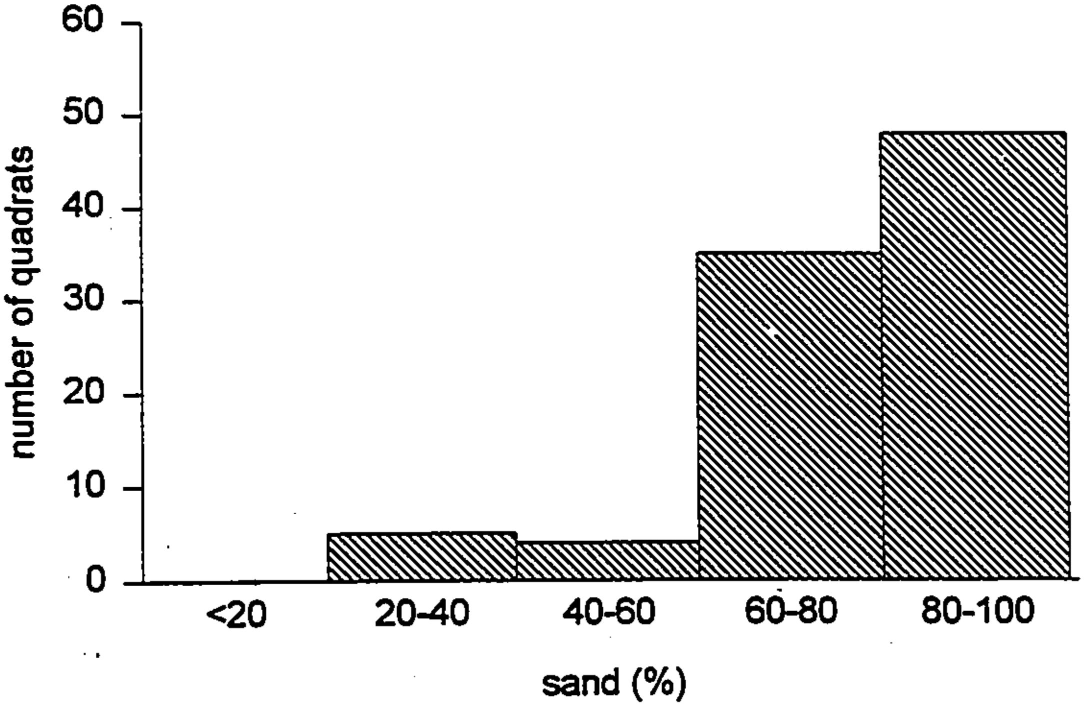
FIGURE 3.3. Distribution of quadrats along five environmental variables: (a) pH; (b) P; (c) organic content; (d) sand; (e) duration of flooding.


(a)
60
50
40
30
20
10
0
number of quadrats
5.5-6
6-6.5
6.5-7
7-7.5
>7.5
pH
(b)
60
50
40
30
20
10
0
number of quadrats
<5
5-10
10-15
15-20
20-25
P (ppm)

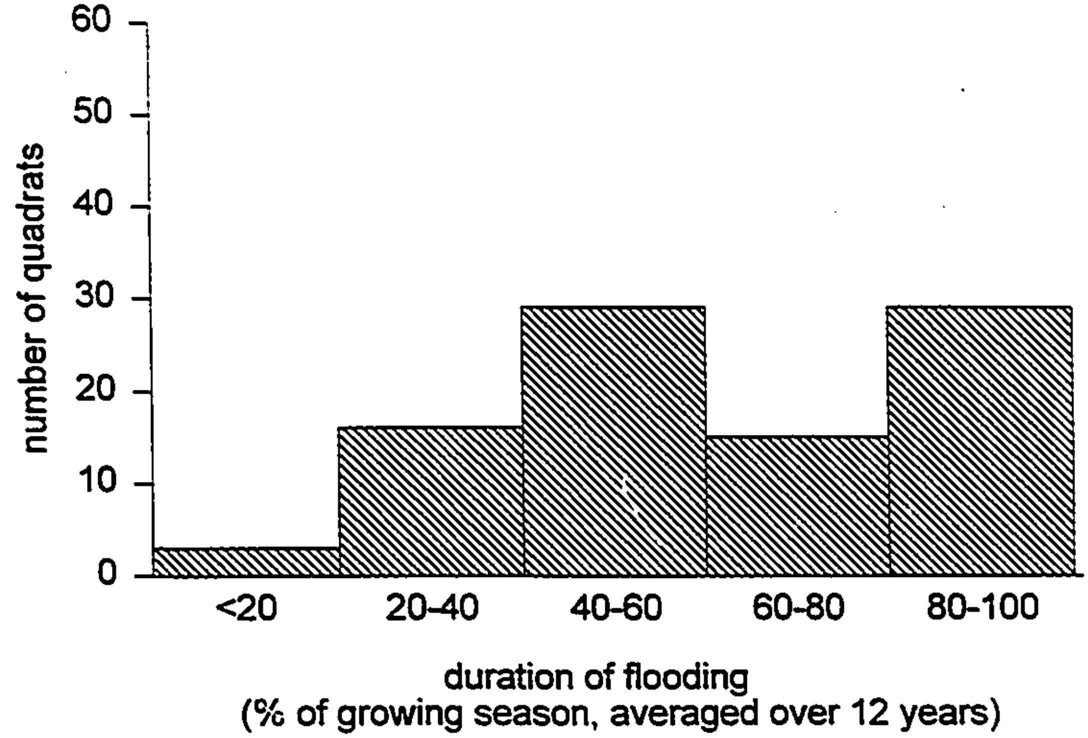
(c)


60
50
40
30
20
10
0
number of quadrats
<5
5-10
10-15
15-20
20-25
loss on ignition (%)

(d)


60
50
40
30
20
10
0
number of quadrats
<20
20-40
40-60
60-80
80-100
sand (%)

(e)



60
50
40
30
20
10
0
number of quadrats
<20
20-40
40-60
60-80
80-100
duration of flooding
(% of growing season, averaged over 12 years)

The distributions of the 92 quadrats with respect to pH, P, loss on ignition and sand content are shown in Figure 3.3 a -d.

Hydrological variables

Useing the elevation data from Day et al. (1988) I calculated values for four hydrological variables for each quadrat: (1) the fraction of the growing season during which flooding occurred, (2) the mean depth of flooding, (3) the end of the first flood and (4) the beginning of the second flood. The first two variables were obvious choices due to their prominence in the literature (see Chapter 2) and the straightforward nature of their calculation. Moreover, the fraction of the growing season flooded was considered a key predictor of the limits of woody plants (Chapter 2) and therefore merited inclusion. Although the mean depth of flooding did not emerge as a good predictor of woody cover, it was not highly correlated with other hydrological variables and therefore represented a unique aspect of the variation in flooding. The end of the first flood and the beginning of the second flood were included because they were the components of the best model for the limit of wooded wetland (Chapter 2). I used the beginning and end of the growing season as identified in Chapter 2. The distribution of the 92 quadrats with respect to duration of flooding is illustrated in Figure 3.3. e.

Long- term water level records were obtained from Environment Canada for the gauges at Westmeath and Brittania. Two of the sites (Andrew Hayden Park and Westmeath Provincial Park) were located near gauges and the records could be used directly for the calculation of hydrological variables. The locations of the other three sites were not as ideal. There are small sets of rapids between the gauge at Brittania and the sites at Lucerne Boulevard and Moussette Park and there was a distance of approximately 15 km between the Brittania gauge and the site at Constance Bay. In order to test for discrepancies between levels at the gauge and at the sites, each site was visited 10 times. Changes in water levels at the sites were compared with changes recorded at the Brittania gauge. There were only small differences between site and gauge readings; the long-term records from the gauge were adjusted according to calibration curves (R^2 =.99, R^2 =.99 , R^2 =.98).

The values for the hydrological variables were averaged over 5 time intervals (1, 3, 7, 12 and 18 growing seasons). It is not clear what period is required before flooding will have an impact on herbaceous vegetation. In the case of woody plants (Chapter 2), the results obtained using an interval of 12 years were the most accurate, although the intervals of 7 and 18 years still led to accuracies greater than 80%. I expected that a shorter time interval would be important in the case of herbaceous vegetation, and therefore retained the 3- and 7 -year intervals and added a one- year interval. The longer periods (12 and 18 years) were retained to allow for comparisons with other studies. For example, Auble et al. (1994) used a 19- year timeframe, though they now believe that changes in the vegetation are occurring more rapidly (Auble et al. 1995).

Analyses

Correlations.

A series of among variable correlations (Sigmastat, Jandel Scientific1994) were used to compare (1) all substrate variables, (2) all hydrological variables with each other and (3) each hydrological variable over time.

In addition, the membership of functional groups identified by traits was examined to ensure that identical groups were not included in the analyses.

Logistic regression.

Each functional group was analyzed separately using logistic regression (SAS Institute 1991). Groups were omitted if they were present in less than 10 quadrats or more than the total number of quadrats less 10 because these unbalanced partitionings were too extreme to lead to accurate models.

I also conducteded a preliminary test of whether or not a logistic function was an appropriate model for the relationship between the groups and the environmental variables. The proportion of quadrats with representation from a given functional group was graphed over intervals of four of the independent variables (fraction of the growing season flooded, mean depth of flooding, pH and loss on ignition). These variables were considered to be an adequate representation of the independent axes from the environmental variables. If the distribution of the group along a given axis was not monotonic then a significant outcome was treated with caution.

Each functional group that was defined by a range of a quantitative trait was analyzed separately. For example, seven analyses were conducted for the seven functional groups defined by stem diameter (< 1mm, 1 - 1.9 mm, 2 - 4.9 mm, 5 - 9.9 mm, 10 - 19.9 mm, 20 - 29.9 mm and ≥ 30 mm.). It was not possible to use a polytomous logistic regression to consolidate the analysis because of its assumption that only one value of the response or dependent variable would be included per sample. For example, there was usually more than one functional group as defined by stem diameter in each quadrat. However, a polytomous model (incorporating several classes of stem size in the analysis) would require that only one class of stem diameter be assigned for each sample or quadrat (e.g., stem diameter for sample 1 = class with stem diameter between 2 to 5 mm). This would not directly indicate whether or not smaller- or larger- stemmed plants were present and would therefore change the nature of the question being addressed.

Use of separate logistic regresssions was not a disadvantage, as there is evidence that the parameters obtained using a set of binary models differ only slightly from those obtained using a polytomous model (Hosmer and Lemshow 1994). Further, in some statistical packages the polytomous regression is simply the simultaneous solution of the separate binary models (Steinberg and Colla 1991).

Criteria for evaluating models

Because of the number of independent variables I conducted separate preliminary analyses for the hydrological and substrate data. First, the presence/absence or dominance/nondominance of each functional group was modeled as a function of all possible combinations of the four hydrological variables. This was followed by a similar analysis with all possible combinations of the substrate variables with one provision; percent sand, percent clay and percent gravel composition were never included in the same model as they were necessarily constrained by each other. Thus, each of these two analyses included 4 variables at most, which made the evaluation of all possible combinations a manageable task. The best predictors from these preliminary analyses were then tested in all possible combinations in a final analysis.

The selection of the strongest trait-environment relationships was accomplished in two steps. First, the best of the models for each functional group was identified by comparing the AIC scores. The lower the score, the better the model (Appendix 2.2). Where scores were similar, the model with fewer variables was chosen. Second, the best models for the different functional groups were compared on the basis of their accuracy, sensitivity and specificity. In order to be included in this final selection a model had to have an accuracy of at least 70% and both a sensitivity and a specificity of at least 60%. Accuracy was defined as the percentage of the quadrats from the original data for which the presence or absence of a functional group was correctly predicted by the model. Sensitivity was a measure of the performance of model in predicting the presence of the functional group (number of predicted occurrences/total number of occurrences). Specificity was a measure of its performance in predicting the absence of a functional group (number of predicted absences/total number of absences).

For each of the final models, the standardized deviance residuals were graphed as a function of the predicted values to check the fit of the logistic function. A curved distribution would indicate a poor fit.

Finally, a set of inclusion and exclusion rules predicting the presence or absence (dominance/nondominance) of the functional groups were derived from the logistic equations. As in Chapter 2, probability ranges of < .3 and > .7 were chosen to identify ranges of the intervals where functional groups would be absent or present, respectively.

Results

Correlations

Table 3.3 shows that the two hydrological variables that were the most highly correlated were the fraction of the growing season flooded (gs) and the end of the first flood (eff). The beginning of the second flood (bsec) was generally independent of these. Results from the 12-year interval have been included in this chapter; results for the other intervals are in Appendix 3.7.

Each hydrological variable had been averaged over five different intervals (1, 3, 7, 12, 18 years). When the values for the different intervals were compared, both gs ($r > .9$) and eff ($r > .9$) were found to be strongly correlated over time (Appendix 3.7). The correlations for bsec and the mean depth of flooding (md) were low over the first two or three intervals but were higher after 7 years ($r > .9$).

Most of the substrate variables were correlated (Table 3.4). The loss on ignition was related to all the other variables. The few nonsignificant pairs included phosphorous and pH, phosphorous and gravel, pH and sand, and silt/clay and gravel.

Composition of functional groups

There were obvious overlaps in the classification of species (Appendices 3.1 to 3.5). However, no two functional groups were identical and thus none was eliminated from the analysis. The greatest degree of overlap was the complete nestedness of the family Cyperaceae and Hutchinson's sagittarids within the monocots. In addition, Hutshinson's herbids were essentially a functional group of dicots plus one fern.

Of the 69 species recorded in the raw data, 17 were dominant in at least one quadrat. Dominant species were generally matrix or interstitial, graminids or graminoids, with either an upright single stem or an upright multilayer of leaves. Further, these species were generally in the functional groups defined by larger values for quantitative traits (e.g., stem diameter > 30mm). Some functional groups had only one or two members from the dominant species and were therefore omitted from the analysis of dominance. For example, Lythrum salicaria was the only dicot species that was dominant, Hutchinson's sagittarids and herbids included only 2 dominant species each, and there were no dominant isoetids.

TABLE 3.3. Pearson product moment coefficients for hydrological variables, as averaged over 12 growing seasons. Probability values are in parenthesis. (n = 92).

Variable		gs	md	eff	bsec
Fraction of the growing season flooded	gs	1.00			
Mean depth of flooding	md	0.40 (<0.001)	1.00		
End of the first flood	eff	0.97 (<0.001)	0.51 (<0.001)	1.00	
Beginning of the second flood	bsec	0.047 (0.65)	-0.51 (<0.001)	-0.047 (0.66)	1.00

TABLE 3.4. Pearson product moment coefficient (r) for substrate variables. Probability values are in parenthesis. (n = 92).

Variable		org	gra	sa	scl	P	pH
organic content (%)	org	1.00					
gravel (%)	gra	-0.69 (<0.001)	1.00				
sand (%)	sa	-0.25 (0.015)	-.069 (<0.001)	1.00			
silt/clay (%)	scl	0.54 (<0.001)	-0.15 (0.15)	-0.61 (<0.001)	1.00		
phosphorous (ppm)	P	0.61 (<0.001)	-0.028 (0.79)	-0.34 (<0.001)	0.50 (<0.001)	1.00	
pH	pH	-0.54 (<0.001)	0.34 (<0.001)	-.068 (0.52)	-0.27 (<0.01)	-0.12 (0.25)	1.00

Best models

Tables 3.5 and 3.6 list the thirteen models that met the criteria for accuracy, sensitivity and specificity. The models for aquatic (floating leaves/flexuous stems) and herbid plants are graphed in figures 3.4 and 3.5. Seven of these predicted the presence/absence of a functional group and six, the dominance/nondominance. Three of the latter were subsequently omitted because it was not possible to define a realistic environmental range at which they would be absent using the threshold value of $p < .3$.

The predictions for the distribution of the herbaceous functional groups are illustrated in Figures 3.6 and 3.7. These figures are combinations of inclusion and exclusion rules for 4 functional groups, where the former describe the ranges of environmental variables where the probability of occurrence of a functional group is greater than .7 and the latter, the ranges where the probability is less than .3. The inclusion and exclusion rules for the other best models are not illustrated as the corresponding models involve 3 variables and would therefore requite a more elaborate illustration. However, at least one scenario describing either their absence or presence has been included in Table 3.5.

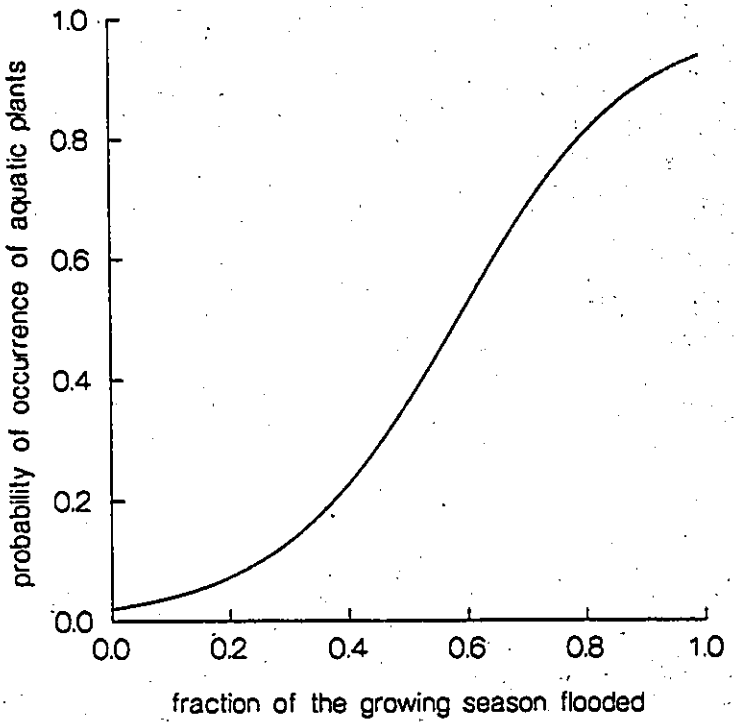
TABLE 3.5. Models predicting the presence or absence of a functional group with accuracy > 70 % and both sensitivity and specificity > 60%. Variables are: pH; gs: fraction of the growing season flooded; sa: percent sand in the soil; P: phosphorous in ppm; org: percent organic content; scl: percent silt/clay. An application in the form of an inclusion or exclusion rule is included in column 4.

Functional group	Equation for calculation of $\ln(p/(1-p))$	Accuracy	Application
Aquatic	6.65 (gs) - 3.88	79%	absent if gs < .45
Hutchinson's herbids	-5.58 (gs) + 4.06	78%	present if gs < .6
Hutchinson's isoetids	4.32 (gs) - 2.63	75%	present if gs > .8
Stem diameter 20-30 mm	13.2 - .34 (pH) - 1.64 (P)	74%	absent only if P < 8 ppm
Stem diameter > 30 mm	3.0 (gs) + 2.5 (pH) + .30 (org) + 20.53	72%	absent only if pH > 7, gs > 0.7
Leaf area < 1 cm^2	-2.02 (pH) - .066 (sa) + 7.76 (or pH, scl)	83% (83%)	absent if pH > 6, sa < 70%
Leaf area > 100cm^2	1.76 (pH) + .19 (org) - .051 (sa) - 8.87	72%	at sa = 70%, absent only if pH < 6 and org < 10%

TABLE 3.5. Models predicting the dominance or non dominance of a functional group with accuracy $> 70\ \%$ and both sensitivity and specificity $> 60\%$. Variables are: pH; gs: fraction of the growing season flooded; sa: percent sand in the soil; P: phosphorous in ppm. An application in the form of an inclusion or exclusion rule is included in Column 4.

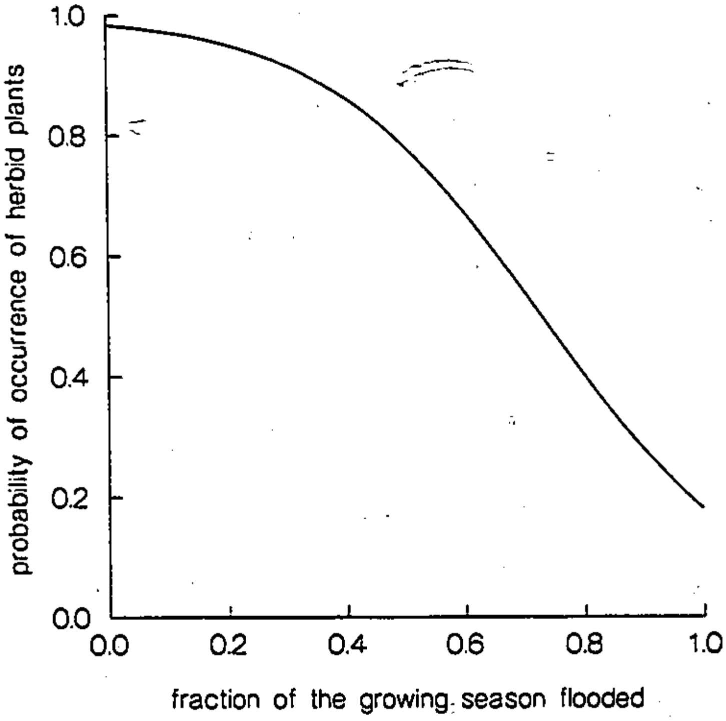
Functional group	Equation for calculation of $\ln(p/(1-p))$	Accuracy	Application
Rhizome number > 4	$3.0\,(\mathrm{pH}) + .34\,(\mathrm{P}) - 23.9$	78%	rarely not dominant
Rhizome number 2-3	$.80\,(\mathrm{pH}) -.057\,(\mathrm{sa}) + 2.9\,(\mathrm{gs})$	73%	rarely not dominant
Canopy diameter > 60 cm	$-1.66\,(\mathrm{pH}) - 12.2$	74%	rarely not dominant
Leafless	$2.78\,(\mathrm{gs}) + .047\,(\mathrm{sa}) - 5.12$	70%	not dominant if $\mathrm{sa} < 70\%$ and $\mathrm{gs} < .4$
Stem diameter 1-2 mm	$2.29\,(\mathrm{gs}) + 1.49\,(\mathrm{pH}) - 8.17$	70%	dominant if $\mathrm{gs} > .4$ and $\mathrm{pH} < 6.5$
Stem diameter 2 -5 mm	$-1.42\,(\mathrm{pH}) + 9.7$	70%	dominant if $\mathrm{pH} < 6$

FIGURE 3.4. Probability of occurrence of aquatic plants as a function of duration of flooding (fraction of the growing season flooded, gs). Model equation is $\ln(p/(1-p)) = 6.65\,(gs) - 3.88$



probability of occurrence of aquatic plants
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
fraction of the growing season flooded

FIGURE 3.5. Probability of occurrence of herbid plants as a function of duration of flooding (fraction of the growing season flooded, *gs*). Model equation is $\ln(p/(1-p)) = -5.58\,(gs) + 4.06$.



1.0
0.8
0.6
0.4
0.2
0.0
probability of occurrence of herbid plants
0.0
0.2
0.4
0.6
0.8
1.0
fraction of the growing season flooded

Trends

As expected, the distribution of aquatic plants yielded an accurate model based on a hydrological predictor, the fraction of the growing season flooded (gs).. At a finer level of division, two functional groups described by Hutchinson's classification (herbids and isoetids) proved to be the more strongly related to environmental variables than other groups defined by qualitative traits. Further, the distribution of these two functional groups could be accurately predicted from a single variable, gs. Among the quantitative traits, stem diameter and leaf area were the only two traits that yielded accurate, predictive models.

Of the phylogenetic groups, the distribution of dicots was related to flooding, and the distribution of Cyperaceae was most strongly related to both duration of flooding and P. Models describing the dominance/nondominance of these functional groups had higher accuracies than those describing their presence/absence, but none approached the performance of the best models.

One variable, gs, emerged as the best hydrological predictor. Unfortunately, the high correlation of this variable over time made it impossible to identify the period required for a change in hydrology to affect vegetation.

In contrast, all of the substrate variables were significant in at least one of the best models. While pH was the most common component, the percent of sand in the soil was also significant in a number of the best models.

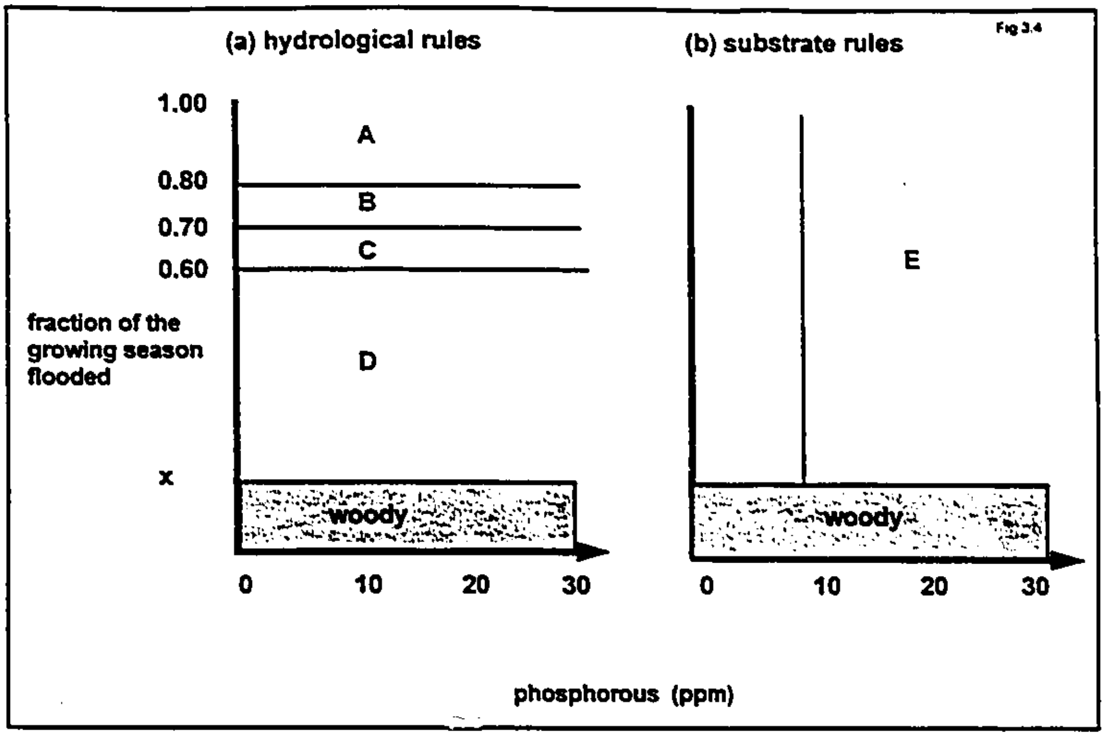


FIGURE 3.6. Inclusion rules for four herbaceous functional groups. The presence of a functional group is based on probabilities of occurrence of > .7. Rules predict the presence of isoetid plants (zone A), aquatic plants (zones A and B), herbids (zone D), plants with stem diameter greater than 3 cm (zone E). There are no predictions for zone C. The lower limit of woody species is from the model described in Chapter 2.

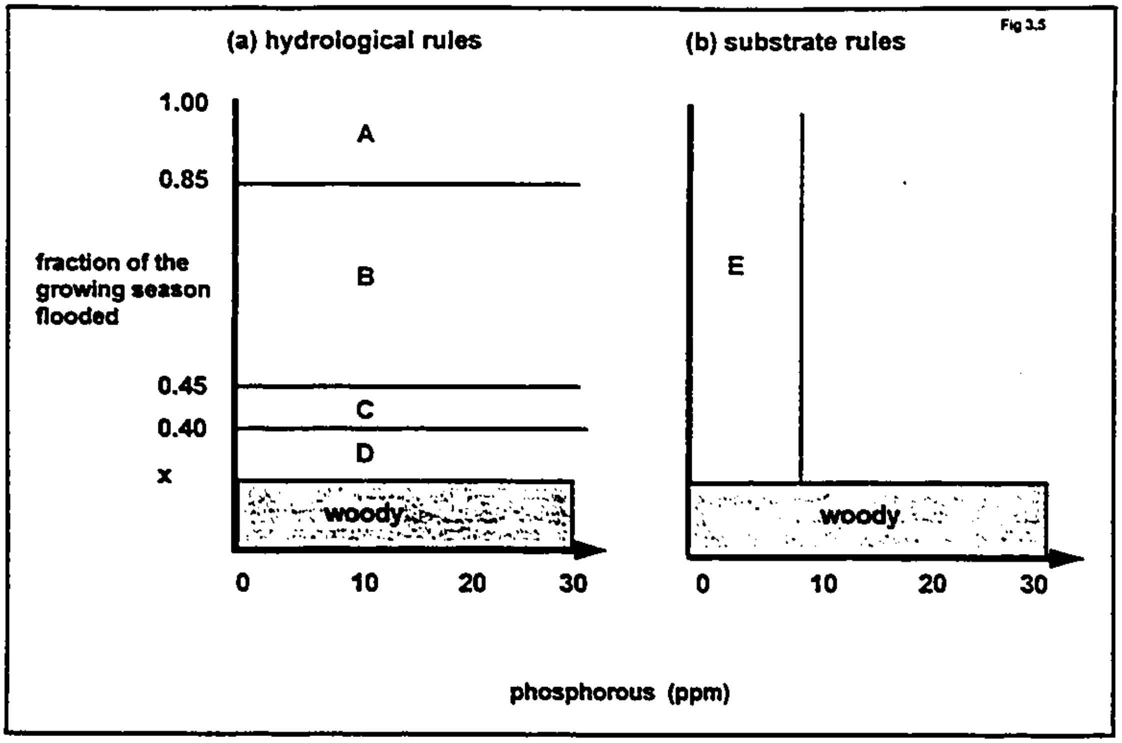


FIGURE 3.7. Exclusion rules for four herbaceous functional groups. The presence of a functional group is based on probabilities of occurrence of < .3. Rules predict the absence of herbids (zone A), aquatic plants (zones C and D), isoetids (zone D), plants with stem diameter greater than 3 cm (zone E). There are no predictions for zone B. The lower limit of woody species is from the model described in Chapter 2.

Discussion

Best models

I have identified ten strong trait-environment relationships that describe the distribution of wetland functional groups. By solving the equations from the logistic regressions, we can calculate the probabilities of occurrence (or of dominance) of a given functional group at different values of environmental variables. Three of these equations use only hydrology, four use substrate variables alone. All but two of the relationships can be described by only one or two variables.

In Figures 3.6 and 3.7 I have illustrated how these relationships can be incorporated into generalized diagrams of wetland vegetation. The two figures are separate representations of inclusion and exclusion rules.

The strong link of the aquatic and herbid functional groups to hydrology is not surprising. It is intuitively obvious that aquatic plants require a minimum amount of flooding and that emergent plants (e.g., herbids) cannot survive too much flooding. However, these limits are more often described as a function of water depth (Sculthorpe 1967, Herdendorf et al. 1986). Using the logistic equation and a threshold probability of .7, we can suggest a minimum duration of flooding as well. This is especially important where there is significant variation in water levels throughout the growing season. Both of these functional groups are important components of wetland vegetation and the quantification of their distribution is essential to protecting the major elements of this vegetation.

One of the most significant results, in terms of conservation, is the model describing the distribution of Hutchinson's isoetids. The isoetids comprise a relatively small functional group (5 species in this data set), but they are likely to include rare species, when surveyed over larger geographic areas. For example, there are five species of Isoetes on the rare species list for Canada (Argus and Pryer 1990), and at least one provincially rare species, Isoetes riparia, has been recorded from an Ottawa River wetland (Brunton and Dilabio 1989). In addition, Sabatia kennedyana Fern. has an isoetid form, although it is an angiosperm, and it has been listed as nationally rare with a priority ranking of 1 (Argus and Pryer 1990). The small stature and slow growth rate of the isoetids make them poor competitors (Boston and Adams 1987) and their protection may become a serious restoration issue.

Unfortunately, the failure of substrate variables to improve the accuracy to this model is suspect. Isoetids typically occur on sandy substrate, although they can apparently be found on richer soils (Boston and Adams 1987). A large number of quadrats were on soils with a sand content exceeding 80% (Fig. 3.3.d). This skewed distribution might explain the absence of a significant statistical effect of percent sand in my models. I would expect that the model describing the distribution of isoetids would have to be further modified.

Only two quantitative traits, leaf area and stem diameter, led to accurate models and these were generally with respect to substrate conditions. The predictors of leaf area in particular (percent sand and percent organic content) indicate that disturbance is having an effect on the distribution of these functional groups. The model which best fits my subjective field observations is the dominance of essentially leafless species where there is frequent flooding and sandy substrate. These are the "reeds" of infertile, exposed shores described by Day et al. (1988).

At first glance, some of the functional groups may appear to be present or absent only at extreme values of the environmental variables. For example, the functional group defined by a stem diameter between 2 and 3 cm is absent only when the levels of phosphorous in the soil is less than 8 ppm. However, many of the quadrats from the data set were within these ranges (Fig 3.3), indicating that there are significant areas of wetland at these apparent extremes.

Poor models.

Two kinds of functional groups were conspicuous by their absence among the best models, groups defined by height and those described by Boutin and Keddy (1993). In contrast, Menges and Waller (1983) found that maximum height was related to elevation of floodplain herbs. There are three major difference between their study and my protocol, which could account for the differences. First, Menges and Waller used the maximum height of species as described by botanical manuals, while I used values from field measurements. I assigned species to a range of functional groups, which made it harder to detect differences. Second, Menges and Waller were working in a floodplain with complete to dissected woody cover; my study system was in areas where the herbaceous functional group was dominant. Third, they described trends rather than using statistical models to test for significant trait-environment relationships.

None of the matrix, interstitial or ruderal guilds appeared in the best models. A tempting explanation for the absence of ruderals is their low numbers at the sites covered by the study. Day et al. (1988) noted the few annuals that appeared in the data set and mentioned the restriction of these species to areas of high sedimentation and disturbance, such as the mouths of creeks.

Alternatively, the poor level of prediction for this group may be due to the nature of disturbance at the study sites and to the definition of the group itself. Ruderal species are generally defined by traits that ensure survival in habitats with frequent disturbance events. These traits include a short period to reproductive maturity (one growing season), the production of large numbers of propagules, and high above-ground to below-ground allocation ratios (Grime 1979). Boutin and Keddy's (1993) classification is consistent with this definition.

However, clonal spread also provides a means of surviving in these habitats, particularly if the disturbance affects seed availability. In a study of barrier island vegetation, Fahrig et al. (1993a) linked capacity for clonal spread with survival at high frequencies of sand overwash. Ninety-five species were categorized according to their cover in habitats with varying frequencies of overwash. In contrast with prevailing theory, the representation of annual plants did not increase with frequency of disturbance.

Similar results were obtained in a comparison of the vegetation of two ecosystems, barrier islands and a short-grass steppe. Fahrig et al. (1993b) described four levels of disturbance for each system, based on frequency of sand overwash and intensity of grazing. In both systems, the cover of plants with long-distance clonal spread increased between moderate and high levels of disturbance. The success of plants with clonal spread was attributed to two factors. First, colonization by clonal spread can occur in the same season as the disturbance event, while colonization by seed requires completion of seed development, dispersal, and germination. This sequence of events will not usually be complete until the year after the time of the disturbance event. Second, some kinds of disturbance can reduce the availability of seeds. Where there is frequent overwash, seeds can be too deeply buried to germinate or survive. Intensive grazing may also reduce the availability of seeds through direct consumption and through destruction of the shoot. Computer simulations of plant response to disturbance were consistent with this interpretation (Fahrig et al. 1993b). Plants with long-distance clonal spread were as successful as annuals if the time to colonization was reduced. They were more successful if the disturbance had a stronger effect on seeds than on shoots.

The principle disturbance events at Day's study sites are wave action and ice scour. If these events are severe enough to destroy plant cover, they may remove a significant portion of the seeds as well. The depth of the seedbanks at these sites has not been described. However, data from other wetland systems provide examples of the importance of the first few centimeters of soil (e.g., Leck and Graveline 1979, Nicholson and Keddy 1983). If the disturbance event affects this layer, then the importance of regeneration from seeds will be reduced, relative to revegetation from clonal spread.. An example of this is described in Wisheu and Keddy's (1991) discussion of the seed bank dynamics of a Nova Scotia river. Thus, the distribution of ruderals, as defined in the conventional manner, will not necessarily be related to variables that reflect mechanical disturbance (e.g., soil sand fraction, organic content).

The poor separation of the matrix and interstitial functional groups, however, raises the question of guild proportionality (Wilson and Roxburgh 1993). I expected that most of the dominant species would be from the matrix functional group. In fact, only 5 of the 17 dominant species belonged to this group, and 11 were from the interstitial functional group. This may be an artifact of the definition of dominance (25% representation by biomass) and of Day et al.'s (1988) original decision to sample by vegetation type. Alternatively, the response of vegetation to environmental gradients may be more accurately reflected in the proportional representation of these functional groups. If this is true, then one functional group would be expected to be dominant at one end of the controlling environmental gradient, the other functional group would be dominant at the opposite end of the gradient, and species from both functional groups would be dominant at some position along the gradient. My results were not inconsistent with this hypothesis, though my analysis does not provide an adequat test.

Significance of traits

A few observations on the significance of the defining traits provides a preview of the accuracy that we might expect for the best models.

The aquatic group (e.g., Nymphoides) is characterized by floating leaves and/or flexuous stems. In both cases, the photosynthetic tissue is supported by water. While this may represent an economy in allocation to support tissue, the plants are at increased risk to damage from hydrological forces. Floating leaves, in particular, can be destroyed by turbulence and high winds (Sculthorpe 1967). The predictive rules for this group are related to hydrology only. The absence of indicators of fetch, or other measures of exposure, may limit their accuracy.

Herbid plants (e.g., Lythrum) have emergent stems, and aerial leaves that are elliptical, lanceolate or compound. This morphology is typical of many terrestrial species as well. It may be that the leaf morphology (dorsiventral orientation and absence of extensive aerenchyma,) is not suited to the mechanical turbulence and oxygen stress of flooding (Sculthorpe 1967). However, it is more likely that leaf morphology one of a set of traits characteristic of this functional group, many of which may limit flood tolerance. Thus, the significance of hydrology in this model may involve a complex of mechanisms.

Isoetids (e.g., Eriocaulon) are distinguished by their slow growth rates, small stature, and stiff, linear leaves that are often in a basal rosette. This group includes several evergreen species (Boston and Adams 1987, Wisheu and Keddy 1989). Isoetids represent a classic example of the stress-tolerators described by Grime (1979). Therefore, it is not surprising that they are generally found on sandy or infertile substrate. Their compact morphology is also advantageous where the mechanical impact of wave action is significant. The lack of substrate variables is suspect.

The rest of the functional groups are defined by leaf area or stem diameter. Leaf area is related to the most important plant functions, light capture and carbon gain. Selection for larger leaves represents a trade off between the benefit (dry matter production) and costs of carbon gain (investment of resources in support tissue, enzymes, water loss, Givinish 1987). It is not surprising, therefore, that several trends in leaf area can be related to environmental factors (Givinish 1987). Of these, two are pertinent to my study. (1) Effective leaf area increases along gradients of humidity and/or soil fertility and (2) decreases with reduction in light (Givinish 1987). The extremes of leaf size are represented in the list of predictive rules; plants with very small leaves (< 1 cm^2, e.g., Galium) and plants with the largest leaves (> 100cm^2, e.g., Pontederia). The distribution of the former is linked to high sand content and pH, while the latter are predicted at low sand fractions and high organic content. Sandy substrate suggests low nutrient levels, as well as sorting by wave action (disturbance). The predictions of the rules are therefore consistent with the observed increase in leaf area along the nutrient gradient, as well as with the expected reduction in leaf area with mechanical disturbance (Sculthorpe 1967).

A third functional group was defined by leaf area; the leafless plants or plants with inconspicuous leaves (e.g., Equisetum). This morphology presents the minimum surface area for resistance to (thus damage by) water turbulence, as well as an investment in height rather than photosynthetic tissue. The rules linked this group to areas with frequent flooding and high sand fractions; that is, an environment susceptible to frequent disturbance from wave action.

Four functional groups were defined on the basis of stem diameter. Large stem diameters represent an investment in support tissue and in resistance to damage from mechanical disturbance. According to the predictions of my rules, the plants with the largest stems (e.g., Typha) occur where there is high organic content in the soil and where there are adequate levels of phosphorous, pH and flooding. The predictors for small-stemmed plants are pH and flooding. The role of a macronutrient, phosphorous, in the models might allow a high investment in support tissue, while the importance of flooding might require it.

Conclusion

As predicted in the introduction, a strong trait-environment relationship emerged at the level of aquatic and emergent vegetation. Nine additional relationships were described for the functional groups defined at a finer level of classification. At least one of these relationships, the one describing the distribution of isoetids, is suspect because of the absence of substrate variables in the model.

The classifications that were tested ran the gamut from intuitive, qualitative groupings (Hutchinson 1975) to divisions of a series of purely quantitative measurements. In the end, three of the functional groups from the most accurate models were the product of the researcher's experience and extensive knowledge of the system (Hutchinson 1975). The other seven were based on ranges of single quantitative traits. At least one of these functional groups (leaf area ≅ 0) could be described qualitatively (leafless). This suggests that the identification of ecologically meaningful groups does not have to involve complex criteria or advanced statistical techniques.

Finally, a set of testable predictions were generated from the most accurate models. I have used graphs of the distribution of functional groups to illustrate the application of these predictions in the form of inclusion and exclusion rules. These rules provide potential guidelines for wetland management.

CHAPTER 4

A TEST OF THE MODEL OF THE LOWER LIMIT OF WOODED WETLAND

Introduction

One of the fundamental divisions of wetland vegetation is the distinction between woody and herbaceous functional groups. Both functional groups represent significant elements of the diversity of the riparian vegetation of the northern temperate zone. I have described the problem of the incursion of woody plants into areas of herbaceous cover (Chapter 2). Several studies have indicated that hydrology is a controlling factor in this unchecked succession (e.g., Jaworski et al. 1979). I have interpreted these studies as evidence that there are flooding regimes which will prevent incursion by woody plants and I have developed a model that describes the flood conditions at which it will not be the dominant functional group. My model incorporates two hydrological variables, the end of the first flood and the beginning of the second flood, and I will refer to it as the two-flood model.

There have been at least two other quantifications of the distribution of the woody functional group, and testable predictions can be derived from both. The first quantification describes the flood tolerance of mature trees at a Tennessee Valley reservoir (Hall and Smith 1955). The most water tolerant species did not survive if the average duration of flooding exceeded 40% of the growing season for six consecutive years. We can therefore predict that the woody functional group will not occur at these flood levels.

The second quantitative prediction comes from work on inland ponds. Schneider (1994) noted that the lower limit of woody cover coincided with the extent of drawdown over the three previous growing seasons. Her sites were in New York state, but her observations are consistent with the description of succession in a Minnesota wetland, where willows survived long periods of flooding if there had been two to three years of drawdown after the initial colonization (Harris and Marshall 1963). These observations indicate that woody plants require a minimum flood-free time for establishment, in order to be tolerant of prolonged flooding. The testable prediction is that the woody functional group will be dominant in areas where there has been a drawdown of two or three years.

In this portion of my research I tested the accuracy of these three sets of quantitative predictions: the two-flood model, the suggested flood tolerance of mature trees, and the minimum time to establishment. The test sites were in the Ottawa and Saint Lawrence River drainage basins, and the test was a comparison of the observed functional group with the predictions generated from the hydrological data. The predictions and the observations pertain to the dominant functional group or plant cover, not the presence or absence of individual woody plants.

Methods

Data

Data were collected from 7 test sites (Table 4.1) along the Mississippi, Ottawa and St. Lawrence Rivers (Figure 2.1). I selected sites that were close to water level gauges because long- term hydrological records were necessary for the tests. All sites were within 20 km of a gauge and two were within 2 km of a gauge. The sites included a range in exposure to wave action, river discharge and drainage area. One site (Westmeath) was adjacent to a site used to develop my model (Chapter 2) and therefore provided a test of the accuracy of the model in the same area.

The data from two of the seven sites (Lac Saint-Louis and Lac des Deux Montagnes) were extracted from a report by le Groupe Dryade (1985). The authors had recorded the elevation of the upper and lower boundaries of the ten dominant vegetation types found in 62 transects at Lac St. Louis. Elevations were expressed with respect to gauge readings at Pointe- Claire. I extracted the elevation of the lower boundary of woody cover for each transect. The data also included a subjective assessment of the exposure to wave action at each transect, based on a five-category scale (very high exposure, high exposure, intermediate exposure, low exposure and no exposure).

In the case of Lac des Deux Montagnes the transect data were not accessible. I therefore used the lower boundary of two of their vegetation types, poplar and silver maple, as these are usually the lowest representation of the woody functional group on the shorelines where they occur. The average elevation of these lower limits were available.

I collected data from the five other sites in the fall of 1993. The sampling protocol involved first identifying the lower boundary or limit of woody cover at 15 to 20 points along the shore (Chapter 2). I then recorded the elevation of these points with respect to a known water level (Appendix 4.1). These data were used to test the predictions of the

TABLE 4.1. Location and time of sampling and location of water gauges.

Site	Year of sampling	Coordinates	River	Gauge
Appleton, Ont.	1993	45° 11′ N 76° 07′ W	Mississippi	Appleton
Westmeath, Ont.	1993	45° 53′ N 75° 54′ W	Ottawa	Westmeath
Luskville, Qué.	1993	45° 21′ N 75° 48′ W	Ottawa	Brittania
Waddington, N.Y.	1993	44° 50′ N 75° 18′ W	St. Lawrence	Iroquois Dam
Lac des Deux Montagnes, Qué.	1982	45° 24′ N 74° 01′ W	Ottawa	Ste-Anne-de-Bellevue
Cap St. Jacques, Qué.	1993	74° 01′ W 45° 23′ N	Ottawa, St. Lawrence	Ste-Anne-de-Bellevue
Lac St. Louis, Qué.	1984	45° 20′ N 73° 57′ W	St. Lawrence	Pointe-Claire

flood tolerance of mature trees and of the minimum time for establishment of the woody functional group. I generated a second data set to test the two-flood model. I added 5 cm to, and subtracted 5 cm from, the elevation of the points at the boundary between the two functional groups. In this manner, I generated pairs of points, one in the area dominatedby the woody and the other in the area dominated by the herbaceous functional groups, respectively (Chapter 2).

Tests

(1) The two-flood model.

The two variables of the two-flood model were the end of the first flood (eff) and the beginning of the second flood (bsec) (Chapter 2). These variables were accurate predictors (>80%) when they were averaged over intervals of 7, 12 and 18 growing seasons. Although the highest accuracy was obtained using the 12-year average, the performance of the models for the two other intervals was only slightly lower and both were therefore included in the tests. The equations for each interval are listed in Table 4.2.

I first tested the predictions of each equation separately, using the appropriate averages of eff and bsec (7, 12 or 18 years). I calculated the average values for these variables for each point, for each of the 7, 12 and 18 growing seasons previous to the

TABLE 4.2. Equations from logistic model based on the end of the first flood (eff) and the beginning of the second flood (bsec). (From analysis in Chapter 2).

Interval	Equation
7 years	$\ln(p/(1-p)) = .11\,(bsec) - .21(eff)$
12 years	$\ln(p/(1-p)) = .16\,(bsec) - .23\,(eff) + 1.42$
18 years	$\ln(p/(1-p)) = .12\,(bsec) - .17\,(eff)$

collection of data. I then calculated the probability of dominance of the woody functional group for each point by using the equation for the appropriate time interval. If the probability was greater than .7, I predicted that the woody functional group would be dominant. If it was less than .3 I predicted that the herbaceous functional group would be dominant. If it was between .3 and .7 then the point was considered to be in a transitionzone at the boundary of the two functional groups and no prediction was made. These points were removed from the test. The accuracy was calculated using the remaining points (probability >.7 and <.3).

I expected that many of the errors in prediction would involve points that were closest to the boundary between the two functional groups. Therefore, I generated a composite of the predictions of the three equations. Woody cover was predicted for a point only if all the equations yielded a probability greater than .7. Similarly, herbaceous cover was predicted only if the probability was less than .3, using all of the three equations. If there was a discrepancy in the predictions of any two equations then the point was considered to be in the transition zone. In this manner, the transition zone was effectively broadened. An illustration of the change in the range of the transition zone is included in Appendix 4.2.

Accuracy was defined as the ratio of the predicted to the observed values (e.g., number of points correctly identified as having woody cover / total number of points). I calculated the accuracy of prediction of woody and herbaceous cover separately.

Finally, I tested for a relationship between the accuracy of the model and degree of exposure, using the data from the Lac St. Louis site and a Chi-square test (Sigma Stat, Jandel Scientific, 1994). The five categories were reduced to three (high, intermediate and low exposure, Table 4.4) to provide sufficient numbers for the test. The categories of very high and high exposure were combined, as were low exposure and no exposure.

(2) Flood tolerance of woody species.

The predicted maximum flood tolerance of the woody functional group was 40% of the growing season for 6 consecutive years. In order to test this I calculated the mean and range of elevation of the limit of woody cover at each site. The duration of flooding at these elevations was then averaged over both the 6 and the 12 growing seasons previous to the collection of data. The interval of six years was taken directly from the prediction; the longer interval was included because of its significance in the accuracy of the two-flood model (Chapter 2).

(3) Time to establishment of woody plants.

I examined water level records for drawdowns at the lower limit of woody cover at each site. The average elevation of this limit was compared with the maximum and average water levels of each of the 18 growing seasons previous to the collection of data. If the average elevation was greater than the maximum water level for a given growing season, then there would have been drawdown throughout that season. Comparison with the average water level was included as an indication of the duration of flooding (e.g. if the elevation of the limit of woody cover was greater than the average water level, then the duration of flooding was likely less than the entire growing season).

Results

(1) The two-flood model.

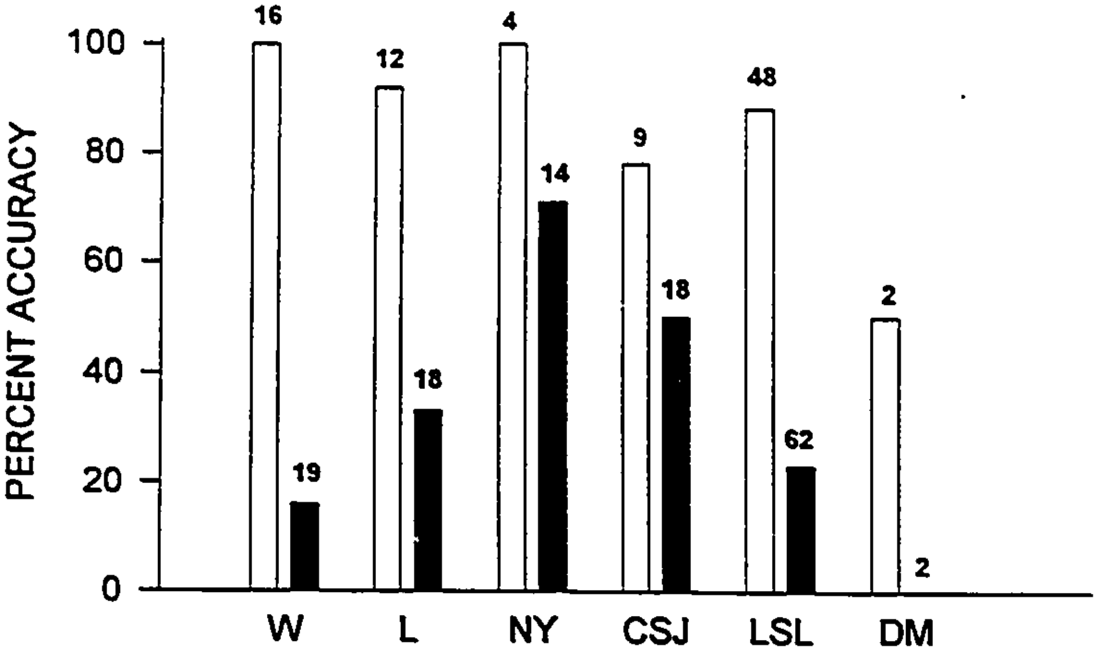
Figures 4.1 to 4.4 summarize the accuracy of prediction of the dominant functional group for each site.

In general, the model was more accurate in predicting woody cover than herbaceous cover. Two sets of predictions proved to be highly accurate in this regard. These were (1) predictions based on the eighteen-year interval (Figure 4.1) and (2) the composite approach (Figure 4.2). Their accuracy ranged from 50% of the points, at Deux Montagnes, to 100 % of the points, at Westmeath. The data from Deux Montagnes include only 2 points. If these are omitted then the accuracy for the equation for the eighteen - year interval ranges from 78% to 100%, and the accuracy of the composite of predictions ranges from 60% to 100%.

FIGURE 4.1. Accuracy of the two-flood model using the equation and averages for the 18-year interval. The y-axis is the percentage of the data points for which the functional group was correctly identified (white) or that were assigned to the transition zone (solid). The sample size is indicated at the top of each bar. Abbreviations for sites are: **W**: Westmeath; **L**: Luskville; **NY**: Waddington, N.Y.; **CSJ**: Cap St-Jacques; **LSL**: Lac St-Louis; **DM**: Deux Montagnes.

Fig. 4.1

(a) woody



(b) herbaceous

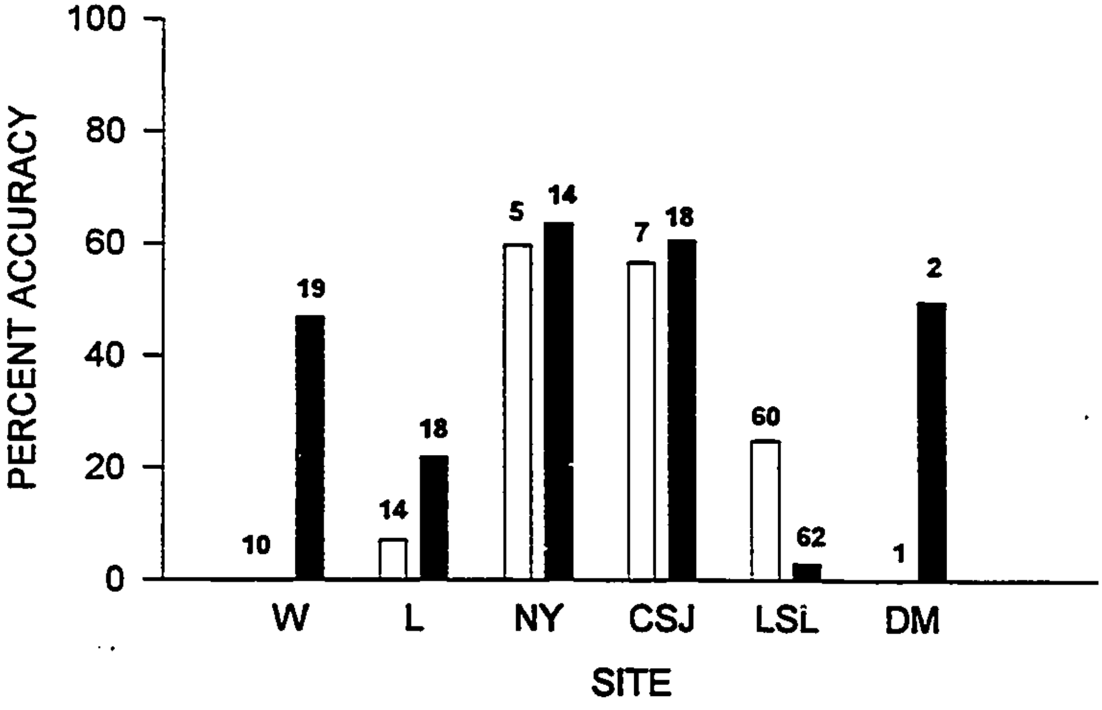
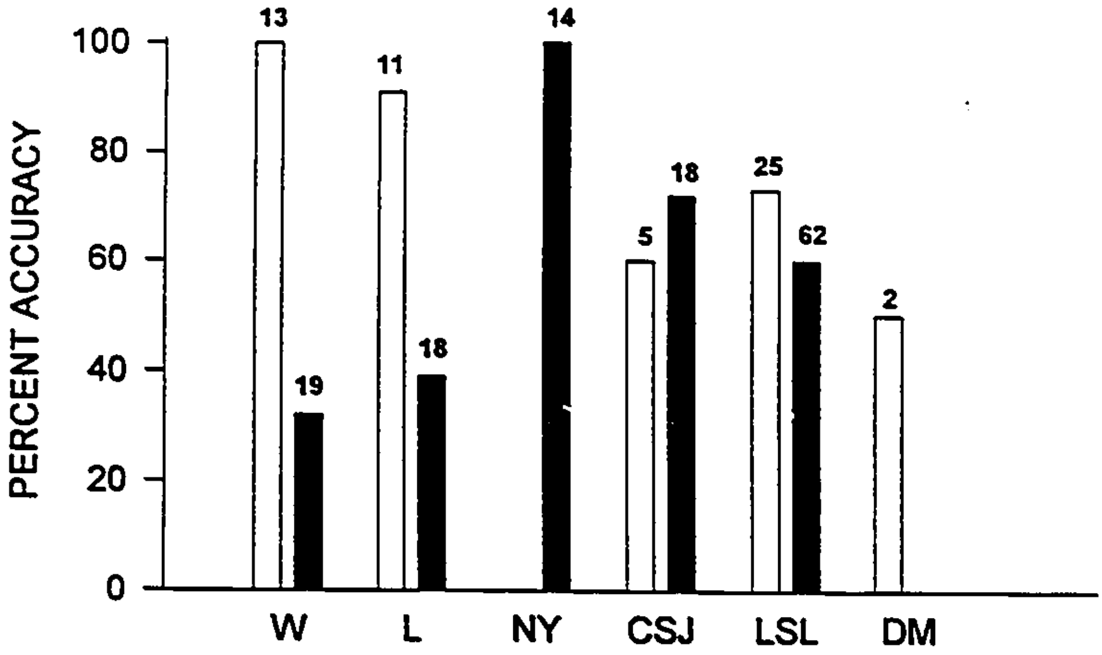


FIGURE 4.2. Accuracy of the two-flood model using the equation and averages for the three intervals (7, 12 and 18 growing seasons). The y-axis is the percentage of the data points for which the functional group was correctly identified (white) or that were assigned to the transition zone (solid). The sample size is indicated at the top of each bar. Abbreviations for sites are: **W:** Westmeath; **L:** Luskville; **NY:** Waddington, N.Y.; **CSJ:** Cap St-Jacques; **LSL:** Lac St-Louis; **DM:** Deux Montagnes.

Fig. 4.2

(a) woody



(b) herbaceous

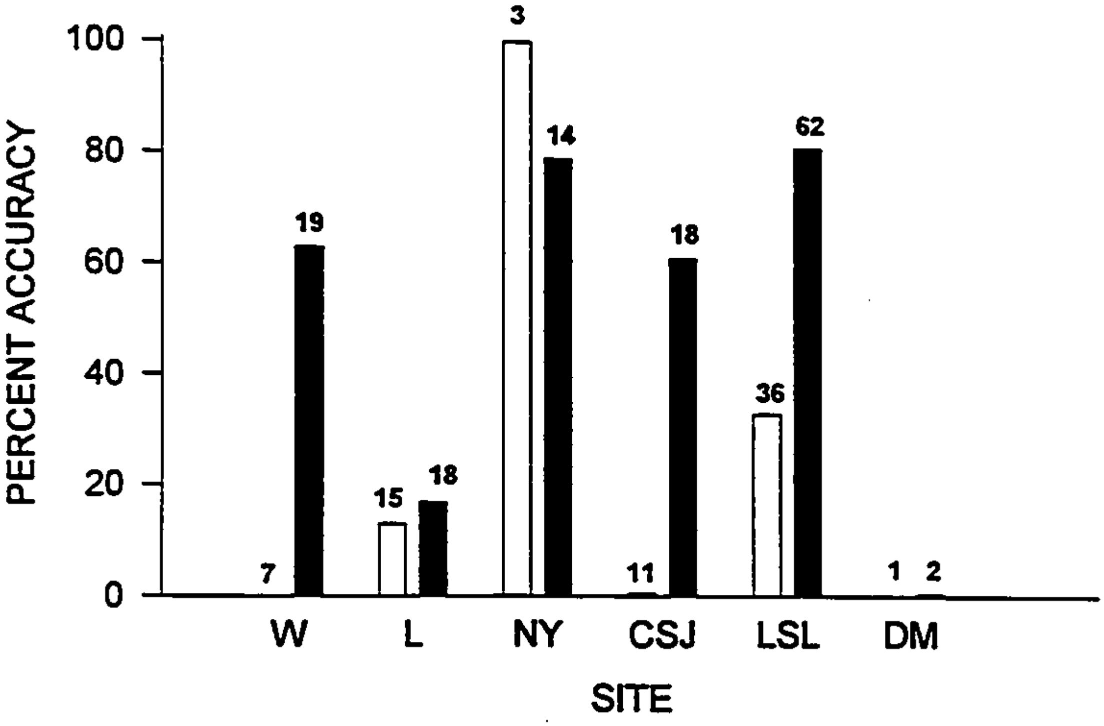
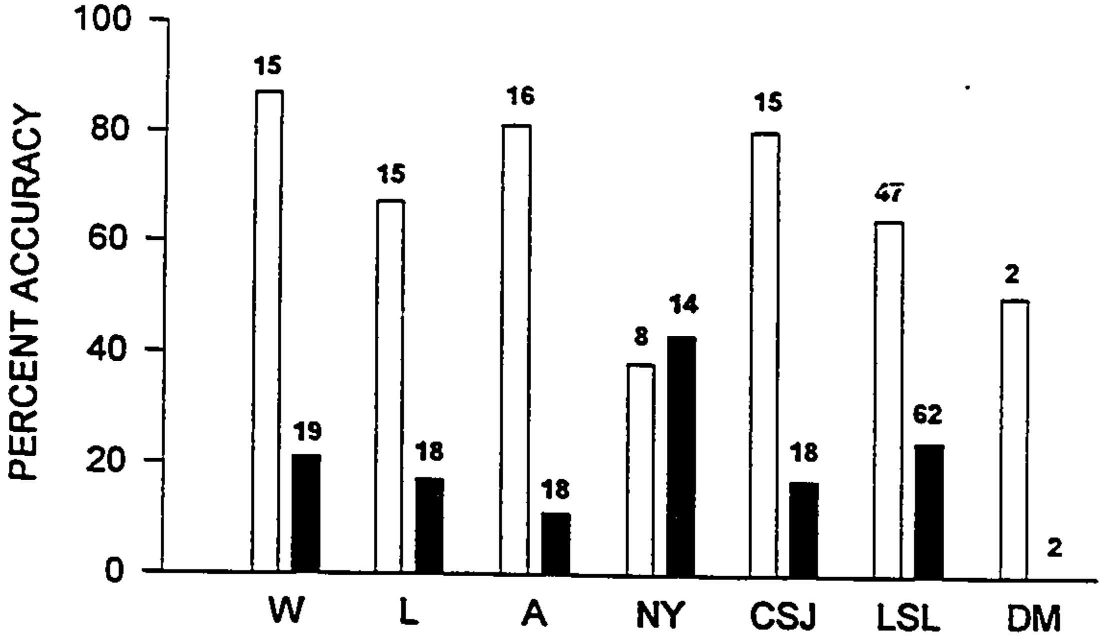
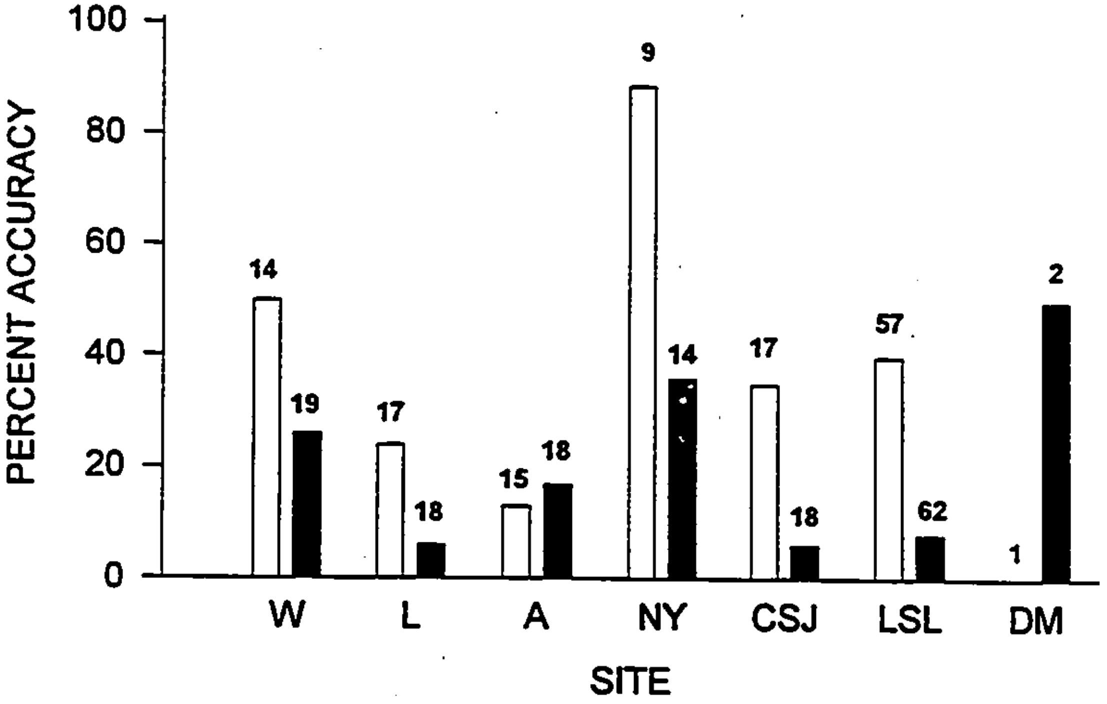


FIGURE 4.3. Accuracy of the two-flood model using the equation and averages for the 7-year interval. The y-axis is the percentage of the data points for which the functional group was correctly identified (white) or that were assigned to the transition zone (solid). The sample size is indicated at the top of each bar. Abbreviations for sites are: **W**: Westmeath; **L**: Luskville; **A**: Appleton; **NY**: Waddington, N.Y.; **CSJ**: Cap St-Jacques; **LSL**: Lac St-Louis; **DM**: Deux Montagnes.

Fig 4.3



(a) woody

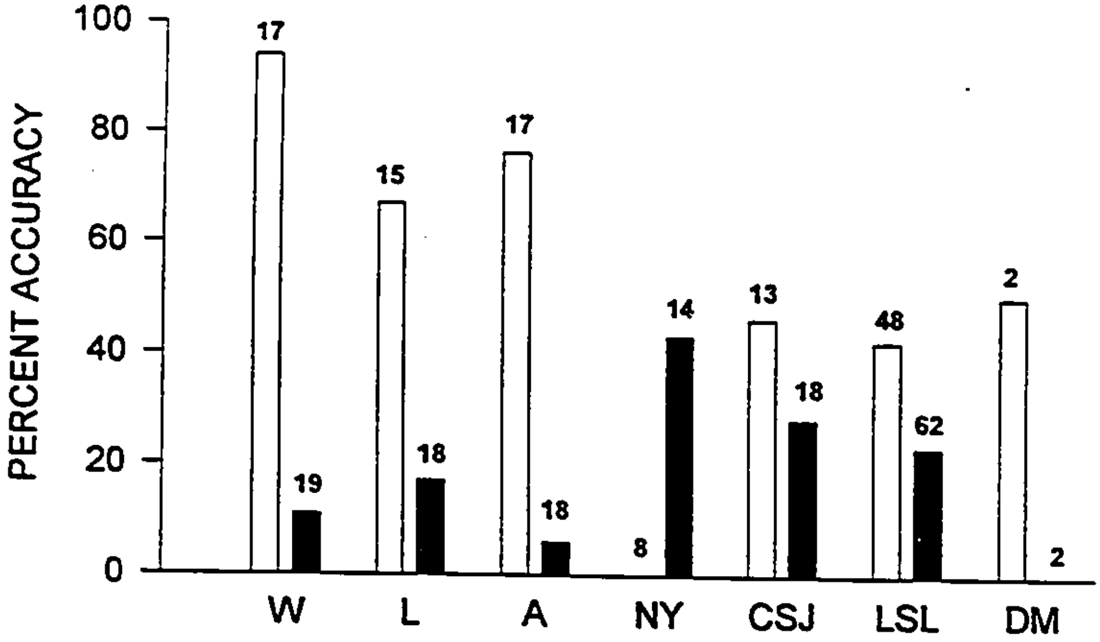


(b) herbaceous

FIGURE 4.4. Accuracy of the two-flood model using the equation and averages for the 12-year interval. The y-axis is the percentage of the data points for which the functional group was correctly identified (white) or that were assigned to the transition zone (solid). The sample size is indicated at the top of each bar. Abbreviations for sites are: **W:** Westmeath; **L:** Luskville; **A:** Appleton; **NY:** Waddington, N.Y.; **CSJ:**.Cap St-Jacques; **LSL:** Lac St-Louis; **DM:** Deux Montagnes.

Fig. 4.4

(a) woody



(b) herbaceous

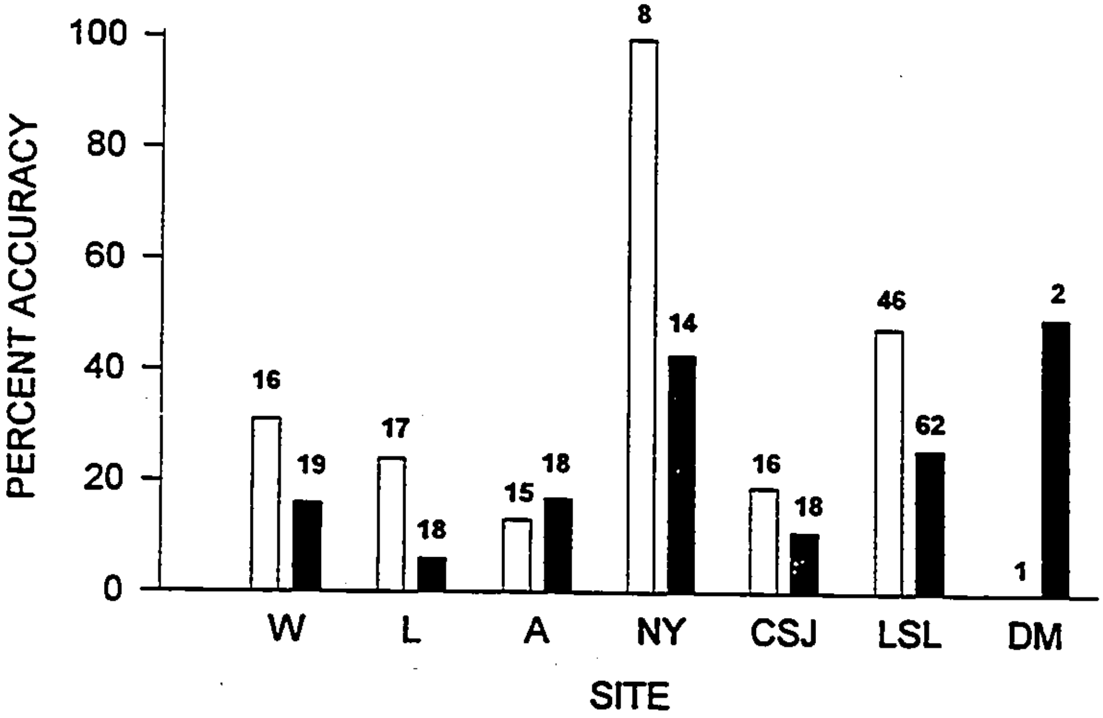


TABLE 4.3. Flood conditions (mean and range of duration of flooding) at the lower limit of woody cover. Drawdown years and years where the mean water level was higher than the lower limit of woody cover are indicated for each site.

Site	Mean duration of flooding [1] (%)	Range in duration of flooding [2] (%)	Water records	Years with no flooding at boundary	Years with mean water level greater than lower limit of woody cover
Appleton, Ont.	19 (23)	8.7 - 41	1980-92		
Westmeath, Ont.	19 (23)	17 - 31	1975-92	1987	1979,1985
Luskville, Qué.	22 (26)	15 - 98	1975-92		1979
Waddington, N.Y.	15 (11)	.27 - 16	1975-92	1986,1987	
Lac des Deux Montagnes, Qué.	8 (14)	not available	1963-81		1967,1970,1972-1974,1976,1979
Cap St. Jacques, Qué.	11 (15)	4.6 - 59	1975-92	1987	1987
Lac St. Louis, Qué.	17 (32)	8.0 - 65	1965-83	1966-68, 1970	1972-1974

1. Six-year average (12 year average).
2. The maximum and minimum duration of flooding at the boundary between woody and herbaceous plants, for the twelve year- period prior to sampling.

The composite of predictions did assign more points to the transition zone, but this did not increase the accuracy of prediction. In some cases it actually reduced the accuracy, by removing points that been correctly identified using the equation from a single interval. The most notable example was the assignment of all the points from the Waddington site to this zone.

The accuracy of prediction of the herbaceous cover was low, especially when based on the longer time intervals.

The Chi-square test failed to detect a significant relationship between exposure and the accuracy of the model (X^2=6.62, *df* = 4, *p*= .16, *power* = .5).

(2) Flood tolerance of woody species.

Table 4.3 shows that the limit of woody cover falls short of its predicted flood tolerance at every site, for both the 6 and 12-year periods. The duration of flooding was well below 40% of the growing season (8% to 32%), indicating that it seldom, if ever, exceeded the 40% mark. However, there were low areas of woody cover that were flooded for most of the growing season at three sites (Luskville, Cap St-Jacques and Lac St- Louis) (Table 4.3, Range in duration of flooding).

TABLE 4.4. Contingency table for exposure data from Lac St. Louis (le Groupe Dryade 1985). Entries are the number of points at which the observed functional group was correctly predicted, using 12-year averages of the end of the first flood and the beginning of the second flood.

	Predicted vegetation type			
Exposure categories	Wooded	Herbaceous	Transition	Total
High	10	12	10	32
Intermediate	12	4	8	24
Low	30	26	12	68
Total	52	42	30	124

(3) Time to establishment of woody plants.

The lower limit of woody cover was flooded at for at least part of the growing season for most years. Moreover, there were only two cases of consecutive dry years (Waddington and Lac St. Louis) for the period examined (Table 4.3).

The limit was above the average water level for most years. The wooded wetland at Cap St-Jacques was the most frequently flooded (7/20 years with mean water levels greater than average elevation of the boundary of woody cover).

Discussion

Two-flood model

My overall goal was to identify quantitative guidelines for controlling the incursion of woody plants into areas dominated by herbaceous plants. The two-flood model provides such a guideline. The accuracy of more than 75% for the 18-year interval is noteworthy, given that the test data represented a narrow elevation range. This was a conservative test. The accuracy of the model would likely have been higher if I had sampled throughout the test sites and not just at the limit of woody cover.

The two-flood model was weak in identifying the points where the herbaceous functional group was dominant. It generated a high probability of dominance by the woody functional group at several of these points. This is not a fatal flaw, given that my goal has been to identify conditions that will prevent incursion by woody plants. It means that predictions will underestimate the areas of herbaceous cover (herbaceous cover will extend to areas higher on the shore than predicted and woody cover will not extend as low on the shore as predicted). It does weaken the generality of the model. Moreover, it underlines the difficulty of predicting the occurrence (or dominance) rather than the absence (or non dominance) of a functional group.

The poor results in predicting the dominance of herbaceous plants may be related to the role of disturbance in determining their distribution. I had expected that the degree of exposure would be an index of disturbance. However, the Chi-square test failed to detect a significant relationship between the accuracy of prediction and exposure category. Nonetheless, the short duration of flooding (less than 40% of the growing season) at the lower limit of woody cover suggests that hydrology is not the only factor. There are two reasons why disturbance is likely a significant factor. First, the significance of mechanical disturbance in the distribution of wetland vegetation has been well documented. For example, Ware and Penfound (1949) described the destruction of vegetation by flash floods, sand cover and blowouts in an Oklahoma floodplain. Johnson (1994) related seedling mortality to ice scour and flood peaks on the Platte River, Nebraska. Second, the area of woody cover is limited to a higher portion of the shore than predicted, a pattern described for another shoreline (Keddy 1983). In a study of the effect of shrub removal, Keddy (1989) found that the greatest increase in abundance was in herbaceous species with fast growth and high production of many small seeds (e.g., Eleocharis palustris). Moreover, the removal of shrubs from exposed shoreline had less effect than removal from protected shorelines. The evidence suggested that disturbance was the overriding factor in the distribution of species on exposed shores, while biotic interactions, such as facilitation or competition, were important at protected sites.

Paradoxically, disturbance can facilitate or prevent colonization by woody plants depending on the time, nature and intensity of the event. Studies of river vegetation in western North America show that Populus and Salix require bare substrate for germination (Rood and Mahoney 1994). The decline of these species has been attributed, in part, to reductions in spring flood levels and to a consequent reduction in the area of substrate appropriate for germination (Johnson et al. 1976, Rood and Mahoney 1994). Conversely, disturbance, in the form of ice scour, can decimate entire populations of tree seedlings (Johnson 1994). In short, the recruitment and persistence of woody species is dependent on a complex set of events. It is therefore all the more important to identify key predictors and to describe the limits of their application, as I have attempted to do with hydrology.

Sensitivity of the two-flood model over different intervals.

I expected the equation for the twelve-year interval to yield the highest accuracy, as it was the best model in the original analysis (Chapter 2). In the test, however, its accuracy was lower than that of the equation for the eighteen- year interval. In addition, its accuracy was lower for the St. Lawrence River sites than for the Ottawa River sites. I have not tested the significance of these differences, but they raise a note of caution. The two-flood model does not account for all of the variation in hydrology. It is more accurate when its variables (eff and bsec) are averaged over long intervals. Differences that occur over shorter periods are thereby reduced. This would explain why the discrepancy between rivers for the 12-year interval disappeared when eff and bsec were averaged over longer periods.

Alternative guidelines

Neither the duration of flooding nor the occurrence of drawdowns proved to be accurate predictors of the boundary between wooded and herbaceous cover. Nonetheless, the maximum flood tolerance of mature trees (40% of the growing season) could provide an exclusion rule; that is, a prediction of where woody cover will be absent. The boundary between the woody and herbaceous functional groups was flooded for less than 40% of the growing season at all sites. The 40% limit suggested by Hall and Smith (1955) is based on woody species at a reservoir and at a lower latitude. Presumably, the disturbance from wave action, strong currents and ice scour was lower at their site than along major rivers of Canada's eastern temperate zone. An exclusion rule for our region might involve a lower percentage of the growing season and might be more accurately applied to small lakes and sheltered shores.

The failure to find consecutive years of drawdown may be a flaw of the test more than of the rule. There were two limitations to my protocol. First, 18 years is a short period for tree species. The life-span of silver maple, commonly found in the study sites, approaches 125 years (Fowells 1975). Thus, some of the trees at the lower limit of woody cover may have colonized the area more than 18 years before the data collection. However, there were young trees and shrubs at the lower limit at some sites (Westmeath and Luskville) which indicates that an extended period of drawdown may not be necessary for establishment of woody species.

A second weakness of my test was the use of the maximum water level as an indicator of the hydrological conditions for the entire season. Peak floods generally last for only short periods. If a plant is flooded for only 2 to 3 days in the spring, the season may still be a dry one from a biological perspective. If these short floods have no impact on woody species, then formulating a decision rule based on drawdown would necessarily involve determining what duration of flooding is or is not biologically significant. This would involve an undertaking similar to the study described in Chapter 2, and is beyond the scope of my project.

Conclusion

Accurate exclusion rules for wooded wetland can be generated using the two-flood model described in Chapter 2. The accuracy is higher when the variables (eff and bsec) are averaged over long intervals, such as 18 growing seasons.

The data did not confirm or disprove the validity of guidelines based on the flood tolerance of mature trees (suggested value = 40% of the growing season) or of a minimum time for establishment of woody species. It is possible that the maximum tolerance of 40% of the growing season is not appropriate for major rivers of the northern temperate zone. It is also possible that the role of drawdown in the establishment of woody plants would be detected with complete water level records and data for the ages of the woody plants at a site.

CHAPTER 5

A TEST OF DECISION RULES FOR HERBACEOUS FUNCTIONAL GROUPS

Introduction

The major goal of my research has been to generate and test decision rules for plant functional groups in riverine wetlands. In Chapter 3, I identified 10 strong relationships between herbaceous plants and environmental variables (Tables 5.1 and 5.2). I then illustrated how the model parameters for each relationship could be used to generate predictions in the form of inclusion and exclusion rules. The inclusion rules described the range of environmental variables where the probability of presence (or dominance) of a functional group exceeded .7 and exclusion rules described the range where the probability of presence (or dominance) would be less than .3. In this last part of my thesis, I have tested the accuracy and generality of these relationships by comparing the predictions generated in this manner, with data from other regions and from Ottawa River sites not previously included in the analysis. The test sites represent a geographical range from the Prairie, Low Boreal, Atlantic Boreal, and Eastern Temperate Regions of Canada (National Wetlands Working Group 1988). In addition, they include different kinds of wetlands, from prairie ponds to lake or river shores.

TABLE 5.1. Models predicting the presence or absence of a functional group (accuracy >70 % and both sensitivity and specificity > 60%) (from Chapter 3). Variables are: pH; gs: fraction of the growing season flooded; sa: percent sand; P: phosphorous in ppm; org: percent organic content; scl: percent silt/clay.

Functional group	Equation for calculation of $\ln(p/(1-p))$	Accuracy
Aquatic	6.65 (gs) - 3.88	79%
Hutchinson's herbids	-5.58 (gs) + 4.06	78%
Hutchinson's isoetids	4.32 (gs) - 2.63	75%
Stem diameter 20-30 mm	13.2 - .34 (pH) - 1.64 (P)	74%
Stem diameter > 30 mm	3.0 (gs) + 2.5 (pH) + .30 (org) + 20.53	72%
Leaf area < 1 cm^2	-2.02 (pH) - .066 (sa) + 7.76[1]	83%
Leaf area > 100cm^2	1.76 (pH) + .19 (org) - .051 (sa) - 8.87	72%

1. Similarly high accuracy achieved using pH and scl.

TABLE 5.2. Models predicting the dominance or non dominance of a functional group (accuracy > 70 % and both sensitivity and specificity > 60%) (from Chapter 3). Variables are: pH; gs: fraction of the growing season flooded; sa: percent sand.

Functional group	Equation for calculation of $\ln(p/(1-p))$	Accuracy
Leafless	$2.78 (gs) + .047 (sa) - 5.12$	70%
Stem diameter 1-2 mm	$2.29 (gs) + 1.49 (pH) - 8.17$	70%
Stem diameter 2 -5 mm	$-1.42 (pH) + 9.7$	70%

Methods

Data

I collected data from two sites along the Ottawa River and extracted data from three documents, Gaudet (1993), Walker (1968) and le Groupe Dryade (1985). The location and nature of the data collection are summarized in Table 5.3. Details follow. It should be noted that only a few of the models could be tested with each of the data sets, as the required variables were not always the ones measured in a given study. The variables that were pertinent are indicated in the description of each data set.

Ottawa River Sites

Transect data were collected at two sites along the Ottawa River between Sept. 1 and Sept. 25, 1994. The first site was located near Luskville, Qué. (45° 31' N, 76° 6' W) This wetland included an area of herbaceous cover that extended for over 1 km along the shore and exceeded 100 m in width at some points. Large portions of this wetland were above the mean water level and thus were not flooded for most of the growing season (wet meadow). Spartina and Lythrum were abundant on these upper shores. Areas that were more frequently flooded (emergent marsh) were dominated by Eleocharis and Scirpus. The range of standing crop varied from stands of Typha and Sparganium (high biomass) to patches sparsely vegetated by Eleocharis, Cyperus or Juncus (low biomass).

TABLE 5.3. Source and nature of data for testing trait-environment relationships for herbaceous functional groups. Variable abbreviations are: gs: fraction of the growing season flooded; org: percent organic content; sa: percent sand in the soil; P phosphorous (ppm).

Source	Location and date	Sample unit	Vegetation units	Variables
Toner (field work) 1994	Ottawa River Valley 1994	transect	species (Braun-Blanquet cover scores)	gs, org, sa
Gaudet 1993	Ottawa River Valley, Ont. Axe Lake, Ont. Wilson's Lake,N.S.	quadrat (.5 m x .5 m)	species (frequency)	P, pH, org
Walker 1968	Saskatchewan aspen and prairie region	transect	dominant species	gs,org, sa
Groupe Dryade 1985	Lac St-Louis and Lac des Deux Montagnes Quebec	transect and quadrat	vegetation type	gs, sa

Previous work at this wetland includes Moore and Keddy (1989), Gaudet (1993) and Gaudet and Keddy (1995).

The second site was at Fitzroy Provincial Park (45° 28' N, 76° 14' W). Although the area of the wetland was smaller, it covered a wide range of the disturbance gradient from protected embayment to exposed shoreline. The wet meadow represented a large portion of the area and was dominated by Lythrum. The composition of the emergent marsh varied; the most abundant genera were Pontederia, Equisetum and Scirpus.

Data were collected for 11 transects, 6 at Luskville and 5 at Fitzroy Provincial Park. The locations of the transects were subjectively chosen to cover the range in standing crop and exposure. Each transect was 1 meter wide and extended from the edgeof the woods to either (i) the lower boundary of continuous vegetative cover or (ii) a water depth of 25 cm. At this depth, the transition from emergent to aquatic functional groups had usually occurred. I chose transects, rather than quadrats, as my sample unit because they provided a more complete range of elevation data, and thus, of hydrological conditions. The data available from published sources did not generally have precise measurements of either elevation or hydrology.

For each transect I collected three categories of data: elevation, soil and vegetation.

Elevation. Elevations were measured with respect to a known water level (obtained on the day of sampling, from the nearest gauge). Each transect was divided according to elevation increments of approximately 4 to 7 cm. (I had originally planned to divide the transect by 5 cm increments, but this degree of accuracy proved difficult to achieve). As well, each segment of the transect had to be at least 1 m in length, regardless of the change in elevation over that distance. The slope was usually steeper at higher elevations, and a 1 m segment frequently had elevation ranges of 8 to 10 cm. Because the segments were defined by elevation (except when 1 m long), they varied in length (1 to 17 m). For each elevation, I averaged the fraction of the growing season that it was flooded over the twelve years previous to and including the year of sampling. Elevation data are presented in Appendix 5.1.

Soil. Soil samples were collected at three points along each transect , at the highest, middle and lowest elevation. Five cores (5 cm in diameter and 3 cm in depth) were collected at each point. Samples were frozen and stored until December, 1995, when they were thawed at room temperature and subsamples were analyzed for loss on ignition and sand fractions. The loss on ignition was measured as the change in mass following combustion for 24 hours at temperatures between 430° C and 480° C. The lower range of temperatures was chosen to reduce the chances of structural changes in the soil (Black 1965).

To estimate the sand fraction of the soil, I first followed the procedure described by Day et al. (1988); that is, removal of organic content by ignition, followed by dry sieving. I found that this protocol led to overestimates of the amount of sand in my samples, due to the presence of aggregates. I therefore obtained a second estimate of the sand fraction by combining dry-sieving and decantation to remove the silt and clay fraction. I used the following protocol. First, I weighed out a subsample of approximately 1 g for each sample. I then dry-sieved with a 53µ -filter to remove some of the silt/clay. Water was added to the remaining material and aggregates were broken into particles through gentle pressure with a cork (Folk 1974). The smallest particles were removed through decantation (Folk 1974). More water was added and the last step was repeated until only a clear liquid remained when the mixture was allowed to settle for 2 to 3 seconds. The remaining material was dried and weighed, and expressed as a percentage of the original material. Because the organic content was low for most samples, it was not considered to be a large source of error. Nonetheless, the values were considered to be coarse estimates rather than precise measurements. Data for loss on ignition and percent sand in the soil are presented in Appendix 5.2.

Vegetation. I recorded all the species found in each segment of each transect and scored their abundance through the cover scale of Braun-Blanquet (Table 5.4)

Data from Gaudet.

Gaudet's (1993) data set was composed of species and soil data from 217 quadrat samples (.5 x .5 m). I used the data from wetlands in the Ottawa Valley (Luskville and Breckenridge), the Georgian Bay area of the Great Lakes (Axe Lake) and Nova Scotia (Wilson's Lake and Ellenwood Lake). I extracted the species data from the original data sheets. For each quadrat the species had been listed and their frequency recorded for 9 subdivisions of the quadrat, the highest possible score being 9/9. I omitted a quadrat if

TABLE 5.4. Method of scoring species abundance for field work: based on the Braun-Blanquet scale (Adapted from Barbour et al. 1980).

Abundance of a species within site or quadrat	Score
2 occurrences, rare	r
3 - 5 occurrences, < 5% cover, occasional	+
> 5 occurrences, < 5% cover	1
cover 5% - 25%	2
cover 25% - 50%	3
cover 50% - 75%	4
cover >75%	5

trait data were unavailable for any of its species. Substrate data were available for each quadrat. The variables that were relevant for my study were pH and phosphorous.

Data from Walker

Walker (1968) surveyed the major vegetation types of wetlands of the aspen grove region, near Saskatoon, Sask. His data set included a list of species that were dominant (frequency > 50%) in at least one stand, and the mean and range of their distribution with respect to a set of environmental variables. Three variables were pertinent to my project, the duration of flooding, soil organic content and sand fraction of the soil. However, in all three cases the variables had been scored on an ordinal scale, which I converted to estimates of real values. The duration of flooding in a stand had been scored according to the water depth as recorded for two dates (July 15 and September 1). I assumed that July 15 represented Walker's approximation of the midseason. Using this as a reference point, I extracted a coarse estimate of the fraction of the growing season flooded from his scores (Table 5.5a). Similarly, percent sand and percent organic content had been described in broad categories, based on sieving (2 mm mesh) and hand-texturing. The accuracy of this method had been verified with the Bououcos method in a preliminary study conducted the previous year. My translation of these scales are presented in Table 5.5b - c. I did not specify a percentage of organic content beyond 25%, as this was near the maximum of the range in the data set used in my original analysis (Chapter 3).

TABLE 5.5. Conversion of scales for environmental predictors The first row of scores is from Walker (1968), the second row is the conversion for this analysis.

(a) Duration of flooding

Scale from Walker	water depth >30cm, Sept.1	water depth 0cm-30cm, Sept.1	water depth >0,July 15 <0, Sept.1	water depth =0,July 15	water depth <0,July 15
Actual fraction of growing season flooded	1	.75	.50	.30	<.30

(b) Organic content

Scale from Walker	nil	very little	moderate	high	peaty
Estimated % organic content	0	<5%	>25%	>25%	>25%

(c) Sand fraction

Scale from Walker	sand	sandy loam	loam	clay loam
Estimated % sand	>90%	>70%	<40%	<20%

Because Walker had recorded only dominant species, his data were used to test the predictions for dominant functional groups. His sampling unit had been the stands that could be identified by dominant species, as opposed to the quadrats or transects of the other data sets. The tests of the rules were therefore based on the proportionof species found in the predicted environmental range for their functional group.

Finally, in addition to his description of emergent species, Walker reported the average range of the aquatic functional group, which I compared with the predicted range.

Data from le Groupe Dryade

The Groupe Dryade (1985) report described the shoreline vegetation of Lac Saint-Louis and Lac des Deux Montagnes. The authors had previously identified major vegetation types of these shores. In their 1985 report, they described the range of environmental conditions associated with the distribution of each group. These data included precise measurement of elevation (mean, maximum and minimum), as well as a subjective assessment of the degree of exposure and a broad classification of soil texture (e.g., sand, loam). I had already used some of their data in my test of the lower limit of woody cover. However, they had described the distribution of vegetation types as defined by species composition, not by traits. Only two of these matched the herbaceous functional groups defined in my study, an aquatic group and a group dominated by Lythrum salicaria (a herbid). Therefore, only two data could be extracted to test the predictions for the functional groups, the upper limit of the aquatic functional group and the lower limit of the herbid functional group. The duration of flooding was calculated for the elevation of each of these two points, and compared with the predicted limits of the corresponding functional group.

Test

The tests of the models were evaluations of the accuracy of a set of rules for some of the environmental conditions one could expect to find along the Ottawa River. They did not include statistical tests of significance and were not a thorough test of the models. However, they were expected to provide an indication of the strength of a given model.

The protocol for testing each of the ten relationships consisted of four steps. First, I generated predictions in the form of inclusion and exclusion rules. To formulate an inclusion rule, I chose the probabilities of greater than .7 as the range where the group should be present. I then identified ranges of the environmental variables that yielded these probabilities, using the equation from the logistic regression model (Tables 5.1 and 5.2). The inclusion rule was simply the prediction that the functional group would be present in this environmental range. To generate an exclusion rule, I used a probability range of less than .3 and defined the range of environmental variables that yielded these probabilities. The rules are listed in Table 5.6.

In the second step, I selected the data sets that included the appropriate environmental variables for a test of the rules.

In the third step, I identified the species from these data sets that were included in the functional group predicted by the rule. This information allowed me to identify the distribution of the functional group with respect to the variables from the test data set.

Finally, I compared these distributions with the ranges identified in the inclusion or exclusion rule. Two classes of comparisons were drawn, one for inclusion rules, one for exclusion rules. To test an inclusion rule, I counted the number of sample units (e.g., transects, quadrats) from the test data set that fell within the predicted distribution of the functional group. The accuracy was calculated as the proportion of these of sample units with representation from the functional group. In the case of exclusion rules, I counted the number of sample units from which the functional group was predicted to be absent. The accuracy in this case was the proportion of these sample units with no representation from the functional group.

An example will help clarify the steps involved. The distribution of the aquatic functional group is related to the duration of flooding. The first step is to generate inclusion and exclusion rules. Solving for the appropriate equation in Table 5.1, I find that the probability of occurrence of aquatic plants is greater than .7 when flooding lasts longer than .7 of the growing season. I also find that the probability of occurrence is less than .3 when flooding lasts less than .45 of the growing season. These are my predictive rules. To test these rules I need a data set with both hydrological and vegetation data. The data set from the Ottawa River sites fits these criteria. It includes a list of species found at different durations of flooding, recorded from 11 transects. I identify all the species in this data set that have the traits that distinguish the functional group (flexuous stem and/or floating leaves). For each transect, I identify the set of segments that have been flooded for longer than .7 of the growing season. I count the number of transects that have representation from the aquatic functional group in any of these segments. This number, divided by 11, represents the accuracy of my first prediction. Similarly, I identify the segments of each transect that were flooded for less than .45 of the growing season. I count the number of transects with no representation from the aquatic functional group in these segments. This number, divided by 11, represented the accuracy of my second prediction. I repeat this process for each of the 10 functional groups listed in Table 5.1.

In the case of one-variable models, it was not difficult to identify the range where there was a high or low probability of occurrence of a functional group. However, if a model included two or three variables, then there was more than one solution that would produce probabilities of .3 or .7. In these cases, I generated several predictions for both ranges of probabilities (>.7 and <.3) and selected the 2 or 3 that were most likely to be represented by the environmental data. Table 5.6 lists the predictions for these models, as well as for the one-variable models. (My model of the lower limit of woody plants was also based on two variables. However, I had used a different approach to test its predictions. I had solved the logistic equation for each sample point directly and compared the observed functional group with the predicted group for that probability (Chapter 4). It was not possible to follow the same procedure here because the environmental data were often an approximation or were incomplete.)

The last complication in generating testable predictions was the discrepancy in the scoring procedure for the abundance of species and for the definition of dominance. The data used to identify the relationships, from Day et al. (1988), were based on biomass. In the analysis, a functional group was dominant if it represented at least 25% of the biomass. By contrast, the test data included a range of measures, such as cover and frequency. Plants with a low biomass can still have high frequency and cover scores, so the definitions of dominance were adjusted as follows. The Ottawa River sites included cover data for species starting with cover >5%. For this data set, a functional group was considered dominant if the total cover of its member species exceeded 50% (which is consistent with Walker's definition). If no functional group met this criterion, then a functional group was dominant if the majority of species listed for a sample were from that functional group. Similarly, the data set from Gaudet (1993) included measures of frequency, based on a maximum of score of 9. A functional group was dominant if the score of any of its member species was 9, or if 3 of its species were among the 5 species with the highest frequency scores.

The data from Walker (1968) and the Groupe Dryade (1985) included only the dominant species or vegetation type, so there was no need to transform their data.

TABLE 5.6. Decision rules (inclusion and exclusion) generated from trait-environment relationships. A functional group is expected to be present (inclusion rule) if the probability calculated from the logistic equation is greater than .7 and is expected to be absent (exclusion rule) if the probability is less than .3. Note: If a model included three variables, one of the variables was assigned a fixed value, while the other two were varied. The values were chosen to reflect the range represented by the data sets used for the test. The rules do not represent a full range of predictions for the models.

Functional group	Test	Prediction
Aquatic	present	if **gs** > .70
	absent	if **gs** < .45
Herbid	present	if **gs** < .60
	absent	if **gs** > .85
Isoetid	present	if **gs** > .8
	absent	if **gs** < .45
Stem diameter 2 - 3 cm	absent	if **P** < 8 ppm
Stem diameter > 3 cm	present	if **org** = 5 % and **gs** > .9 or if **org** = 5% and **gs** > .5 and **pH** > 8
	absent	if **org** = 5% and **pH** < 6.5 or if **org** = 5% and **pH** < 7 and **gs** < .7 or if **org** = 5% and **pH** < 7.5 and **gs** < .2
Leaf area <1 cm^2	present	if **sa** > 70% and **pH** < 5.5 or if **sa** > 80% and **pH** < 6
	absent	if **sa** < 30% or if **sa** < 70% and **pH** > 6.5
Leaf area >100 cm^2	present	if **sa** = 30% and **org** > 10% or if **sa** = 70% and **org** > 20%
	absent	if **sa** = 70% and **org** < 10 and **pH** < 6
Leafless	dominant	if **sa** > 80% and **gs** > .8
	not dominant	if **sa** < 70% and **gs** < .4 or if **sa** < 90% and **gs** < .2

Stem diameter 1 - 2 mm	dominant	if gs > .4 and **pH** < 6.5 or if gs > .7 and **pH** < 6
	not dominant	if gs < .3 and **pH** > 6.5 or if gs < .6 and **pH** > 7
Stem diameter 2 - 5 mm	dominant	if **pH** < 6
	not dominant	if **pH** > 7

Results

The accuracies for the tests for each functional group are summarized in Table 5.7. Two models performed well in predicting both the presence and the absence of the corresponding functional groups; those that described the distribution of the aquatic and herbid plants. In contrast, the model describing the distribution of the isoetids failed to accurately identify where they would be absent. The sole variable in this model was the duration of flooding and the isoetids were present throughout the range of flood conditions. In the case of the functional group of species with stem diameter between 2 and 3 cm, the model was more accurate in predicting its absence than its presence. A similar result was obtained for the model describing where the plants with inconspicuous leaves would or would not be dominant.

Generally low accuracies were obtained for rules for two groups; plants with a stem diameter greater than 3 cm, and plants with a stem diameter between 2 and 5 mm. The data were not adequate to provide tests of two models, those describing the distribution of the functional group defined by leaf area < 1 cm^2 and the functional group defined by a stem diameter between 1 and 2 mm.

TABLE 5.7. Accuracy of decision rules generated from trait-environment relationships for herbaceous functional groups. Entries are the proportion of the sample units (transects, quadrats, species, vegetation types) that matched the predictions of presence/dominance (inclusion), or absence/non dominance (exclusion) of the listed functional group.

		Data set used in testing predictions					
		Toner	Gaudet	Gaudet	Gaudet	Walker	Groupe Dryade
Functional group		Ottawa Valley	Ottawa Valley	Axe Lake	N.S.		
Aquatic	present	8/11	-	-	-	1/1	0/1
	absent	9/11	-	-	-	1/1	1/1
Herbid	present	8/11	-	-	-	1/1	1/1
	absent	11/11	-	-	-	1/1	0/1
Isoetid	present	10/11	-	-	-	-	-
	absent	1/11	-	-	-	-	-
Stem diameter 2 - 3 cm	absent	-	16/20	9/12	18/18	-	-
Stem diameter > 3 cm	present	2/8	-	-	-	-	-
	absent	4/9	-	-	-	-	-
Leaf area <1 cm^2	no test	-	-	-	-	-	-
Leaf area >100 cm^2	present	0/2	-	-	-	3/3	-
	absent	-	-	-	-	1/2	-
Leafless	dominant	5/8	-	-	-	0/3	-
	not dominant	7/7	-	-	-	-	-
Stem diameter 1 - 2 mm	no test	-	-	-	-	-	-
Stem diameter 2 - 5 mm	dominant	-	7/28	1/1	5/5	-	-
	not dominant	-	0/27	-	-	-	-

I have included a description of the hydrological range of the functional groups from the Ottawa River transects (Table 5.8) In addition, I have described their range along the phosphorous and pH gradients covered by Gaudet's data. These data are provided in order to describe the extent to which the distribution of some functional groups (e.g., isoetids) did not fit the model predictions.

The other relevant data, not listed elsewhere, are the upper limit of the aquatic and the lower limit of herbid functional groups from le Groupe Dryade(1985). These points had been flooded for .94 and .88 of the growing season, respectively.

TABLE 5.8. Distribution of functional groups with respect to environmental gradients. The upper limit of flooding of the herbids and the lower limits of the aquatic, isoetid and leafless functional groups were not applicable. Abbreviations of variable are: gs: fraction of growing season flooded; P: phosphorous.

	Functional group	Variable	Range of upper limit	Range of lower limit
(A)	Aquatic	gs^1	.38 - .76	
	Herbid	gs^1		.27 - .82
	Isoetid	gs^1	.13 - .39	
	Stem diameter 2 - 3 cm	P (ppm)^2	2 - 13	19 - 25
	Stem diameter > 3 cm	gs^1	.18 - 1.0	.20 - .91
	Leaf area <1 cm^2	throughout range		
	Leaf area >100 cm^2	throughout range		
(B)	Leafless	gs^1	.27 - .53	
	Stem diameter 1 - 2 mm	gs^1	.36 - .4	.38 - .63
	Stem diameter 2 - 5 mm	pH^2	4.8 - 6.2	5.8 - 8.7

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1 duration of flooding data from Ottawa River sites (11 transects)

2 substrate data from Gaudet (1993).

3 found throughout transect

Discussion

Models and rules.

Four models yielded accurate predictions. The first two were the distribution of the (1) aquatic and (2) herbid functional groups, as a function of flooding. The others predicted the distribution of (3) plants with a stem diameter of between 2 and 3 cm, as a function of phosphorous and (4) plants with inconspicuous leaves, as a function of flooding and soil sand fraction. In the cases of the first two models, both the absence and the presence of the functional groups were predicted with accuracy. Thus, the models can be used to generate both inclusion and exclusion rules. The models for the functional groups based on leaf area and stem diameter, however, were more accurate in predicting the absence of these groups and are more appropriate for generating exclusion rules. The final set of rules are listed in Table 5.9. The distribution of three of the groups is illustrated in Figures 5.1 and 5.2. My results indicate that simple models, based on only one or two environmental variables, can accurately describe the distribution of wetland functional groups.

Table 5.9. Final list of predictive rules for herbaceous plants.

	Rules
1a	Aquatic plants will be present if the duration of flooding exceeds .70 of the growing season.
1b	Aquatic plants will be absent if the duration of flooding is less than .45 of the growing season.
2a	Herbids will be present if the duration of flooding is less than .60 of the growing season.
2b	Herbids will be absent if the duration of flooding exceeds .85 of the growing season.
3	Plants with stem diameters of 2 to 3 cm will be absent if phosphorous levels are less than 8 ppm.
4	Plants with inconspicuous leaves will not dominate if flooding lasts less than .40 of the growing season and the sand fraction in the soil is less than 70%; or if flooding lasts less than .20 of the growing season and if the sand fraction is less than 90%.

The most accurate models were those which were consistent with qualitative descriptions in the literature. An obvious example is the relationship between the aquatic functional group and hydrology (e.g., Sculthorpe 1967, Hutchinson 1975). The aquatic plants were sometimes absent from the predicted range of values, which might be explained by the absence of some measure of disturbance in the model.

The distribution of plants with a stem diameter between 2 and 3 cm is also qualitatively described in the literature. This group includes the larger wetland species, such as Typha angustifolia, that are generally absent from habitats with low nutrient levels (e.g., Grime 1979, Gaudet 1993). A third functional group, plants with inconspicuous leaves, is typically associated with areas of high mechanical disturbance from wave action. These are the "reed swamps" and the Equisetum fluviatile sociation of Spence (1964), found in habitats that are characterized by frequent flooding and a high sand fraction in the soil.

Conversely, the model describing the distribution of the isoetids was inconsistent with trends described from other studies and proved to be inaccurate in my test. Isoetids are typically found in sandy habitats (Boston and Adams 1987) and my model was based on hydrology alone. (The substrate variables had not added to the accuracy of the model in the original analysis). The failure of the model is significant because of the number of rare species that might be included in this functional group (e.g., the nationally threatened Sabatia kennedyana). However, it is not unexpected, given the absence of substrate variables in the model.

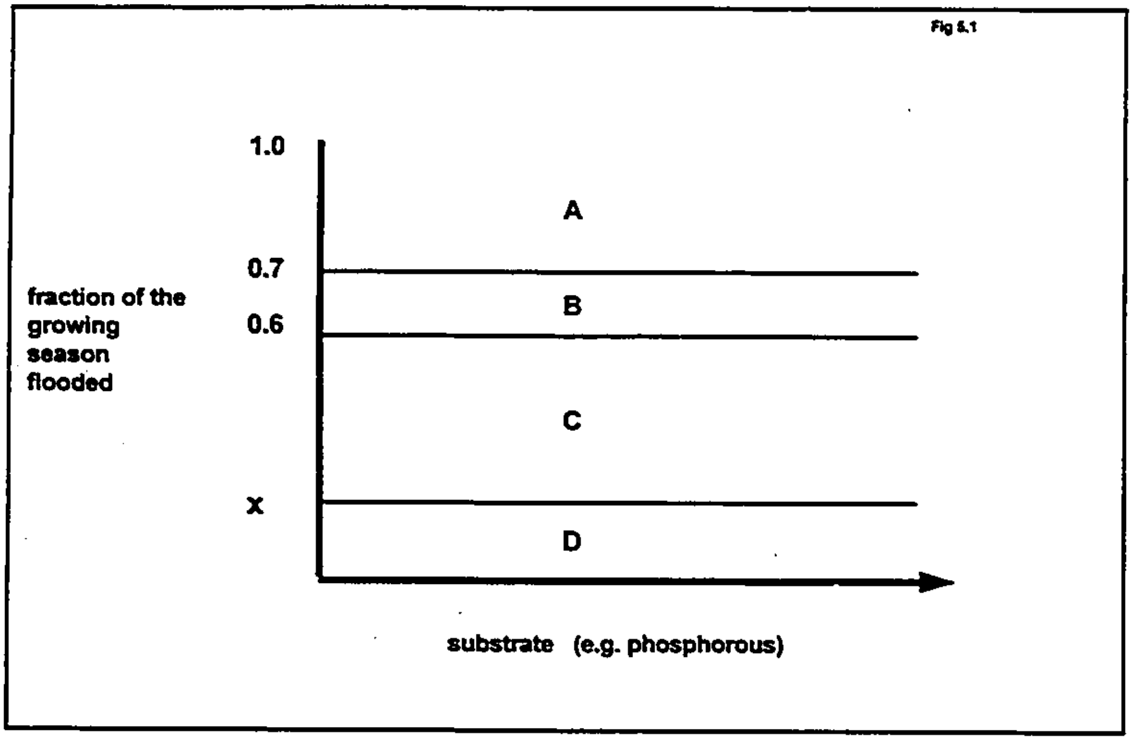

FIGURE 5.1. The distribution of 3 wetland functional groups as predicted by inclusion rules. The functional groups are present in the range of flooding where the model yields a probability of occurrence of greater than .7. Rules predict the presence of aquatic plants (zone **A**), herbids (zone **C**) and the dominance of woody plants (zone **D**). There are no predictions for zone **B**. The lower limit of woody plants (**x**) is a function of two hydrologic variables, the end of the first flood and the beginning of the second flood.

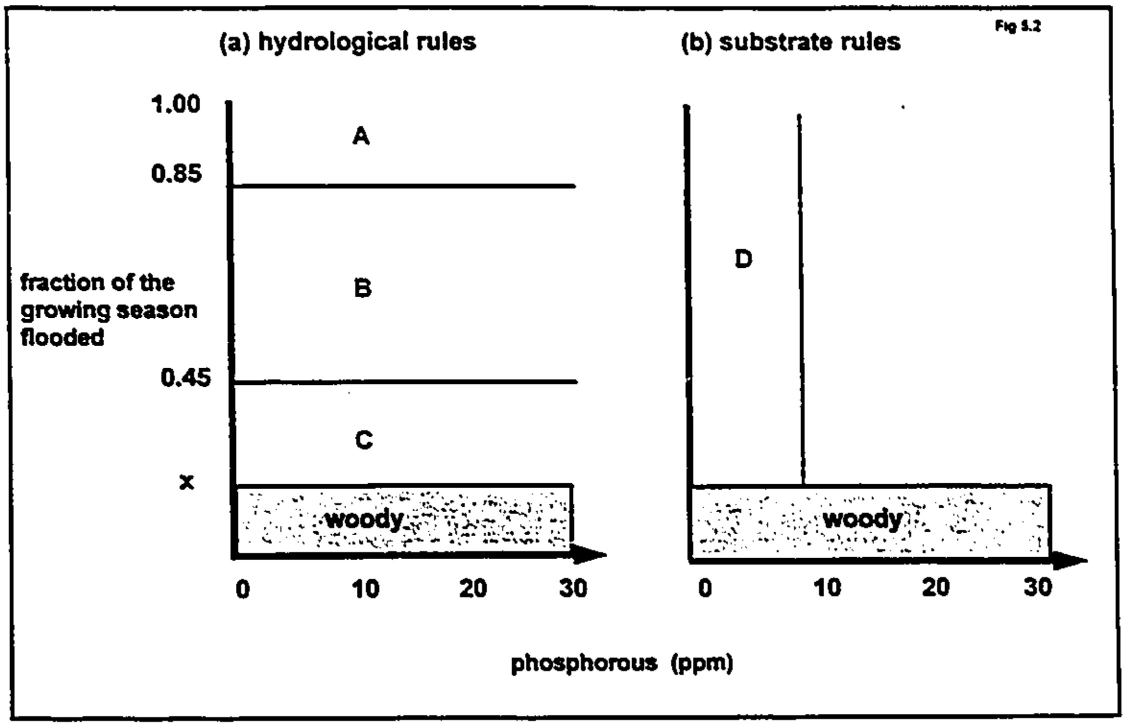

FIGURE 5.2. The distribution of 5 wetland functional groups as predicted by exclusion rules. The functional groups are absent in the range of flooding and nutrient levels where the model yields a probability of occurrence of less than .3. Rules predict the absence of herbids (zone A), aquatic plants (zone C), and plants with stem diameter between 2 and 3 cm (zone D). There are no predictions for zone B. The lower limit of woody plants (x) is a function of two hydrologic variables, the end of the first flood and the beginning of the second flood.

Other inaccurate models were those describing the dominance or distribution of functional groups defined by stem diameters of 2 to 5 mm and greater than 3 cm. The first model was based on pH. The pH gradient is a fundamental axis for defining wetland classes and their characteristic vegetation, from the low pH of bogs to the circumneutral or slightly alkaline values for marshes (National Wetlands Working Group 1988). There are obvious changes in the stature and morphology of species found in these two habitats. The inaccuracy of my rule may be due to the smaller scale of within marsh comparisons (as opposed to comparisons between classes of wetlands). However, this was one of the largest functional groups and it included widespread species, such as Spartina pectinata and Eleocharis smallii. It is therefore more likely that the result from Chapter 3 was not accurate.

The prediction for plants with stem diameters greater than 3 cm was based on the fraction of the growing season flooded. This group was found throughout the range of flood duration at the Ottawa River sites (Table 5.8). This inaccurate result is sufficient to disprove the model, despite the presence of other variables.

The poor performance of the model for the isoetids and the error for other hydrological models may be explained, in part, by the absence of variables related to disturbance. Soil organic content and sand fractions had been included in the original analysis, but had not significantly improved the models. Both of these substrate properties are affected by wave action. The mechanical impact of waves removes organic and small-grained material, such as silt and clay. The remaining substrate is coarsegrained and generally low in nutrients. However, these variables are not necessarily accurate indicators of other important forms of disturbance, such as ice scour. Therefore, their absence in the models does not mean that the effect of disturbance is insignificant. For example, the distribution of herbids fell well short of the flood tolerance of the group in some of the transects from the Ottawa River sites. It is likely that the disturbance had a role in the discrepancy, as cover was reduced in the lower segments of these transects. It is also likely that a more precise treatment of disturbance would generate accurate models for groups such as the isoetids.

Mechanism

I have generated rules that relate the distribution of plant functional groups to environmental variables. However, it is difficult to determine if these patterns are the product of abiotic factors alone. The distribution of plants with inconspicuous leaves is a case in point. The model predicts that they will be dominant only in areas with sandy substrate and frequent flooding. Their streamlined form and allocation to height allow them to survive the impact of disturbance (wave action) and stress (prolonged flooding). Their abundance is reduced at lower levels of stress and disturbance. It is not clear whether the decline is due to competitive displacement or whether the lower levels of stress and disturbance represent less favourable conditions for this functional group. The evidence from other wetland studies suggests that competition is an important factor. For example, Keddy (1989) found that the response of herbaceous plants to shrub removal varied with exposure and stress. Fewer herbaceous species invaded artificial clearings on exposed shores. In addition, the number of herbaceous species was reduced in all clearing during a season of unusually high water levels. More recently, Twolan-Strutt and Keddy (in press) documented an increase in competitive intensity from low to high biomass wetlands. These results suggest that the relative importance of competition in shoreline communities declines with stress and disturbance.

Summary, a hint of generality

One of the significant aspects of the results was the geographical range and variety of wetland classes represented by the test data. Four of the ten models that were tested performed well, in some cases with data from at least two different regions. The predictions that were related to hydrology, in particular, were consistently accurate among regions.

There were two discrepancies in the results from different regions. The first was not serious enough to dismiss the corresponding decision rules. It involved the aquatic and herbid functional groups in the data from the Groupe Dryade (1985). The aquatic functional group was absent from a range where it should have occurred. I have already discussed the role of disturbance in limiting the distribution of functional groups and this is a plausible explanation of the inaccurate result. The discrepancy between prediction and observation for the herbids is minor (the difference between .85 and .88). Error in measurement, alone, could account for the apparent discrepancy.

The second regional difference involves Walker's data, and plants with inconspicuous leaves. No species from this functional group were dominant in the predicted range (the frequently flooded, sandy habitats). The results from the Ottawa River sites were also poor, and both sample sizes were small. Thus, it is unlikely that there is a statistically significant difference in these accuracies. However, it is worth noting that the conditions where this functional group dominates in the Ottawa River system are generally characterized by frequent flooding and exposure to the mechanical disturbance of wave action. The hydrology and nature of disturbance of Prairie glacial wetlands differs greatly from that of a river, particularly a major river of the eastern temperate zone. Prairie wetlands operate on short cycles (5 to 30 years) of dramatic changes in water levels, and the dominant vegetation changes with each phase of the cycle (van der Valk and Davis 1976, National Wetland Working Group 1988). In years of drawdown conditions, pioneer species colonize the area from seed. With time and the return of higher water levels, perennial emergent species form the dominate cover. They are eventually displaced by aquatic species or open water, as they succumb to deep flooding, grazing, disease and senescence (van der Valk and Davis 1976). This rapid change in hydrology and cover makes it difficult to predict vegetation from variables that are generally averaged over time, such as the fraction of the growing season flooded. There may be a lag between the occurrence of a set of hydrological conditions and the response of the vegetation. Thus, variables that reflect rapid changes (e.g., time since drawdown, length of previous drawdown) are potentially more accurate for these systems.

It is also worth noting the differences in the nature of disturbance between our rivers and prairie systems. The wave action of a large river is simply absent in small bodies of water. Thus, it is difficult to predict the distribution of a functional group adapted to frequent flooding and mechanical disturbance in such a system. This indicates that the differences in disturbance regimes across wetland classes will limit the generality of some rules. It is reasonable to expect that some calibration of these models will be required to accommodate these differences.

The difficulty in quantifying the impact of disturbance need not be an obstacle to predicting wetland vegetation. No doubt, one of the problems lies in the number of forms of disturbance (e.g., grazing, ice scour, wave action, infestation) and the single events that can occur. However, there are strategies for measuring disturbance, despite its complexity. For example, Johnson (1994) incorporated an index of ice scour in a linear regression model describing seedling mortality. Effective solutions may involve tracking major events such as unusually high floods or ice flows. Ironically, these are the events whose impacts we often try to mitigate, through flood control and river regulation. We should be able to predict the role of these events in maintaining wetland diversity, given the amount of time and energy that we have spent trying to eliminate them. In the interim, I offer these predictive models of hydrology, and to a lesser extent, substrate, as the foundation for this future work.

CHAPTER SIX

CONCLUSION

FIVE PREDICTIVE MODELS

General trends

The investigation of trait-environment relationships represents an efficient avenue of research in systems where there are steep abiotic gradients and large species pools. I have used this approach to develop quantitative models that describe the distribution or dominance of five functional groups in riverine wetlands (Table 6.1). The functional groups are all defined by simple traits: woody or not woody; presence or absence of flexuous stems and/or floating leaves; emergent leaves with lanceolate, elliptical or ovate shape; a stem diameter between 2 and 3 cm; or inconspicuous leaves. I have generated a set of testable predictions from the models. Where those predictions proved to be accurate, they have been incorporated into inclusion or exclusion rules for the corresponding functional groups (Table 6.1). The rules describe some of the functional groups that are likely to be present or absent (dominant or not dominant) at specific ranges of environmental variables of a given wetland. As such, they provide quantitative guidelines for wetland management.

The advantages of my approach have been the simplicity and generality of the results. The models, or rules, quantify relationships between one or two environmental variables and a functional group. The strongest relationships were accurate among sites along the Ottawa River and, in some cases, among regions as well.

The final list of rules reflects three trends. First, the most accurate models were quantifications of relationships already qualitatively described in the literature. For example, the delineation of woody cover by hydrology is assumed in the general descriptions of shoreline vegetation (e.g., Nilsson 1992) and the distribution of aquatic

TABLE 6.1. Functional groups for which accurate decision rules were generated and the nature of the rules.

	Functional group	Rules
Present/absent	Aquatic	inclusion and exclusion
	Herbid	inclusion and exclusion
	Stem diameter 2 - 3 cm.	exclusion
Dominant/not dominant	Woody	exclusion
	Leaf area = 0	exclusion

species is, by definition, related to hydrology. While my findings may seem trivial at first glance, they represent one of the few cases of testable, quantitative predictions.

Second, predictions of the absence (or non dominance) of a functional group were generally more accurate than predictions of its presence (or dominance). There are many conditions that can eliminate a functional group (e.g. flood, ice scour), and only one need occur in order for the group to be absent. Conversely, there may be several requirements for the survival of a functional group. Thus, generating accurate inclusion rules could well involve more complex models than the one- and two- variable models that I have described.

Finally, the highest accuracy was achieved where hydrology appeared to be paramount. It was, in fact, difficult to detect and incorporate the significance of substrate or disturbance, despite its prominence in the literature. This failing is particularly significant for functional groups that are likely to include rare species and it identifies an area of research that requires new and innovative methodology.

Significance: predictive rules.

"The goal of biology, ecology, or any science is prediction." (Peters 1980). Yet the history of predictive rules in ecology has been fraught with controversy. Diamond (1975) proposed a set of assembly rules for the avian community of a New Guinea archipelago. His interpretation of incidence functions was roundly criticized (Connor and

Simberloff 1979) and led to a prolonged discussion of choice of null models. A more recent controversy involved an exchange between Wilson (1995) and Fox and Brown (1995) over the appropriate interpretation and testing of an assembly rule for communities of small mammals.

Attention to statistical rigour is important for any science. However, it can detract from the more basic question of, "What is our goal?" If our goal is to detect pattern, then a thorough examination of the various constraints and possibilities for null models is essential. In contrast, if our goal is prediction, then we will choose a statistical method that will generate prediction (e.g., regression models) and our test will be the accuracy of the output (e.g., rules, equations). Our discussion will not revolve around null models. Rather, it will tend to questions such as, "What is predictable?" (Rigler 1982) and "What would be a valid manner of operationalizing a given factor?"

The goal of my research is prediction. I have demonstrated that the distribution of some plant functional groups can be predicted from quantitative rules. My results are certainly not a final word on riparian functional groups. They do, however, provide a counter-weight to the current controversy and pessimism over our ability to generate predictive rules.

Significance: plant ecology

The concepts and tools of plant community ecology reflect the extent to which we relate the organization of vegetation to gradients. Most of our models, questions and statistical repertoire bear the imprint of gradient analysis. For example, Grime's (1977) model of community organization compresses the variation in plant form and function into two gradients, stress and disturbance. In addition, theoretical questions are often discussed and analyzed in the context of gradients. An example raised in an earlier discussion (Chapter 5) involved the relative importance of competition along exposure gradients. Finally, a succession of statistical techniques have related community composition to environmental gradients (polar ordination, Bray and Curtis 1957; reciprocal averaging, Hill 1973; CCA).

My analysis was based on two kinds of gradients, flooding (e.g., duration, time) and components of the substrate (e.g., percent sand, organic content). Ironically, one of the weaknesses of my approach is related to my emphasis on gradients. My choice of independent variables failed to account for the impact of environmental fluctuations and single events. Moreover, I averaged the hydrological variables, specifically to reduce the impact of single events. This was an effective strategy for the prediction of the limits of woody plants, as a significant response usually requires a prolonged flood event (e.g., dieback after 3 years of high water, Jaworski et al. (1979). However, the limitation of my approach was apparent in my comparison of riparian and prairie glacial wetlands.

The effects of some events are impossible to ignore (e.g., fire, hurricane) and may represent essential elements of the successional cycle (fire in a boreal forest). Less dramatic events can also have a major impact on an ecosystem. For example, drawdowns in prairie marshes provide opportunities for regeneration of species. These apparently innocuous events can significantly alter community composition (van der Valk and Davis

1976). These single events are analogous to the "ecological crunches" described by Wiens (1977). His discussion was in the context of competition and resource availability. Nonetheless, his caution against ignoring environmental fluctuation and single events is pertinent to the study of riparian systems. Where single events have significant impacts, it is necessary to choose variables that incorporate the time and magnitude of effect.

Significance: conservation ecology

> Yet will I stay my steps and not go down to the marshland,-
> Muse and recall far off, rather remember than see, -
> Lest on too close sight I miss the darling illusion,
> Spy at their task even here the hands of chance or change.
>
> Charles G.D. Roberts. 1883. From Tantramar Revisited.

Throughout my project I have emphasized three elements that are particularly related to conservation ecology. First, I have reiterated the question of what is and what is not likely to be predictable. I have addressed this question by generating predictions and testing their accuracy. The issue of moving from description to prediction may seem trivial. However, most wetland studies fall short of this step. Multivariate analysis (DCA, CCA) are regularly used to identify significant gradients or explain variability (e.g., Jean and Bouchard. 1993). This work is important in laying the foundation for prediction. However, much of this descriptive work has been done and we are now in a position to generate testable predictions.

The second element related to conservation ecology is the list of predictive rules. These are potential management tools for the protection of the three fundamental units of riparian vegetation, the woody, emergent and aquatic functional groups. The additional rules, related to leaf area and stem diameter, indicate that we have not exhausted the possibilities for prediction of riparian vegetation.

Finally, I have emphasized simple, untransformed predictors. This may be particularly important in the case of wetland restoration or creation, where the starting point may be a bare or terrestrial ecosystem. For example, restricting flooding to less than 60% of the growing season will favour herbid rather than aquatic plants. Complex models make an already daunting task even more difficult. Most wetland restoration work has involved ponds or estuarine systems. There has been markedly less effort to restore riparian wetlands (Mitsch and Gosselink 1986). Simple predictive models may make the proposition more attractive.

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Appendix 2.1. Calculation of effective fetch and peak flow and drainage variables.

Although site selection was designed to minimize the effect of disturbance, we decided to test for effects of exposure to waves or destructive floods by calculating three additional variables for each of the study sites: (1) effective fetch, (2) effective fetch multiplied by average wind speeds and frequencies and (3) peak flow. A fourth variable, soil drainage, was also included. Details for these four calculations follow.

(1) To measure effective fetch the shoreline of each site was divided into 3 sections. For each section, the distances of open water were measured for 16 directions, each separated by 22.5°, starting with North. Distances for five of the sites were measured from maps at a scale of 1:20000 (Ontario Ministry of Natural Resources and Environment Canada 1990). A topographical map (1:25000) (Gouvernement du Quebec, Ministere de l'Energie et des Ressources, Service de la Cartographie 1983) was used for the site at Westmeath.

The effective fetch (F_E) for each of the sixteen directions was determined through a modified version of the formula described by the U.S. Army Coastal Engineering Research Centre (Anonymous 1977) and used by Keddy (1984).

$$F_E = [F(\alpha) \cos \alpha + F(\alpha + 22.5) \cos (\alpha + 22.5) + F(\alpha - 22.5) \cos(\alpha - 22.5)] \div [\cos \alpha + 2\cos(\alpha + 22.5)]$$

where α is set to 0 for each F_E calculated. These values were then averaged over the sixteen directions for each portion of shoreline.

(2) For a second measure of fetch the distances in (1) were multiplied by wind speed and percent frequency before using the formula for effective fetch. Wind speeds from May, June and July were averaged over 6 years (1984- 1986 and 1988 - 1990) using records from the weather stations mentioned previously. These three months were chosen to coincide with the high water levels of spring and early summer, when wave damage in the wet meadow and wooded wetland would have been more likely to occur. The year 1987 and previous years were omitted because of incomplete data.

(3) Peak flow was calculated by dividing the maximum discharge that occurred during the growing season for each of the four intervals by the river width. This variable was intended as an indicator of catastrophic events.

(4) Finally, sites were ranked according to drainage based on soil types read from geological maps (Department of Chemistry, Ontario Agricultural College, and Experimental Farm Services, Dominion Department of Agriculture 1962, Research Branch, Canada Department of Agriculture 1962 and 1967, Soil Research Institute 1964, Ontario Institute of Pedology 1982,). Rankings included four categories, very good, good, imperfect and poor drainage.

Appendix 2.2 Interpretation of logistic regression and comparison of models.

The presence or absence of a functional group is a binary dependent variable. Thus, the appropriate tool of analysis is a logistic regression. Using the LOGISTIC procedure (SAS 1994), I tested the relationship between the presence/absence of each functional group and all possible combinations of the independent variables. The performance of the models were compared on the basis of the Akaike Information Criterion (AIC). This is a variation of the log likelihood ratio that accounts for differences in the number of independent variables, as well as the number of levels of response. (The number of levels of response were two throughout the project, e.g., presence or absence.). The formula is

$$\mathrm{AIC} = -2\,LogL + 2\,(k + s)$$

where k is the number of ordered values for the dependent variable and s is the number of independent variables. The lower the AIC score, the better the model (Hosmer and Lemeshow 1989, SAS Institute 1990). The logic behind this is not obvious and some explanation is appropriate. The description that follows is taken from Hosmer and Lemeshow (1989).

The two levels of response of a binary dependent variable are 1 and 0. The probability that the response will be 1 is ¶, and the probability that a response will be 0 is (1 - ¶). The LOGISTIC procedure fits a logistic model to the data through a series of iterations that maximize the **likelihood function.** The likelihood function, l(B),is the product of each data point (x_i, y_i) multiplied by the probability assigned by the logistic function.

$$l(\mathbf{B}) = \Pi\ \varsigma\,(x_i)$$

Thus, if $y_i = 1$, then the term for that point in the likelihood function will be the value for ¶ at x_i, as calculated from the logistic equation. If yi = 0, then the term will be (¶ - 1) at x_i. The actual calculations are usually done using the log of the likelihood function or the **log likelihood.**

$$\mathbf{L(B) = ln\ [\ \mathit{l}\ (B)] = \Sigma\ \{y_i\ ln\ [\P\ (\mathit{x_i})] + (\ 1 - \mathit{y_i}\ )\ ln\ [1 - \P(\ \mathit{x_i})]\}}$$

From this equation we can see that the log likelihood will be greater if ¶ is large where $y_i = 1$, and low where $y_i = 0$. Thus, the better model will assign high probabilities to the points where $y_i = 1$ and low probabilities to the points where $y_i = 0$.

However, the deviance for the model is actually calculated from the **likelihood ratio.**

Deviance = - 2 ln [likelihood of the current model/ likelihood of the saturated model]

As the log likelihood increases, the likelihood ratio approaches 1, but the value for the deviance decreases. It is the deviance which forms the basis for the AIC score. Thus, the lower the AIC score, the better the model.

On a final note, the significance of an independent variable is calculated by comparing the deviance of the model without the variable and with the variable.

G = (Deviance of the model without the variable)
- (Deviance of the model with the variable)

This statistic follows a Chi-square distribution.

Appendix 2.3. Matrix of Pearson product moment correlations of hydrological variables for three intervals, the 3 **(a)**, 7 **(b)** and 18 **(c)** years previous to the collection of field data. Probability values are in parenthesis, unless <.001 (***), <.01 (**) or <.05 (*). N=222.

a. 3 year interval data.

Variable		Pearson product moment coefficients						
		gs	eff	lsec	md	nf	tbf	bsec
fraction of the growing season flooded	gs	1.00						
end of first flood	eff	.97	1.00					
		***						
length of second flood	lsec	.31	.36	1.00				
		***	***					
mean depth of flooding	md	.037	.027	.026	1.00			
		(.58)	(.68)	(.70)				
number of floods	nf	.67	.57	.12	-.058	1.00		
		***	***	(.066)	(.39)			
lag before midseason flood	tbf	.19	.15	.014	.19	-.19	1.00	
		**	*	(.84)	**	**		
beginning of second flood	bsec	.60	.60	.18	.013	.47	-.085	1.00
		***	***	**	(.84)	***	(.20)	

b. 7 year interval data.

Variable		Pearson product moment coefficients						
		gs	eff	lsec	md	nf	tbf	bsec
fraction of the growing season flooded	gs	1.00						
end of first flood	eff	.86 ***	1.00					
length of second flood	lsec	.52 ***	.48 ***	1.00				
mean depth of flooding	md	.51 ***	.63 ***	.13 (.054)	1.00			
number of floods	nf	.65 ***	.51 ***	.35 ***	.19 **	1.00		
lag before midseason flood	tbf	-.14 (.038)	-.30 ***	-.10 (.13)	-.32 ***	-.26 ***	1.00	
beginning of second flood	bsec	.55 ***	.67 ***	.060 (.37)	.48 ***	.20 **	-.20 **	1.00

c. 18 year interval data.

Variable	Pearson product moment coefficients							
		gs	eff	lsec	md	nf	tbf	bsec
fraction of the growing season flooded	gs	1.00						
end of first flood	eff	.82 ***	1.00					
length of second flood	lsec	-.64 ***	-.70 ***	1.00				
mean depth of flooding	md	.13 (.054)	.46 ***	-.39 ***	1.00			
number of floods	nf	.58 ***	.61 ***	-.61 ***	.34 ***	1.00		
lag before midseason flood	tbf	-.16 *	-.29 ***	.21 **	-.23 ***	-.34 ***	1.00	
beginning of second flood	bsec	.66 ***	.75 ***	-.55 ***	.30 ***	.42 ***	-.36 ***	1.00

Appendix 2.4. Elevation of points derived from lower boundary of woody cover (+5 cm, -5 cm) and values for hydrological variables averaged over the twelve growing seasons previous to the collection of data (1981 - 1992). Trait values: 1: woody cover; 0: herbacoues cover. Sites are: 1: Andrew Hayden Park; 2: Breckenridge; 3: Fitzroy Provincial Park; 4: Lucerne Boulevard; 5: Masson; 6: Westmeath Provincial Park. Elevations are with respect to the Survey of Canada Geodetic Datum.

Site	Elevation of point	Trait	Fraction of growing season flooded	Mean depth of flooding (m)	End of first flood (days)	Number of floods	Begining of second flood (days)	Lag before midseason flood (days)	Length of second flood (days)
1	58.14	1	0.38	0.55	60.75	2.67	99.73	8.45	40
1	58.18	1	0.35	0.54	58.33	2.67	102	8.9	41
1	58.18	1	0.35	0.54	58.33	2.67	102	8.9	41
1	58.19	1	0.35	0.54	57.17	2.75	97.5	7.7	23
1	58.2	1	0.34	0.53	56.92	2.58	96.55	7.27	23.5
1	58.21	1	0.34	0.53	56.75	2.67	98.2	7.5	23.5
1	58.21	1	0.34	0.53	56.75	2.67	98.2	7.5	23.5
1	58.22	1	0.33	0.53	56.58	2.5	100.2	7	24
1	58.22	1	0.33	0.53	56.58	2.5	100.2	7	24
1	58.23	1	0.33	0.53	56.58	2.58	100.4	6.6	24.5
1	58.26	1	0.32	0.52	55.25	2.33	114.11	5.33	27.5
1	58.26	1	0.32	0.52	55.25	2.33	114.11	5.33	27.5
1	58.26	1	0.32	0.52	55.25	2.33	114.11	5.33	27.5
1	58.26	1	0.32	0.52	55.25	2.33	114.11	5.33	27.5
1	58.26	1	0.32	0.52	55.25	2.33	114.11	5.33	27.5
1	58.26	1	0.32	0.52	55.25	2.33	114.11	5.33	27.5
1	58.26	1	0.32	0.52	55.25	2.33	114.11	5.33	27.5
1	58.36	1	0.28	0.48	50.58	1.92	94.67	12.5	31
1	58.41	1	0.26	0.46	42.42	1.83	91	15.67	56
2	58.13	1	0.41	0.51	63.58	3.17	89	7.1	7
2	58.18	1	0.38	0.5	60.75	2.75	98.45	7.73	21
2	58.2	1	0.37	0.49	59.42	2.42	104.44	11.44	21.5
2	58.22	1	0.35	0.49	58.33	2.58	101.8	8.6	22.5
2	58.23	1	0.35	0.49	57.17	2.75	106.5	7.7	23
2	58.23	1	0.35	0.49	57.17	2.75	106.5	7.7	23
2	58.24	1	0.34	0.48	56.92	2.75	95.55	7.27	5
2	58.24	1	0.34	0.48	56.92	2.67	95.55	7.27	5
2	58.25	1	0.34	0.48	56.75	2.58	97.3	6.6	23.5
2	58.26	1	0.33	0.48	56.58	2.42	97.5	6.7	24.5
2	58.27	1	0.32	0.48	55.75	2.5	99.56	6.44	24.5
2	58.27	1	0.32	0.48	55.75	2.5	99.56	6.44	24.5
2	58.3	1	0.31	0.47	55.08	2.33	113.11	5.33	26.5
2	58.3	1	0.31	0.47	55.08	2.33	113.11	5.33	26.5
2	58.32	1	0.31	0.46	52.75	2	119.88	8.75	27
2	58.32	1	0.31	0.46	52.75	2	119.88	8.75	27
2	58.32	1	0.31	0.46	52.75	2	119.88	8.75	27

2	58.35	1	0.29	0.45	47.17	2	111.86	13.71	27.5
2	58.38	1	0.28	0.44	46.42	1.92	110.33	12	32.5
2	58.4	1	0.27	0.43	45.83	1.75	103.4	12.4	56
2	58.43	1	0.26	0.41	42.33	1.83	90	15.67	56
3	58.215	1	0.09	0.59	54.67	2.58	95.1	2.8	46
3	58.245	1	0.08	0.58	52.17	2.33	94.89	5.33	26.5
3	58.34	1	0.07	0.55	43.42	2.08	89.71	15.57	32.5
3	58.365	1	0.07	0.53	43.42	1.92	92	17.5	29.5
3	58.37	1	0.07	0.53	43.42	1.82	92	17.5	30
3	58.485	1	0.07	0.43	39.67	1.75	78.2	11.6	36.5
3	58.49	1	0.07	0.43	39.58	1.75	78.2	11.8	39
3	58.51	1	0.07	0.41	39.25	1.67	79.2	10.4	61
3	58.55	1	0.06	0.43	32.42	2.17	59.71	8	63
3	58.6	1	0.05	0.42	28.08	2.17	59.88	14.38	65
3	58.615	1	0.05	0.43	22.58	2.33	37	17.89	66
3	58.65	1	0.05	0.43	21.92	2.42	37	12.33	66
3	58.67	1	0.04	0.44	21.17	2.08	37.5	17.63	66
3	58.71	1	0.04	0.43	25.42	1.83	40.86	11.86	66
3	58.76	1	0.04	0.39	24.17	1.75	43.13	10.88	68
3	58.795	1	0.04	0.37	22.5	1.67	34.29	12.57	0
3	58.83	1	0.04	0.34	21.75	1.67	34.43	12.43	0
4	57.97	1	0.58	0.47	85.17	3.75	110.58	9.67	16.5
4	58.01	1	0.52	0.47	75.17	3.42	100.92	8.25	20.43
4	58.07	1	0.47	0.47	68.5	3	92.56	15.11	27
4	58.1	1	0.43	0.48	66.33	2.92	101	8.89	14.33
4	58.1	1	0.43	0.48	66.33	2.92	101	8.89	14.33
4	58.13	1	0.4	0.48	63.58	2.92	90.9	6.5	12.5
4	58.15	1	0.39	0.48	62.75	2.67	100.9	8	18
4	58.16	1	0.38	0.47	62	2.67	95.3	5.7	20.5
4	58.2	1	0.36	0.46	59.08	2.67	103.44	10	21.5
4	58.21	1	0.35	0.46	58.33	2.67	101	8.8	22.5
4	58.21	1	0.35	0.46	58.33	2.67	101	8.8	22.5
4	58.25	1	0.33	0.45	56.67	2.5	97.5	6.9	5
4	58.27	1	0.32	0.45	55.33	2.33	113.11	5.33	27.5
4	58.27	1	0.32	0.45	55.33	2.33	113.11	5.33	27.5
4	58.29	1	0.31	0.44	55.08	2	125.13	7.25	30
4	58.31	1	0.3	0.43	52.58	2	120.25	8.63	28
4	58.32	1	0.3	0.42	52.33	2	120.38	7.88	36
4	58.35	1	0.28	0.42	46.5	2.17	103.14	10.71	32.5
4	58.37	1	0.27	0.41	46.08	1.83	111	10.67	56
5	41.44	1	0.28	0.29	41.08	2.75	98.11	10.44	13
5	41.455	1	0.27	0.28	40.67	2.67	91	13.8	0
5	41.46	1	0.27	0.28	36	2.5	91	13.9	35
5	41.47	1	0.26	0.28	35.83	2.58	91.3	13.4	35
5	41.48	1	0.25	0.27	35.25	2.58	91.6	12.4	0
5	41.505	1	0.24	0.26	31.75	2.5	78.78	7.78	62
5	41.505	1	0.24	0.26	31.75	2.5	78.78	7.78	62
5	41.535	1	0.22	0.26	30	2.5	70.63	8.13	62
5	41.535	1	0.22	0.26	30	2.5	70.63	8.13	62
5	41.54	1	0.22	0.26	29.92	2.42	98.11	7.38	57
5	41.54	1	0.22	0.26	29.92	2.42	98.11	7.38	57
5	41.55	1	0.21	0.26	29.5	2.25	71.25	7.25	63
5	41.55	1	0.21	0.26	29.5	2.25	71.25	7.25	63
5	41.555	1	0.21	0.26	25.17	2.42	59.9	10.3	63

5	41.56	1	0.2	0.25	24.42	2.5	56.82	9.91	63
5	41.58	1	0.19	0.25	23.75	2.58	61.6	9.5	65
5	41.59	1	0.19	0.24	22.92	2.58	35.67	9.89	67
5	41.6	1	0.18	0.24	22.83	2.42	36.11	9.22	68
5	41.69	1	0.12	0.24	14	2.83	20.2	9.7	0
6	1.918	1	0.22	0.51	24.67	2.67	48.75	18.63	14.5
6	1.933	1	0.22	0.51	24.42	2.67	48.75	18.5	15.5
6	1.978	1	0.2	0.52	23.5	2.33	51.88	13.6	67
6	1.988	1	0.19	0.52	23.25	2.33	51.88	15.25	64
6	2.008	1	0.18	0.53	23.08	2.17	52.13	13.88	64
6	2.008	1	0.18	0.53	23.08	2.17	52.13	13.88	64
6	2.018	1	0.18	0.53	22.83	2.08	52.25	13.5	64
6	2.038	1	0.17	0.53	17.92	2	47.67	17.89	64
6	2.038	1	0.17	0.53	17.92	2	47.67	17.89	64
6	2.068	1	0.16	0.54	17.42	2	48.11	16.56	65
6	2.083	1	0.16	0.54	17.33	1.83	34.5	17.88	65
6	2.133	1	0.14	0.53	15.5	1.83	31.89	16.33	65
6	2.148	1	0.14	0.53	17.67	1.83	34.56	13.44	66
6	2.153	1	0.14	0.53	17.67	1.83	34.67	10.67	66
6	2.238	1	0.12	0.53	16.92	1.58	39.43	13	68
6	2.243	1	0.12	0.53	16.92	1.67	39.43	13	68
1	58.14	0	0.44	0.56	66	2.75	76.25	7.78	14
1	58.18	0	0.41	0.56	63.75	2.92	75.5	6.8	6
1	58.18	0	0.41	0.56	63.75	2.92	75.5	6.8	6
1	58.19	0	0.4	0.56	63.5	3	76.58	6.1	7.33
1	58.2	0	0.4	0.56	63.42	3	76.67	5.8	8.5
1	58.21	0	0.39	0.56	62.58	2.67	84.42	8.1	21
1	58.21	0	0.39	0.56	62.58	2.67	84.42	8.1	21
1	58.22	0	0.38	0.56	62	2.58	82.75	7.8	41
1	58.22	0	0.38	0.56	62	2.58	82.75	7.8	41
1	58.23	0	0.38	0.55	60.75	2.67	92.5	8.09	41
1	58.26	0	0.36	0.54	59.33	2.5	78.5	11	23
1	58.26	0	0.36	0.54	59.33	2.5	78.5	11	23
1	58.26	0	0.36	0.54	59.33	2.5	78.5	11	23
1	58.26	0	0.36	0.54	59.33	2.5	78.5	11	23
1	58.26	0	0.36	0.54	59.33	2.5	78.5	11	23
1	58.26	0	0.36	0.54	59.33	2.5	78.5	11	23
1	58.26	0	0.36	0.54	59.33	2.5	78.5	11	23
1	58.36	0	0.32	0.52	55.25	2.33	85.58	5.33	27.5
1	58.41	0	0.3	0.5	52.33	2	80.92	7.88	31
2	58.13	0	0.5	0.5	70.42	3.17	91.67	12.78	12.33
2	58.18	0	0.45	0.5	68.08	3.08	78.33	11.67	13.33
2	58.2	0	0.43	0.5	66.42	3	74	7.33	14.33
2	58.22	0	0.42	0.51	64.67	2.5	77.67	11.78	6.5
2	58.23	0	0.41	0.51	63.58	3.17	74.17	7.1	7
2	58.23	0	0.41	0.51	63.58	3.17	74.17	7.1	7
2	58.24	0	0.4	0.5	63.5	3.08	75.75	6.1	7.33
2	58.24	0	0.4	0.5	63.5	3.08	75.75	6.1	7.33
2	58.25	0	0.39	0.51	63	2.83	80.75	15.6	21
2	58.26	0	0.39	0.51	62.5	2.75	79.5	5.9	20
2	58.27	0	0.38	0.5	60.75	2.75	87.25	6.36	14.33
2	58.27	0	0.38	0.5	60.75	2.75	87.25	6.36	14.33
2	58.3	0	0.37	0.49	59.42	2.42	78.33	11.44	21.5
2	58.3	0	0.37	0.49	59.42	2.42	78.33	11.44	21.5

2	58.32	0	0.35	0.49	58.33	2.58	84.83	8.6	22.5
2	58.32	0	0.35	0.49	58.33	2.58	84.83	8.6	22.5
2	58.32	0	0.35	0.49	58.33	2.58	84.83	8.6	22.5
2	58.35	0	0.34	0.48	56.75	2.58	81.08	6.6	23.5
2	58.38	0	0.32	0.48	58	2.5	74.83	4.6	26.5
2	58.4	0	0.31	0.47	55.08	2.33	84.83	5.33	26.5
2	58.43	0	0.3	0.45	55	2	80.17	8.38	28
3	58.215	0	0.1	0.62	58.58	3.17	68.33	4.7	7
3	58.245	0	0.09	0.62	57.75	2.75	74.08	6.9	21.5
3	58.34	0	0.08	0.58	52.25	2.42	71.08	5.44	26.5
3	58.365	0	0.08	0.56	47.58	2.42	62.42	10.75	26.5
3	58.37	0	0.08	0.55	47.33	2.58	62.42	10.75	27
3	58.485	0	0.07	0.51	41.67	2.25	39.92	11	32.5
3	58.49	0	0.07	0.51	41.67	2.08	39.92	11	32.5
3	58.51	0	0.07	0.49	40.75	2.08	40	10.83	32.5
3	58.55	0	0.07	0.46	40.5	1.92	27.42	11.6	63
3	58.6	0	0.07	0.42	39.25	1.67	32.92	10.6	61
3	58.615	0	0.07	0.41	35.67	2	35.42	15.5	62
3	58.65	0	0.06	0.43	32.42	2.17	34.83	8	63
3	58.67	0	0.06	0.42	33.33	1.92	35.58	10.67	65
3	58.71	0	0.05	0.42	23.75	2.33	41.25	17.44	66
3	58.76	0	0.05	0.44	21.75	2.17	25	18.25	66
3	58.795	0	0.04	0.43	20.58	2.08	24.5	10.88	66
3	58.83	0	0.04	0.42	25.17	1.83	24	11.43	67
4	57.97	0	0.73	0.46	114.58	2.5	118.92	19.82	20.33
4	58.01	0	0.68	0.46	99.25	3.25	108.83	7.45	15
4	58.07	0	0.58	0.47	85.17	3	110.58	9.67	16.5
4	58.1	0	0.54	0.47	79.08	3.5	96.67	8	19.14
4	58.1	0	0.54	0.47	79.08	3.5	96.67	8	19.14
4	58.13	0	0.5	0.48	70.42	3	83.33	6.5	26.25
4	58.15	0	0.48	0.47	69.58	3.08	64.17	11.5	21.4
4	58.16	0	0.47	0.47	69	2.83	61.17	17.5	27
4	58.2	0	0.43	0.48	66.33	2.92	75.75	8.89	14.33
4	58.21	0	0.42	0.47	65.25	3.25	79.5	8.67	8.67
4	58.21	0	0.42	0.47	65.25	3.25	79.5	8.67	8.67
4	58.25	0	0.39	0.48	62.75	2.67	84.08	8	18
4	58.27	0	0.38	0.47	60.75	2.67	90.25	7.82	14.67
4	58.27	0	0.38	0.47	60.75	2.67	90.25	7.82	14.67
4	58.29	0	0.37	0.46	59	2.5	77.67	11.78	21.5
4	58.31	0	0.35	0.46	58.33	2.67	84.17	8.8	22.5
4	58.32	0	0.35	0.46	57.25	2.75	88.92	7.3	23.5
4	58.35	0	0.33	0.45	56.33	2.5	81.25	6.9	5
4	58.37	0	0.32	0.45	55.25	2.33	84.83	5.33	27.5
5	41.44	0	0.37	0.31	58	4	86.42	4.33	23.33
5	41.455	0	0.35	0.31	56	3.25	66.5	3.9	35
5	41.46	0	0.35	0.31	55.83	3.08	66.5	3.7	39.67
5	41.47	0	0.34	0.3	55.75	2.75	80.17	5	29
5	41.48	0	0.33	0.3	55.33	2.5	86.08	7.89	29
5	41.505	0	0.31	0.29	48.33	2.25	76.42	16.5	30
5	41.505	0	0.31	0.29	48.33	2.25	76.42	16.5	30
5	41.535	0	0.29	0.28	41.25	2.58	62.75	17.44	33.5
5	41.535	0	0.29	0.28	41.25	2.58	62.75	17.44	33.5
5	41.54	0	0.28	0.29	41.08	2.75	73.58	10.44	33.5
5	41.54	0	0.28	0.29	41.08	2.75	73.58	10.44	33.5

5	41.55	0	0.28	0.28	41	2.5	74.42	11.44	33.5
5	41.55	0	0.28	0.28	41	2.5	74.42	11.44	33.5
5	41.555	0	0.27	0.28	36	2.67	75.83	13.8	0
5	41.56	0	0.27	0.28	36	2.5	75.83	13.9	35
5	41.58	0	0.25	0.27	35.25	2.58	76.33	12.4	0
5	41.59	0	0.25	0.27	34.75	2.58	76.42	11	62
5	41.6	0	0.24	0.27	31.92	2.42	59.67	17.67	62
5	41.69	0	0.19	0.24	22.92	2.58	26.75	9.89	67
6	1.918	0	0.29	0.48	36.5	4	63.25	5.82	16.67
6	1.933	0	0.28	0.5	31.58	3.92	52.67	9.55	10
6	1.978	0	0.25	0.5	25	3.17	34.25	17.4	12.5
6	1.988	0	0.24	0.5	25.42	3	31.33	19.33	12.5
6	2.008	0	0.23	0.5	24.75	2.83	23	18.25	14
6	2.008	0	0.23	0.51	24.75	2.83	23	18.25	14
6	2.018	0	0.22	0.52	24.67	2.67	33.17	18.63	14.5
6	2.038	0	0.21	0.52	24.42	2.5	34.75	16.38	64
6	2.038	0	0.21	0.52	24.42	2.5	34.75	16.38	64
6	2.068	0	0.2	0.51	23.92	2.25	35.08	17	64
6	2.083	0	0.19	0.52	23.25	2.33	35.25	15.25	64
6	2.133	0	0.18	0.52	18.08	1.92	35.5	13.38	64
6	2.148	0	0.17	0.52	17.92	2	36.25	17.67	64
6	2.153	0	0.17	0.53	17.83	2.08	36.25	17.11	64
6	2.238	0	0.14	0.53	20.25	1.75	23.08	12	65
6	2.243	0	0.14	0.53	17.75	1.83	26.33	13.56	66

Appendix 2.5. Elevation of points derived from lower boundary of woody cover (+5 cm, -5 cm) and values for hydrological variables averaged over the seven growing seasons previous to the collection of data (1986 - 1992). Trait values: 1: woody cover; 0: herbaceous cover. Sites are: 1: Andrew Hayden Park; 2: Breckenridge; 3: Fitzroy Provincial Park; 4: Lucerne Boulevard; 5: Masson; 6: Westmeath Provincial Park. Elevations are with respect to the Survey of Canada Datum.

Site	Point	Trait	Fraction of growing season flooded	End of first flood (days)	Begining of second flood (days)
1	58.14	1	0.34	53	105.57
1	58.18	1	0.32	50.43	104.8
1	58.18	1	0.32	50.43	104.8
1	58.19	1	0.31	50	105
1	58.2	1	0.31	49.57	101.83
1	58.21	1	0.3	49.43	106
1	58.21	1	0.3	49.43	106
1	58.22	1	0.3	49.29	106.6
1	58.22	1	0.3	49.29	106.6
1	58.23	1	0.29	49.29	106.6
1	58.26	1	0.28	47.29	128.6
1	58.26	1	0.28	47.29	128.6
1	58.26	1	0.28	47.29	128.6
1	58.26	1	0.28	47.29	128.6
1	58.26	1	0.28	47.29	128.6
1	58.26	1	0.28	47.29	128.6
1	58.26	1	0.28	47.29	128.6
1	58.36	1	0.24	42	124
1	58.41	1	0.23	35.71	100.25
2	58.13	1	0.37	54.71	82.5
2	58.18	1	0.34	53	104.14
2	58.2	1	0.33	51	106.2
2	58.22	1	0.32	50.43	105.4
2	58.23	1	0.31	50	124
2	58.23	1	0.31	50	124
2	58.24	1	0.31	49.57	100.83
2	58.24	1	0.31	49.57	100.83
2	58.25	1	0.3	49.43	105.2
2	58.26	1	0.29	49.29	105.6
2	58.27	1	0.29	47.86	103.6
2	58.27	1	0.29	47.86	103.6
2	58.3	1	0.28	47	127.6
2	58.3	1	0.28	47	127.6
2	58.32	1	0.27	43	121.8
2	58.32	1	0.27	43	121.8
2	58.32	1	0.27	43	121.8
2	58.35	1	0.25	43	141
2	58.38	1	0.24	42.14	123
2	58.4	1	0.24	41.43	124.67
2	58.43	1	0.23	35.57	99.25

3	58.215	1	0.1	46.57	102
3	58.245	1	0.1	42.57	96
3	58.34	1	0.09	37.71	102.5
3	58.365	1	0.09	37.71	102.5
3	58.37	1	0.09	37.71	102.5
3	58.485	1	0.07	32.57	82
3	58.49	1	0.07	32.43	82
3	58.51	1	0.07	32	83.67
3	58.55	1	0.06	28.43	74.33
3	58.6	1	0.06	22.14	60.8
3	58.615	1	0.05	20.57	28.4
3	58.65	1	0.05	20.14	28.4
3	58.67	1	0.04	19.43	27.25
3	58.71	1	0.04	27	31
3	58.76	1	0.04	25	37.25
3	58.795	1	0.04	22.43	37.75
3	58.83	1	0.03	22	38
4	57.97	1	0.52	73	100.86
4	58.01	1	0.47	69.86	98.29
4	58.07	1	0.42	61.57	91.4
4	58.1	1	0.39	58.43	105.8
4	58.1	1	0.39	58.43	105.8
4	58.13	1	0.36	54.71	85
4	58.15	1	0.35	54.14	106.67
4	58.16	1	0.34	53	99.29
4	58.2	1	0.32	50.43	103.8
4	58.21	1	0.32	50.43	103.8
4	58.21	1	0.32	50.43	103.8
4	58.25	1	0.29	49.29	105.6
4	58.27	1	0.28	47.29	127.6
4	58.27	1	0.28	47.29	127.6
4	58.29	1	0.27	46.86	130.2
4	58.31	1	0.26	43	122.4
4	58.32	1	0.26	43	122.6
4	58.35	1	0.25	42.14	107.25
4	58.37	1	0.24	41.86	124.33
5	41.44	1	0.24	33.86	84
5	41.455	1	0.23	33.43	73.67
5	41.46	1	0.23	25.43	73.67
5	41.47	1	0.22	25.29	73.67
5	41.48	1	0.22	24.86	73.67
5	41.505	1	0.2	19.71	46.8
5	41.505	1	0.2	19.71	46.8
5	41.535	1	0.18	17.86	47.8
5	41.535	1	0.18	17:86	47.8
5	41.54	1	0.18	17.86	84
5	41.54	1	0.18	17.86	84
5	41.55	1	0.17	17.29	48.4
5	41.55	1	0.17	17.29	48.4
5	41.555	1	0.17	17.14	41.17
5	41.56	1	0.16	17	41.33
5	41.58	1	0.15	16.14	47.6
5	41.59	1	0.15	15.86	18.75
5	41.6	1	0.15	15.86	19

5	41.69	1	0.09	13.57	17.6
6	1.918	1	0.19	26.57	58.25
6	1.933	1	0.18	26.29	58.25
6	1.978	1	0.16	25.57	59.25
6	1.988	1	0.16	25.29	59.25
6	2.008	1	0.16	25	59.5
6	2.008	1	0.16	25	59.5
6	2.018	1	0.15	24.71	59.75
6	2.038	1	0.15	16.43	50
6	2.038	1	0.15	16.43	50
6	2.068	1	0.14	16	50.4
6	2.083	1	0.14	16	23.5
6	2.133	1	0.12	15.57	24.25
6	2.148	1	0.12	19.43	30.25
6	2.153	1	0.12	19.43	30.25
6	2.238	1	0.1	18.71	36.33
6	2.243	1	0.1	18.71	36.33
1	58.14	1	0.4	57.86	76.29
1	58.18	1	0.37	54.86	72.43
1	58.18	1	0.37	54.86	72.43
1	58.19	1	0.36	54.71	73.71
1	58.2	1	0.36	54.57	73.86
1	58.21	1	0.35	53.86	91.43
1	58.21	1	0.35	53.86	91.43
1	58.22	1	0.34	53	104.57
1	58.22	1	0.34	53	104.57
1	58.23	1	0.34	53	105.14
1	58.26	1	0.33	50.86	75.43
1	58.26	1	0.33	50.86	75.43
1	58.26	1	0.33	50.86	75.43
1	58.26	1	0.33	50.86	75.43
1	58.26	1	0.33	50.86	75.43
1	58.26	1	0.33	50.86	75.43
1	58.26	1	0.33	50.86	75.43
1	58.36	1	0.28	47.29	91.86
1	58.41	1	0.26	43	88.29
2	58.13	1	0.45	63.43	64
2	58.18	1	0.41	61.14	80.43
2	58.2	1	0.4	58.57	72.57
2	58.22	1	0.38	56.14	74.71
2	58.23	1	0.37	54.71	70.71
2	58.23	1	0.37	54.71	70.71
2	58.24	1	0.36	54.71	72.86
2	58.24	1	0.36	54.71	72.86
2	58.25	1	0.35	54.29	86.14
2	58.26	1	0.35	53.71	99.43
2	58.27	1	0.34	53	99.29
2	58.27	1	0.34	53	99.29
2	58.3	1	0.33	51	75.86
2	58.3	1	0.33	51	75.86
2	58.32	1	0.32	50.43	75.29
2	58.32	1	0.32	50.43	75.29
2	58.32	1	0.32	50.43	75.29
2	58.35	1	0.3	49.43	75.14

2	58.38	1	0.28	52	74
2	58.4	1	0.28	47	91.14
2	58.43	1	0.26	47.29	87.43
3	58.215	1	0.12	51	58.14
3	58.245	1	0.12	49.86	57.71
3	58.34	1	0.1	42.57	68.43
3	58.365	1	0.1	42.29	61.86
3	58.37	1	0.1	42	61.86
3	58.485	1	0.08	35.29	56.29
3	58.49	1	0.08	35.29	56.29
3	58.51	1	0.08	35.14	56.43
3	58.55	1	0.08	33.86	34.86
3	58.6	1	0.07	32	35.71
3	58.615	1	0.06	31.86	36
3	58.65	1	0.06	28.43	31.86
3	58.67	1	0.06	31	36.14
3	58.71	1	0.06	22.14	43.43
3	58.76	1	0.05	20.14	15.57
3	58.795	1	0.04	18.43	14.57
3	58.83	1	0.04	26.71	13.29
4	57.97	1	0.66	98.14	129.43
4	58.01	1	0.6	81.86	83
4	58.07	1	0.52	73	100.86
4	58.1	1	0.48	70.14	97.29
4	58.1	1	0.48	70.14	97.29
4	58.13	1	0.45	63.43	64
4	58.15	1	0.44	62.86	64
4	58.16	1	0.43	62	52.14
4	58.2	1	0.39	58.43	75.57
4	58.21	1	0.38	57.14	81.86
4	58.21	1	0.38	57.14	81.86
4	58.25	1	0.35	54.14	91.43
4	58.27	1	0.34	53	104.14
4	58.27	1	0.34	53	104.14
4	58.29	1	0.33	50.29	74.71
4	58.31	1	0.32	50.43	74.14
4	58.32	1	0.31	50	88.71
4	58.35	1	0.29	48.71	75.43
4	58.37	1	0.28	47.29	91.14
5	41.44	1	0.34	50	76
5	41.455	1	0.32	47.71	60.29
5	41.46	1	0.31	47.71	60.29
5	41.47	1	0.3	47.71	61.71
5	41.48	1	0.29	47.14	71.86
5	41.505	1	0.26	36.14	55.14
5	41.505	1	0.26	36.14	55.14
5	41.535	1	0.25	34	41.57
5	41.535	1	0.25	34	41.57
5	41.54	1	0.24	33.86	60
5	41.54	1	0.24	33.86	60
5	41.55	1	0.23	33.86	60.71
5	41.55	1	0.23	33.86	60.71
5	41.555	1	0.23	25.43	63.14
5	41.56	1	0.23	25.43	63.14

5	41.58	1	0.22	24.86	63.14
5	41.59	1	0.21	24.71	63.14
5	41.6	1	0.2	19.86	34.43
5	41.69	1	0.15	15.86	10.71
6	1.918	1	0.27	31.71	46
6	1.933	1	0.25	31.29	51.29
6	1.978	1	0.21	26.71	36.14
6	1.988	1	0.21	27.71	31
6	2.008	1	0.2	26.57	16.71
6	2.008	1	0.2	26.57	16.71
6	2.018	1	0.19	26.57	34.14
6	2.038	1	0.18	26.29	34.14
6	2.038	1	0.18	26.29	34.14
6	2.068	1	0.17	25.86	34.57
6	2.083	1	0.16	25.29	34.71
6	2.133	1	0.15	16.57	35
6	2.148	1	0.14	16.43	36.29
6	2.153	1	0.14	16.43	36.29
6	2.238	1	0.12	23.71	12.86
6	2.243	1	0.12	19.57	18

Appendix 2.6. Elevation of points derived from lower boundary of woody cover (+5 cm, -5 cm) and values for hydrological variables averaged over the eighteen growing seasons previous to the collection of data (1975 - 1992). Trait values: 1: woody cover; 0: herbacoues cover. Sites are: 1: Andrew Hayden Park; 2: Breckenridge; 3: Fitzroy Provincial Park; 4: Lucerne Boulevard; 5: Masson; 6: Westmeath Provincial Park. Elevations are with respect to the Survey of Canada Geodetic Datum.

Site	Point	Trait	Fraction of the growing season flooded	End of the first flood (days)	Beginning of the second flood (days)
1	58.14	1	0.38	60.33	99.63
1	58.18	1	0.36	57.72	93.8
1	58.18	1	0.36	57.72	93.8
1	58.19	1	0.36	56.94	90.87
1	58.2	1	0.35	56.72	90.63
1	58.21	1	0.34	56.28	91.33
1	58.21	1	0.34	56.28	91.33
1	58.22	1	0.34	55.89	92.67
1	58.22	1	0.34	55.89	92.67
1	58.23	1	0.34	55.83	92.8
1	58.26	1	0.32	54.56	105.64
1	58.26	1	0.32	54.56	105.64
1	58.26	1	0.32	54.56	105.64
1	58.26	1	0.32	54.56	105.64
1	58.26	1	0.32	54.56	105.64
1	58.26	1	0.32	54.56	105.64
1	58.26	1	0.32	54.56	105.64
1	58.36	1	0.28	49.61	86.33
1	58.41	1	0.26	43.83	96.44
2	58.13	1	0.42	64.33	91.2
2	58.18	1	0.39	59.72	98.56
2	58.2	1	0.38	58.39	103.29
2	58.22	1	0.36	57.06	93.33
2	58.23	1	0.36	56.22	96.6
2	58.23	1	0.36	56.22	96.6
2	58.24	1	0.35	56	89.63
2	58.24	1	0.35	56	89.63
2	58.25	1	0.34	55.83	90.4
2	58.26	1	0.34	55.72	90.53
2	58.27	1	0.33	55.17	91.36
2	58.27	1	0.33	55.17	91.36
2	58.3	1	0.32	53.33	104.64
2	58.3	1	0.32	53.33	104.64
2	58.32	1	0.31	51.39	99.38
2	58.32	1	0.31	51.39	99.38
2	58.32	1	0.31	51.39	99.38
2	58.35	1	0.29	47.39	95.55
2	58.38	1	0.28	46.72	93.3
2	58.4	1	0.27	46.22	90.38
2	58.43	1	0.26	43.72	106.56

3	58.215	1	0.04	53.5	86.27
3	58.245	1	0.04	51.11	83.71
3	58.34	1	0.04	44.5	83.4
3	58.365	1	0.04	44.39	96.56
3	58.37	1	0.04	44.39	96.56
3	58.485	1	0.03	40.22	79.56
3	58.49	1	0.03	40.17	79.56
3	58.51	1	0.03	39.83	85.38
3	58.55	1	0.03	35.06	70.9
3	58.6	1	0.03	32	70
3	58.615	1	0.03	28.22	40.82
3	58.65	1	0.03	27.67	40.82
3	58.67	1	0.03	27.17	39.56
3	58.71	1	0.03	29.39	43.78
3	58.76	1	0.03	28	39.22
3	58.795	1	0.02	25.72	34.13
3	58.83	1	0.02	25.17	34.38
4	57.97	1	0.6	89.67	108.72
4	58.01	1	0.55	77.06	101.82
4	58.07	1	0.48	71.22	89.85
4	58.1	1	0.44	68.61	98.79
4	58.1	1	0.44	68.61	98.79
4	58.13	1	0.42	64.83	92.53
4	58.15	1	0.4	63.89	103.29
4	58.16	1	0.39	61.44	96.47
4	58.2	1	0.37	58.33	93.71
4	58.21	1	0.36	57.72	92.8
4	58.21	1	0.36	57.72	92.8
4	58.25	1	0.34	55.89	90.53
4	58.27	1	0.32	54.72	104.5
4	58.27	1	0.32	54.72	104.5
4	58.29	1	0.31	54.33	111.54
4	58.31	1	0.31	52.17	99.62
4	58.32	1	0.3	52.17	100
4	58.35	1	0.28	47.5	90.36
4	58.37	1	0.27	46.67	96.89
5	41.44	1	0.28	42	95.31
5	41.455	1	0.27	41.56	90.43
5	41.46	1	0.27	38.44	90.43
5	41.47	1	0.26	38.17	90.64
5	41.48	1	0.25	37.78	90.86
5	41.505	1	0.24	34.94	82.23
5	41.505	1	0.24	34.94	82.23
5	41.535	1	0.22	32.39	70.92
5	41.535	1	0.22	32.39	70.92
5	41.54	1	0.21	32.33	95.31
5	41.54	1	0.21	32.33	95.31
5	41.55	1	0.21	32	71.31
5	41.55	1	0.21	32	71.31
5	41.555	1	0.2	28.94	63.8
5	41.56	1	0.2	28.44	61.63
5	41.58	1	0.19	27.61	55.79
5	41.59	1	0.18	26.56	35.62
5	41.6	1	0.18	25.83	35.08

5	41.69	1	0.12	12.94	17.2
6	1.918	1	0.22	29.83	55.15
6	1.933	1	0.21	28.89	53.77
6	1.978	1	0.2	28.11	55.5
6	1.988	1	0.19	27.89	53.36
6	2.008	1	0.19	27.67	53.64
6	2.008	1	0.19	27.67	53.64
6	2.018	1	0.18	27.5	53.73
6	2.038	1	0.17	23.94	58.92
6	2.038	1	0.17	23.94	58.92
6	2.068	1	0.16	23.44	59.42
6	2.083	1	0.16	23.33	50.55
6	2.133	1	0.15	20.94	44.42
6	2.148	1	0.14	22.22	48
6	2.153	1	0.14	22.22	35.8
6	2.238	1	0.12	20.28	38.38
6	2.243	1	0.12	20.28	38.38
1	58.14	0	0.45	68.89	76.99
1	58.18	0	0.42	64.94	82.6
1	58.18	0	0.42	64.94	82.6
1	58.19	0	0.41	64.61	83.39
1	58.2	0	0.41	64.5	86.84
1	58.21	0	0.4	63.78	92.01
1	58.21	0	0.4	63.78	92.01
1	58.22	0	0.39	61.44	88.43
1	58.22	0	0.39	61.44	88.43
1	58.23	0	0.39	60.61	94.93
1	58.26	0	0.37	58.5	78
1	58.26	0	0.37	58.5	78
1	58.26	0	0.37	58.5	78
1	58.26	0	0.37	58.5	78
1	58.26	0	0.37	58.5	78
1	58.26	0	0.37	58.5	78
1	58.26	0	0.37	58.5	78
1	58.36	0	0.32	54.56	87.19
1	58.41	0	0.3	51	76.74
2	58.13	0	0.52	72.39	91.64
2	58.18	0	0.47	68.06	78.09
2	58.2	0	0.45	66.61	75.47
2	58.22	0	0.43	65.06	85.51
2	58.23	0	0.42	64.33	81.31
2	58.23	0	0.42	64.33	81.31
2	58.24	0	0.41	64.17	82.5
2	58.24	0	0.41	64.17	82.5
2	58.25	0	0.41	63.83	89.43
2	58.26	0	0.4	62.67	88.25
2	58.27	0	0.39	59.72	90.97
2	58.27	0	0.39	59.72	90.97
2	58.3	0	0.38	58.39	85.96
2	58.3	0	0.38	58.39	85.96
2	58.32	0	0.36	57.06	82.02
2	58.32	0	0.36	57.06	82.02
2	58.32	0	0.36	57.06	82.02
2	58.35	0	0.34	55.83	79.59

2	58.38	0	0.33	55.94	79.49
2	58.4	0	0.32	53.33	86.36
2	58.43	0	0.3	52.89	75.64
3	58.215	0	0.05	57.89	70.82
3	58.245	0	0.04	56.56	72.99
3	58.34	0	0.04	51.17	68.52
3	58.365	0	0.04	47.83	62.88
3	58.37	0	0.04	47.61	62.88
3	58.485	0	0.04	43.22	56.35
3	58.49	0	0.04	43.22	56.44
3	58.51	0	0.04	42.28	53.9
3	58.55	0	0.03	39.56	50.6
3	58.6	0	0.03	39.83	48.6
3	58.615	0	0.03	37.44	50.56
3	58.65	0	0.03	35.06	50.38
3	58.67	0	0.03	36.28	50.94
3	58.71	0	0.03	29	44.5
3	58.76	0	0.03	27.56	29.43
3	58.795	0	0.03	26.72	29.29
3	58.83	0	0.03	28.83	27.71
4	57.97	0	0.77	123.61	122.91
4	58.01	0	0.71	106.56	111.22
4	58.07	0	0.6	84.5	108.53
4	58.1	0	0.56	79.94	94.11
4	58.1	0	0.56	79.94	94.11
4	58.13	0	0.52	73.11	86.09
4	58.15	0	0.5	72.33	73.04
4	58.16	0	0.49	71.78	71.11
4	58.2	0	0.44	68.61	82.1
4	58.21	0	0.44	66.83	85.8
4	58.21	0	0.44	66.83	85.8
4	58.25	0	0.4	63.89	85.19
4	58.27	0	0.39	60.61	93.1
4	58.27	0	0.39	60.61	93.1
4	58.29	0	0.38	59.11	85.51
4	58.31	0	0.36	57.72	81.58
4	58.32	0	0.36	56.94	84.81
4	58.35	0	0.34	55.67	79.7
4	58.37	0	0.32	54.72	86.22
5	41.44	0	0.4	58.5	77.11
5	41.455	0	0.38	54.94	60.79
5	41.46	0	0.37	54.83	92.29
5	41.47	0	0.36	53	71.82
5	41.48	0	0.34	52.06	73.28
5	41.505	0	0.32	47.06	71.21
5	41.505	0	0.32	47.06	71.21
5	41.535	0	0.29	42.17	70.47
5	41.535	0	0.29	42.17	70.47
5	41.54	0	0.28	42	78.12
5	41.54	0	0.28	42	78.12
5	41.55	0	0.27	41.83	78.71
5	41.55	0	0.27	41.83	78.71
5	41.555	0	0.27	38.44	79.71
5	41.56	0	0.27	38.44	79.71

5	41.58	0	0.25	37.78	80.06
5	41.59	0	0.24	37.06	80.34
5	41.6	0	0.24	35	68.59
5	41.69	0	0.18	26.56	29.32
6	1.918	0	0.3	38.33	68.68
6	1.933	0	0.29	34.94	54.38
6	1.978	0	0.25	30.5	43.1
6	1.988	0	0.25	30.67	42.56
6	2.008	0	0.23	29.94	62
6	2.008	0	0.23	29.94	62
6	2.018	0	0.23	29.83	43.91
6	2.038	0	0.22	28.89	43.77
6	2.038	0	0.22	28.89	43.77
6	2.068	0	0.21	28.39	41.68
6	2.083	0	0.2	27.94	40.77
6	2.133	0	0.18	24.22	41.13
6	2.148	0	0.18	23.89	50.44
6	2.153	0	0.17	23.83	50.44
6	2.238	0	0.15	24.11	40.07
6	2.243	0	0.15	22.33	42.77

Appendix 3.1. Assignment of species to subsets of the species pool based on qualitative traits. Division of herbaceous vegetation into aquatic and emergent subsets, and taxonomic groups of monocots, dicots and the only family (Cyperaceae) represented by at least three genera and at least five species.

Species	Functional group		Taxonomic group		
	emergent	aquatic	monocot	dicot	Cyperaceae
Acorus calamus	1	0	1	0	0
Alisma plantago-aquatica L.	1	0	1	0	0
Calamagrostis canadensis	1	0	1	0	0
Campanula aparinoides Pursh.	1	0	0	1	0
Carex lenticularis	1	0	1	0	1
Carex vesicaria	1	0	1	0	1
Ceratophyllum demersum	0	1	0	1	0
Dulichium arundinaceum	1	0	1	0	1
Eleocharis acicularis	1	0	1	0	1
Eleocharis erythropoda Steudel	1	0	1	0	1
Eleocharis smallii	1	0	1	0	1
Elodea canadensis	0	1	1	0	0
Equisetum arvense	1	0			
Equisetum fluviatile	1	0			
Eriocaulon septangulare	1	0	1	0	0
Hypericum boreale	1	0	0	1	0
Hypericum ellipticum	1	0	0	1	0
Isoetes echinospora Durieu	0	1			
Juncus canadensis	1	0	1	0	0
Juncus pelocarpus	1	0	1	0	0
Juncus subtilis	1	0	1	0	0
Leersia oryzoides	1	0	1	0	0
Lemna minor	0	1	1	0	0
Lycopus uniflorus	1	0	0	1	0
Lysimachia terrestris	1	0	0	1	0
Lythrum salicaria	1	0	0	1	0
Mentha arvensis	1	0	0	1	0
Mimulus ringens	1	0	0	1	0
Myriophyllum tenellum	0	1	0	1	0
Onoclea sensibilis	1	0			
Phalaris arundinacea	1	0	1	0	0
Polygonum amphibium	1	0	0	1	0
Pontederia cordata	1	0	1	0	0
Potamogeton gramineus	0	1	1	0	0
Potamogeton robbinsii	0	1	1	0	0
Potamogeton spirillus	0	1	1	0	0
Potentilla palutris	1	0	0	1	0
Ranunculus aquatilis L.	0	1	0	1	0
Ranunculus flammula	0	1	0	1	0
Sagittaria cuneata	1	0	1	0	0
Sagittaria graminea	1	0	1	0	0
Sagittaria latifolia	1	0	1	0	0
Sagittaria rigida	1	0	1	0	0
Scirpus acutus	1	0	1	0	1

Scirpus americanus	1	0	1	0	1
Scirpus fluviatile	1	0	1	0	1
Sium suave	1	0	0	1	0
Solanum dulcamara	1	0	0	1	0
Sparganium eurycarpum	1	0	1	0	0
Spartina pectinata	1	0	1	0	0
Triadenum fraseri (Spach) Gl.	1	0	0	1	0
Typha latifolia	1	0	1	0	0
Vallisneria americana	0	1	1	0	0
Galium palustre	1	0	0	1	0
Bidens cernua	1	0	0	1	0
Boehmeria cylindrica	1	0	0	1	0
Impatiens biflora	1	0	0	1	0
Iris versicolor	1	0	1	0	0
Vicia cracca	1	0	0	1	0
Convolvulus sp.	1	0	0	1	0
Carex lasiocarpa	1	0	1	0	1
Juncus filiformis	1	0	1	0	0
Carex projecta	1	0	1	0	1
Megalodonta beckii (Torr.) Greene.	0	1	0	1	0
Nitella	0	1			
Alga	0	1			
Nymphaea odorata	0	1	0	1	0
Myriophyllum alterniflorum	0	1	0	1	0
Nymphoides cordata	0	1	0	1	0
Heteranthera dubia	0	1	1	0	0
Veronica sp.	1	0	0	1	0
Potomogetum perfoliatus	0	1	1	0	0

Appendix 3.2. Assignment of species to functional groups based on Hutchinson's life-forms. No values were entered for aquatic species.

Species	life forms			
	graminid	sagittarid	herbid	isoetid
Acorus calamus	1	0	0	0
Alisma plantago-aquatica L.	0	1	0	0
Calamagrostis canadensis	1	0	0	0
Campanula aparinoides Pursh.	0	0	1	0
Carex lenticularis	1	0	0	0
Carex vesicaria	1	0	0	0
Ceratophyllum demersum				
Dulichium arundinaceum	1	0	0	0
Eleocharis acicularis	0	0	0	1
Eleocharis erythropoda Steudel	1	0	0	0
Eleocharis smallii	1	0	0	0
Elodea canadensis				
Equisetum arvense	1	0	0	0
Equisetum fluviatile	1	0	0	0
Eriocaulon septangulare	0	0	0	1
Hypericum boreale	0	0	1	0
Hypericum ellipticum	0	0	1	0
Isoetes echinospora Durieu	0	0	0	1
Juncus canadensis	1	0	0	0
Juncus pelocarpus	0	0	0	1
Juncus subtilis	1	0	0	0
Leersia oryzoides	1	0	0	0
Lemna minor				
Lycopus uniflorus	0	0	1	0
Lysimachia terrestris	0	0	1	0
Lythrum salicaria	0	0	1	0
Mentha arvensis	0	0	1	0
Mimulus ringens	0	0	1	0
Myriophyllum tenellum				
Onoclea sensibilis	0	0	1	0
Phalaris arundinacea	1	0	0	0
Polygonum amphibium				
Pontederia cordata	0	1	0	0
Potamogeton gramineus				
Potamogeton robbinsii				
Potamogeton spirillus				
Potentilla palutris	0	0	1	0
Ranunculus aquatilis L.				
Ranunculus flammula	0	0	1	0
Sagittaria cuneata	0	1	0	0
Sagittaria graminea	0	0	0	1
Sagittaria latifolia	0	1	0	0
Sagittaria rigida	0	1	0	0
Scirpus acutus	1	0	0	0
Scirpus americanus	1	0	0	0
Scirpus fluviatile	1	0	0	0
Sium suave	0	0	1	0
Solanum dulcamara	0	0	1	0

Sparganium eurycarpum	1	0	0	0
Spartina pectinata	1	0	0	0
Triadenum fraseri (Spach) Gl.	0	0	1	0
Typha latifolia	1	0	0	0
Vallisneria americana				
Galium palustre	0	0	0	0
Bidens cernua	0	0	1	0
Boehmeria cylindrica	0	0	1	0
Impatiens biflora	0	0	1	0
Iris versicolor	1	0	0	0
Vicia cracca	0	0	0	0
Convolvulus sp.	0	0	0	0
Carex lasiocarpa	1	0	0	0
Juncus filiformis	1	0	0	0
Carex projecta	1	0	0	0
Megalodonta beckii (Torr.) Greene.	0	0	1	0
Nitella				
Alga				
Nymphaea odorata				
Myriophyllum alterniflorum				
Nymphoides cordata				
Heteranthera dubia				
Veronica sp.	0	0	1	0
Potomogetum perfoliatus				

Appendix 3.3. Assignment of species to functional groups based on classification by Shipley et al. (1989). No values entered for aquatic species.

Species	Canopy types				
	graminoid	multilayer	monolayer	single stem	tussock of stems
Acorus calamus	1	0	0	0	0
Alisma plantago-aquatica L.	1	0	0	0	0
Calamagrostis canadensis	0	1	0	0	0
Campanula aparinoides Pursh.	0	1	0	0	0
Carex lenticularis	1	0	0	0	0
Carex vesicaria	1	0	0	0	0
Ceratophyllum demersum					
Dulichium arundinaceum	0	1	0	0	0
Eleocharis acicularis	0	0	1	0	0
Eleocharis erythropoda Steudel	0	0	0	0	1
Eleocharis smallii	0	0	0	1	0
Elodea canadensis					
Equisetum arvense	0	0	0	1	0
Equisetum fluviatile	0	0	0	1	0
Eriocaulon septangulare	1	0	0	0	0
Hypericum boreale	0	1	0	0	0
Hypericum ellipticum	0	1	0	0	0
Isoetes echinospora Durieu					
Juncus canadensis	1	0	0	0	0
Juncus pelocarpus	1	0	0	0	0
Juncus subtilis	0	1	0	0	0
Leersia oryzoides	0	1	0	0	0
Lemna minor					
Lycopus uniflorus	0	1	0	0	0
Lysimachia terrestris	0	1	0	0	0
Lythrum salicaria	0	1	0	0	0
Mentha arvensis	0	1	0	0	0
Mimulus ringens	0	1	0	0	0
Myriophyllum tenellum					
Onoclea sensibilis	0	0	1	0	0
Phalaris arundinacea	0	1	0	0	0
Polygonum amphibium	0	0	1	0	0
Pontederia cordata	1	0	0	0	0
Potamogeton gramineus					
Potamogeton robbinsii					
Potamogeton spirillus					
Potentilla palutris	0	1	0	0	0
Ranunculus aquatilis L.					
Ranunculus flammula					
Sagittaria cuneata	1	0	0	0	0
Sagittaria graminea	1	0	0	0	0
Sagittaria latifolia	1	0	0	0	0
Sagittaria rigida	1	0	0	0	0
Scirpus acutus	0	0	0	1	0
Scirpus americanus	0	0	0	1	0
Scirpus fluviatile	0	1	0	0	0
Sium suave	0	1	0	0	0

Solanum dulcamara	0	1	0	0	0
Sparganium eurycarpum	0	1	0	0	0
Spartina pectinata	0	1	0	0	0
Triadenum fraseri (Spach) Gl.	0	1	0	0	0
Typha latifolia	1	0	0	0	0
Vallisneria americana					
Galium palustre	0	1	0	0	0
Bidens cernua	0	1	0	0	0
Boehmeria cylindrica	0	1	0	0	0
Impatiens biflora	0	1	0	0	0
Iris versicolor	1	0	0	0	0
Vicia cracca	0	1	0	0	0
Convolvulus sp.	0	0	1	0	0
Carex lasiocarpa	1	0	0	0	0
Juncus filiformis	0	0	0	0	1
Carex projecta	1	0	0	0	0
Megalodonta beckii (Torr.) Greene.					
Nitella					
Alga					
Nymphaea odorata					
Myriophyllum alterniflorum					
Nymphoides cordata					
Heteranthera dubia					
Veronica sp.	0	1	0	0	0
Potomogetum perfoliatus					

Appendix 3.4. Assignment of species to functional groups based on classification by Shipley et al. (1989). No values entered for aquatic species.

Species	Growth forms		
	upright	rosette	creeping
Acorus calamus	1	0	0
Alisma plantago-aquatica L.	0	1	0
Calamagrostis canadensis	1	0	0
Campanula aparinoides Pursh.	1	0	0
Carex lenticularis	1	0	0
Carex vesicaria	1	0	0
Ceratophyllum demersum			
Dulichium arundinaceum	1	0	0
Eleocharis acicularis	0	1	0
Eleocharis erythropoda Steudel	0	1	0
Eleocharis smallii	1	0	0
Elodea canadensis			
Equisetum arvense	1	0	0
Equisetum fluviatile	1	0	0
Eriocaulon septangulare	0	1	0
Hypericum boreale	1	0	0
Hypericum ellipticum	1	0	0
Isoetes echinospora Durieu	0	1	0
Juncus canadensis	1	0	0
Juncus pelocarpus	1	0	0
Juncus subtilis	1	0	0
Leersia oryzoides	1	0	0
Lemna minor			
Lycopus uniflorus	1	0	0
Lysimachia terrestris	1	0	0
Lythrum salicaria	1	0	0
Mentha arvensis	1	0	0
Mimulus ringens	1	0	0
Myriophyllum tenellum			
Onoclea sensibilis	1	0	0
Phalaris arundinacea	1	0	0
Polygonum amphibium	0	0	1
Pontederia cordata	0	1	0
Potamogeton gramineus			
Potamogeton robbinsii			
Potamogeton spirillus			
Potentilla palutris	0	0	1
Ranunculus aquatilis L.			
Ranunculus flammula			
Sagittaria cuneata	0	1	0
Sagittaria graminea	0	1	0
Sagittaria latifolia	0	1	0
Sagittaria rigida	0	1	0
Scirpus acutus	1	0	0
Scirpus americanus	1	0	0
Scirpus fluviatile	1	0	0
Sium suave	1	0	0
Solanum dulcamara	1	0	0

Sparganium eurycarpum	1	0	0
Spartina pectinata	1	0	0
Triadenum fraseri (Spach) Gl.	1	0	0
Typha latifolia	0	1	0
Vallisneria americana			
Galium palustre	0	0	1
Bidens cernua	1	0	0
Boehmeria cylindrica	1	0	0
Impatiens biflora	1	0	0
Iris versicolor	1	0	0
Vicia cracca	0	0	1
Convolvulus sp.	0	0	1
Carex lasiocarpa	1	0	0
Juncus filiformis	1	0	0
Carex projecta	1	0	0
Megalodonta beckii (Torr.) Greene.			
Nitella			
Alga			
Nymphaea odorata			
Myriophyllum alterniflorum			
Nymphoides cordata			
Heteranthera dubia			
Veronica sp.	1	0	0
Potomogetum perfoliatus			

Appendix 3.5. Assignment of species to subsets of the species pool based on qualitative traits. Approximation of functional groups described by Boutin and Keddy (1993). No values entered for aquatic species. No values entered for aquatic species.

Species	Functional group		
	matrix	interstitial	ruderal
Acorus calamus	0	1	0
Alisma plantago-aquatica L.	0	1	0
Calamagrostis canadensis	0	1	0
Campanula aparinoides Pursh.	0	1	0
Carex lenticularis	0	1	0
Carex vesicaria	0	1	0
Ceratophyllum demersum			
Dulichium arundinaceum	0	1	0
Eleocharis acicularis	0	1	0
Eleocharis erythropoda Steudel	0	1	0
Eleocharis smallii	0	1	0
Elodea canadensis			
Equisetum arvense	0	1	0
Equisetum fluviatile	0	1	0
Eriocaulon septangulare	0	0	1
Hypericum boreale	0	1	0
Hypericum ellipticum	0	1	0
Isoetes echinospora Durieu			
Juncus canadensis	0	1	0
Juncus pelocarpus	0	1	0
Juncus subtilis	0	1	0
Leersia oryzoides	0	1	0
Lemna minor			
Lycopus uniflorus	0	1	0
Lysimachia terrestris	0	1	0
Lythrum salicaria	0	0	1
Mentha arvensis	1	0	0
Mimulus ringens	0	0	1
Myriophyllum tenellum			
Onoclea sensibilis	0	1	0
Phalaris arundinacea	1	0	0
Polygonum amphibium	1	0	0
Pontederia cordata	0	1	0
Potamogeton gramineus			
Potamogeton robbinsii			
Potamogeton spirillus			
Potentilla palutris	1	0	0
Ranunculus aquatilis L.			
Ranunculus flammula			
Sagittaria cuneata	0	1	0
Sagittaria graminea	0	0	1
Sagittaria latifolia	1	0	0
Sagittaria rigida	0	1	0
Scirpus acutus	1	0	0
Scirpus americanus	1	0	0
Scirpus fluviatile	1	0	0

Sium suave	0	1	0
Solanum dulcamara	0	1	0
Sparganium eurycarpum	1	0	0
Spartina pectinata	1	0	0
Triadenum fraseri (Spach) Gl.	1	0	0
Typha latifolia	1	0	0
Vallisneria americana			
Galium palustre	0	1	0
Bidens cernua	0	0	1
Boehmeria cylindrica	0	1	0
Impatiens biflora	0	0	1
Iris versicolor	0	1	0
Vicia cracca	0	1	0
Convolvulus sp.			
Carex lasiocarpa			
Juncus filiformis	0	1	0
Carex projecta	0	1	0
Megalodonta beckii (Torr.) Greene.			
Nitella			
Alga			
Nymphaea odorata			
Myriophyllum alterniflorum			
Nymphoides cordata			
Heteranthera dubia			
Veronica sp.	0	0	1
Potomogetum perfoliatus			

Appendix 3.6.a. Quantitative traits. Mean and standard deviation for above-ground biomass and photosynthetic height, as measured in plants in the field. Nomenclature follows Fernald (1950) except where taxon authority is given.

Species	N	Mean biomass (g)	Biomass STDEV	Mean height (cm)	Height STDEV
Acorus calamus	5	6.02	2.49	101	14.5
Alisma plantago-aquatica L.	6	3.94	3.35	39.4	7.3
Bidens cernua	10	1.63	4.8	26.1	19.6
Boehmeria cylindrica	7	1.72	3.82	49	17.6
Calamagrostis canadensis	6	2.63	0.49	79.1	3.34
Campanula aparinoides Pursh.	3	0.11		32	0.84
Carex lenticularis	9	0.69	0.19	53.7	5.9
Carex vesicaria	10	0.97	0.12	67.3	1.75
Carex lasiocarpa					
Carex projecta					
Convolvulus sp.	1			39	
Dulichium arundinaceum	8	0.70	0.31	56.1	1.58
Eleocharis acicularis	11	0.00	0.0015	6.66	1.64
Eleocharis erythropoda Steudel	16	0.05	0.062	33.9	4.2
Eleocharis smallii	9	0.61	0.072	82.9	2.44
Equisetum arvense	7	0.30	0.101	45.6	3.9
Equisetum fluviatile	13	0.55	0.135	67	4.8
Eriocaulon septangulare	5	0.08	0.18	2.57	1.22
Galium palustre	9	0.08	0.14	19	18.22
Heteranthera dubia	1	0.02		1.5	
Hypericum boreale	9	0.08	0.187	10.8	2.05
Hypericum ellipticum	6	0.14	0.045	22.3	1.46
Impatiens biflora	10	2.59	4.95	68.1	35.24
Iris versicolor	5	4.55	2.65	74.1	6.01
Isoetes echinospora Durieu	3	0.06	0.0011	5.63	1.52
Juncus canadensis	1			36	
Juncus pelocarpus	3	0.02	0.0076	10.9	1.75
Juncus subtilis	3	0.00	0.00039	3.57	1.01
Leersia oryzoides	12	0.65	0.23	66	2.83
Lycopus uniflorus	8	0.34	0.11	40.7	4.78
Lys-nm	4	0.12	0.002	3.78	6.16
Lysimachia terrestris	11	1.06	0.24	52.3	3.51
Lythrum salicaria	13	12.39	7.82	104	9.87
Mentha arvensis	7	0.86	1.1	23.6	8.44
Mimulus ringens	7	2.43	4.86	49.1	11.8
Onoclea sensibilis	9	2.48	1.28	57.6	3.28
Phalaris arundinacea	9	5.66	1.41	96.2	3.29
Polygonum amphibium	8	3.08	0.888	37.2	6.44
P-pers	3	1.28	0.19	31.7	0.52
Pontederia cordata	6	9.06	2.4	69.7	6.07
Potentilla palutris	6	5.40	3.11	52.3	1.04
Sagittaria cuneata	3	0.16	0.017	15.1	13.8
Sagittaria graminea	4	0.13	0.17	11.9	8.07

Sagittaria latifolia	12	6.35	4.55	66.8	5.64
Sagittaria rigida	6	0.38	0.638	50.5	8.74
Scirpus acutus	10	4.19	0.25	166	2.01
Scirpus americanus	9	1.63	0.25	114	4.99
Scirpus fluviatile	9	7.37	1.64	131	6.32
Sium suave	12	1.70	3.71	68.8	3.41
Solanum dulcamara	1	2.67		70	
Sparganium eurycarpum	9	14.52	7.25	114	6.11
Spartina pectinata	10	6.15	1.25	125	5.43
Triadenum fraseri (Spach) Gl.	4	0.92	0.376	39.6	3.51
Typha latifolia	6	77.90	15.59	241	4.28
Veronica sp.	1	1.17		23	
Vicia cracca	3	0.57	0.318	48.2	26.1

Appendix 3.6.b. Quantitative traits. Mean and standard deviation for canopy diameter and crown area, as measured in plants in the field. Nomenclature follows Fernald (1950) except where taxon authority is given.

Species	N	Mean canopy diameter (cm)	Canopy diameter STDEV	Mean crown area (cm^2)	Crown area STDEV
Acorus calamus	5	33.9	5.4	150	95
Alisma plantago-aquatica L.	6	28.2	10.9	230	230
Bidens cernua	10	19.2	2.7	89	44
Boehmeria cylindrica	7	21	1.68	100	27
Calamagrostis canadensis	6	36.7	2.29	180	39
Campanula aparinoides Pursh.	3			13	12
Carex lenticularis	9	30.7	7.43	120	140
Carex vesicaria	10	48.6	2.34	280	86
Carex lasiocarpa					
Carex projecta					
Convolvulus sp.	1	57		400	
Dulichium arundinaceum	8	8.2	0.33	17	5.7
Eleocharis acicularis	11	6.25	1.17	6.2	2.6
Eleocharis erythropoda Steudel	16	5.69	6.08	9	67
Eleocharis smallii	9	7.61	2.13	6.2	2.4
Equisetum arvense	7	13.5	25.9	78	390
Equisetum fluviatile	13	14.4	7.65	44	77
Ericcaulon septangulare	5	4.26	1.28	3.2	5
Galium palustre	9	7.67	4.34	14	31
Heteranthera dubia	1	4		1.3	
Hypericum boreale	9	3.93	1.07	3.1	3.8
Hypericum ellipticum	6	5.07	2.25	6	8.1
Impatiens biflora	10	25.5	10.8	180	270
Iris versicolor	5	28.2	4.81	170	110
Isoetes echinospora Durieu	3	9.93	1.69	20	16
Juncus canadensis	1	5.5		6.3	
Juncus pelocarpus	3	2.8	1.39	1	0.65
Juncus subtilis	3	3.83	0.66	2.1	1
Leersia oryzoides	12	21.7	5.1	75	87
Lycopus uniflorus	8	10.9	0.95	26	7.3
Lys-nm	4	10.9	3.27	17	7.8
Lysimachia terrestris	11	11.7	0.56	31	4.2
Lythrum salicaria	13	21.4	3.54	110	55
Mentha arvensis	7	10.6	1.66	25	20
Mimulus ringens	7	9.7	3.65	25	44
Onoclea sensibilis	9	23.8	1.68	120	27
Phalaris arundinacea	9	35.9	7.99	220	160
Polygonum amphibium	8	21.4	3.65	130	38
P-pers	3	22.5	0.81	110	11
Pontederia cordata	6	63.5	10.3	710	380
Potentilla palutris	6	25.8	3.78	120	52

Sagittaria cuneata	3	13.5	0.7	29	1.5
Sagittaria graminea	4	11.7	7	27	59
Sagittaria latifolia	12	49.4	7.95	440	200
Sagittaria rigida	6	15.7	8.4	42	61
Scirpus acutus	10	25.8	13.6	75	120
Scirpus americanus	9	13.4	13.8	27	110
Scirpus fluviatile	9	63	2.9	140	110
Sium suave	12	18.5	7.85	91	180
Solanum dulcamara	1	45		200	
Sparganium eurycarpum	9	55.8	29.24	480	510
Spartina pectinata	10	45.8	2.28	290	150
Triadenum fraseri (Spach) Gl.	4	9.88	2.47	24	21
Typha latifolia	6	71.8	4.86	900	290
Vallisneria americana					
Veronica sp.	1	24		77	
Vicia cracca	3	23.7	4.58	92	35

Appendix 3.6c. Quantitative traits. Mean and standard deviation of stem diameter and measure of leaf area, as measured in plants in the field. Nomenclature follows Fernald (1950) except where taxon authority is given.

Species	N	Mean stem diameter (mm)	Stem diameter STD	Leaf area (cm^2)
Acorus calamus	5	28.26	2.32	69.62
Alisma plantago-aquatica L.	6	18.22	5.67	36.61
Bidens cernua	10	3.71	0.63	5.57
Boehmeria cylindrica	7	3.36	0.22	19.27
Calamagrostis canadensis	6	2.17	0.086	7.37
Campanula aparinoides Pursh.	3	1.08		0.79
Carex lenticularis	9	4.53	1.26	12.46
Carex vesicaria	10	3.94	0.13	19.21
Carex lasiocarpa				
Carex projecta				
Convolvulus sp.	1	1.10		
Dulichium arundinaceum	8	3.63	0.25	3.62
Eleocharis acicularis	11	0.99	0.23	0
Eleocharis erythropoda Steudel	16	1.49	1.02	0
Eleocharis smallii	9	3.14	0.44	0
Equisetum arvense	7	2.71	0.21	0
Equisetum fluviatile	13	3.64	0.35	0
Eriocaulon septangulare	5	1.08	0.01	0.53
Galium palustre	9	0.58	0.13	0.53
Heteranthera dubia	1	1.60		0.2
Hypericum boreale	9	0.85	0.45	0.62
Hypericum ellipticum	6	1.17	0.15	0.79
Impatiens biflora	10	5.67	1.1	2.8
Iris versicolor	5	20.66	0.64	96.35
Isoetes echinospora Durieu	3	7.97	1.36	0.47
Juncus canadensis	1	2.35		
Juncus pelocarpus	3	3.67	2.27	0.46
Juncus subtilis	3	1.45	1.06	0.03
Leersia oryzoides	12	1.71	0.47	14.22
Lycopus uniflorus	8	2.58	0.19	3.21
Lys-nm	4	1.60	0.34	0.82
Lysimachia terrestris	11	4.52	0.35	4.65
Lythrum salicaria	13	13.29	2.71	6.63
Mentha arvensis	7	5.69	15.65	8.75
Mimulus ringens	7	4.96	2.57	3.99
Onoclea sensibilis	9	14.35	14.19	187.92
Phalaris arundinacea	9	4.25	0.4	6.72
Polygonum amphibium	8	3.16	0.49	15.12
P-pers	3	2.87	0.12	23.15
Pontederia cordata	6	67.40	9.45	126.12
Potentilla palutris	6	3.33	0.24	25.15
Sagittaria cuneata	3	6.13	0.32	3.78

Sagittaria graminea	4	6.39	5.91	6.37
Sagittaria latifolia	12	34.80	8.53	127.26
Sagittaria rigida	6	6.88	3.34	3.25
Scirpus acutus	10	11.16	1.45	0
Scirpus americanus	9	6.87	0.427	0
Scirpus fluviatile	9	13.30	0.5	27.68
Sium suave	12	9.18	7.25	9.65
Solanum dulcamara	1	3.00		
Sparganium eurycarpum	9	34.30	24.3	166.08
Spartina pectinata	10	7.81	1.517	31.5
Triadenum fraseri (Spach) Gl.	4	3.23	0.34	6.63
Typha latifolia	6	51.73	10.96	146.43
Vallisneria americana				
Veronica sp.	1	2.05		
Vicia cracca	3	0.88	0.036	0.48

Appendix 3.7. Correlation of the hydrological variables as averaged over different time intervals (1, 3, 7, 12 and 18 growing seasons). Probability values are in parenthesis. (n = 92).

a. fraction of the growing season flooded.

Interval	Pearson product moment coefficients				
	1	3	7	12	18
1	1.00				
3	.98 (<.001)	1.00			
7	.96 (<.001)	.99 (<.001)	1.00		
12	.95 (<.001)	.99 (<.001)	.99 (<.001)	1.00	
18	.93 (<.001)	.98 (<.001)	.99 (<.001)	.99 (<.001)	1.00

b. mean depth of flooding.

Interval	Pearson product moment coefficients				
	1	3	7	12	18
1	1.00				
3	.60 (<.001)	1.00			
7	.49 (<.001)	.92 (<.001)	1.00		
12	.44 (<.001)	.89 (<.001)	.99 (<.001)	1.00	
18	.39 (<.001)	.90 (<.001)	.99 (<.001)	.99 (<.001)	1.00

c. last day of the first flood .

Interval	Pearson product moment coefficients				
	1	3	7	12	18
1	1.00				
3	.99 (<.001)	1.00			
7	.96 (<.001)	.98 (<.001)	1.00		
12	0.95 (<.001)	0.97 (<.001)	0.99 (<.001)	1.00	
18	0.94 (<.001)	0.96 (<.001)	0.99 (<.001)	0.99 (<.001)	1.00

d. beginning of second flood.

Interval	Pearson product moment coefficients				
	1	3	7	12	18
1	1.00				
3	.54 (<.001)	1.00			
7	.36 (<.001)	.77 (<.001)	1.00		
12	.40 (<.001)	.87 (<.001)	.95 (<.001)	1.00	
18	.40 (<.001)	.88 (<.001)	.92 (<.001)	.99 (<.001)	1.00

Appendix 3.8 Correlation among hydrological variables as averaged over 1 **(a)**, 3 **(b)**, 7 **(c)**, 13 **(d)** and 18 **(e)** growing seasons. Variable abbreviations: gs: fraction of the growing season flooded ; md: mean depth of flooding; ld: last day of the first flood; bsec: beginning of second flood. Probability values are in parenthesis. (n = 92).

a. Variables averaged over 1 growing season.

Variable	Pearson product correlation coefficients.			
	gs	md	ld	bsec
gs	1.00			
md	.11 (.27)	1.00		
ld	.93 (<.001)	.050 (.63)	1.00	
bsec	.053 (.61)	.084 (.42)	-.030 (.77)	1.00

b. Variables averaged over 3 growing seasons.

Variable	Pearson product correlation coefficients.			
	gs	md	ld	bsec
gs	1.00			
md	.56 (<.001)	1.00		
ld	.95 (<.001)	.66 (<.001)	1.00	
bsec	.075 (.48)	-.20 (.055)	-.044 (.67)	1.00

c. Variables averaged over 7 growing seasons.

Variable	Pearson product correlation coefficients.			
	gs	md	ld	bsec
gs	1.00			
md	.40 (<.001)	1.00		
ld	.96 (<.001)	.54 (<.001)	1.00	
bsec	-.011 (.92)	-.46 (<.001)	-.089 (.40)	1.00

d. Variables averaged over 13 growing seasons.

Variable	Pearson product correlation coefficients.			
	gs	md	ld	bsec
gs	1.00			
md	.40 (<.001)	1.00		
ld	.97 (<.001)	.51 (<.001)	1.00	
bsec	.047 (.65)	-.51 (<.001)	-.047 (.66)	1.00

e. Variables averaged over 18 growing seasons.

Variable	Pearson product correlation coefficients.			
	gs	md	ld	bsec
gs	1.00			
md	.44 (<.001)	1.00		
ld	.97 (<.001)	.56 (<.001)	1.00	
bsec	.11 (.30)	-.49 (<.001)	.023 (.83)	1.00

Appendix 3.9 Twelve-year averages of hydrological variables for the 92 quadrats from Day et al. (1988).

Fraction of growing season flooded	Mean depth of flooding (m)	End of first flood (days)	Beginning of second flood (days)
0.37	0.59	62.67	92.75
0.28	0.53	50.08	103.67
0.62	0.6	92.33	104.3
0.45	0.61	69.58	95.22
0.54	0.6	85.42	99.33
0.86	0.59	146.67	126.86
0.73	0.59	104.67	128.45
0.61	0.6	91.83	107.2
0.61	0.6	91.83	107.2
0.2	0.45	32.92	38.6
0.22	0.5	36.75	45.33
0.22	0.49	36.5	45.5
0.31	0.55	53.5	109.4
0.2	0.47	34.92	46.6
0.47	0.52	69.58	104.9
1	0.61	194	0
0.53	0.51	84.17	113.8
0.53	0.51	84.17	113.8
0.5	0.51	79.33	106.1
0.52	0.51	82.25	114.4
0.58	0.51	89	95.78
0.44	0.52	69	110.78
0.59	0.51	90.08	90.56
0.43	0.52	67.08	95.7
0.81	0.49	128.42	121.11
1	0.58	188.42	132
1	0.81	194	0
0.96	0.53	167.83	139.2
0.94	0.52	160.17	137.5
1	0.79	194	0
1	1.03	194	0
1	0.77	194	0
1	0.63	194	0
1	0.64	194	0
0.36	0.5	60.17	78.71
0.34	0.5	59	69
0.59	0.51	89.42	90.22

0.51	0.51	80.5	112.9
0.46	0.52	69.58	95.22
0.9	0.63	160.33	137.17
0.92	0.64	167.58	139.8
0.97	0.67	188.42	135
0.93	0.64	167.83	139.4
0.94	0.64	167.92	135.4
0.74	0.62	128.25	123
0.56	0.63	91.08	98.33
0.83	0.62	146.67	126
0.84	0.62	148.67	127.57
0.85	0.62	153.33	123.33
1	0.82	194	0
0.99	0.67	188.5	133
0.99	0.68	188.42	132
1	0.82	194	0
1	0.61	188.42	132
0.86	0.54	146.58	136.71
0.95	0.56	160.33	137.17
1	0.8	194	0
1	0.82	194	0
0.61	0.55	91.5	111.2
0.79	0.53	122.5	123.8
0.78	0.53	120.33	125.7
0.61	0.55	91.67	111.2
0.53	0.55	84.17	113.8
0.35	0.54	59.33	69
0.36	0.54	60.58	78.57
0.54	0.55	84.58	105.6
0.44	0.56	69	110.78
0.56	0.55	85.75	99.33
0.53	0.55	84.17	113.8
0.52	0.55	80.92	113.3
0.51	0.55	80.17	113.9
0.58	0.55	86.83	103.4
0.52	0.55	80.92	113.3
0.51	0.51	59.17	74.25
0.39	0.58	49.75	71
0.58	0.49	60.5	70.17
0.42	0.56	50.25	69.08
0.56	0.49	59.42	69.5
0.2	0.74	32.42	62.88
0.24	0.71	33.92	48.75
0.23	0.7	33.67	49.13
0.23	0.7	33.67	49.13

0.23	0.71	33.58	49.13
0.54	0.5	59.33	73.67
0.73	0.49	95.83	80.89
0.78	0.53	110.75	88.38
0.3	0.66	39.17	55.2
0.26	0.7	35.42	54.9
0.75	0.51	98.08	84.5
0.74	0.5	96.67	82.78
0.76	0.52	103.75	91.56
0.8	0.55	118.67	99.63

Appendix 3.10. Values for substrate variables for the 92 quadrats from Day *et al.* (1988).

Gravel (%)	Loss on ignition (%)	pH	Phosphorous	Sand (%)	Silt/clay (%)
0.15	2.73	7	4	76.45	23.4
4.7	1.95	7.7	6	83.64	11.66
0.01	5.8	6.5	6	66.81	33.18
0.14	1.39	7.7	4	84.47	15.15
0.08	1.2	7.6	3	89.4	10.52
0.04	0.72	7.7	3	91.34	8.62
0.01	0.36	7.8	2	94.17	5.82
0.6	0.76	7.6	6	90.33	9.07
0.49	0.57	7.6	6	94.68	4.84
0.32	2.9	7.3	5	82.26	17.43
0	5.49	7	10	66.09	33.91
0.26	1.87	7.7	4	82.23	17.47
0.39	16.23	7	11	65.26	34.35
2.21	1.65	7.5	3	89.67	8.12
9.55	11.21	6.6	10	70.81	19.64
4.77	8.7	6.7	4	62.9	32.33
11.1	4.71	6.9	4	66.02	22.87
20.07	6.64	7.3	7	59.92	20.01
20.02	5.22	7.3	6	61.83	18.15
0	18.1	5.6	8	75.78	24.22
4.88	14.55	5.8	10	61.93	33.19
0	22.69	5.7	9	72.25	27.75
0	27.45	5.8	11	72.18	27.82
0	29.5	5.7	16	74.48	25.52
0.09	27.49	6	13	77.31	22.6
4.52	17.66	6.1	3	66.39	29.09
3.09	9.33	6.2	6	62.21	34.69
0.14	13.44	6.3	6	59.35	40.51
0.1	18.61	7	8	67.16	32.74
47.74	2.95	7.6	6	36.63	15.62
55.8	1.96	7.3	3	36.39	7.81
50.63	1.87	7.7	7	37.43	11.95
55.25	1.03	7.7	5	33.57	11.19
72.68	3.51	7.3	9	24.83	2.48
0	12.99	7.5	24	57.47	42.53
0	15.93	7.3	19	65.03	34.97
0	16.22	6.3	14	71.09	28.91
0	16.11	6.5	24	77.85	22.15
0	22.14	6.3	13	72.74	27.26

0	2.93	6.7	3	96.36	3.64
0	8.09	6.4	2	93.96	6.04
0	8.37	6.1	2	94.77	5.23
0	6.94	6.4	3	95.09	4.91
0	3.04	6.5	4	95.35	4.65
0	19.35	5.9	11	93.39	6.61
0	7.01	6	2	91.57	8.43
0	8.66	6.3	7	92.1	7.9
0.05	3.61	6.4	3	99.14	0.81
0	17.15	6.1	5	89.08	10.92
0	1.58	6.7	6	98.6	1.4
0	2.17	6.7	6	98.21	1.79
0.01	1.94	6.5	6	97.82	2.17
0	1.47	6.9	6	98.96	1.04
19.6	0.73	7.4	2	76.35	4.05
0.93	0.59	7.7	3	93.8	5.27
0.01	1.85	7.4	4	88.46	11.54
2.7	1.09	7.6	3	80.6	16.7
1.26	5.45	6.4	7	72.47	26.28
5.34	0.51	7.8	2	90.53	4.14
0.82	7.26	6.6	8	62.24	36.94
0.59	7.88	6.4	14	66.15	33.25
3.12	0.7	7.6	3	88.26	8.63
4.02	1.19	7.7	3	83.08	12.9
6.48	2.78	6.9	4	80.09	13.42
9.36	1.61	7.5	6	82.57	8.07
0.04	8.84	5.7	9	63.24	32.72
4.11	4.83	6.8	9	55.19	40.7
3.29	5.4	7.1	9	61.79	34.92
1.74	1.09	7.7	3	89.57	8.69
0.41	2.92	7.6	5	84.99	14.59
9.11	3.54	7.6	5	84.42	6.47
0.58	4.17	7.1	6	72.57	26.85
0.65	2.35	7.4	7	77.06	22.28
0.01	2.25	6.2	4	89.87	10.11
0.04	2.36	6.5	3	94.06	5.89
0.09	1.65	6.9	3	93.29	6.63
0.17	5.2	6	3	81.41	18.42
0.02	2.8	6.3	9	87.41	12.56
0.11	10.72	5.9	4	82.63	17.26
0	6.6	5.7	3	62.05	37.95
0	13.95	5.9	5	69.21	30.79
0	5.45	5.4	3	69.8	30.2
0.41	10.85	6.1	5	74.67	24.92
0.4	0.47	5.8	1	99.03	0.57

0.03	0.61	6.9	2	95.77	4.21
0.08	0.44	6.8	2	98.02	1.9
0	4.77	6	3	73.3	26.7
0	6	5.8	3	69.88	30.12
0.09	1.78	5.8	7	93.69	6.22
0	1.49	6.2	5	96.81	3.19
0.21	1.43	6.4	3	97.08	2.71
0.39	0.92	6.5	6	95.34	4.26

Appendix 4.1a. Elevation of points at lower limit of woody cover at test sites.

Westmeath[*]	Luskville[*]	Appleton[†]	Waddington[‡]	Cape St. Jacques[‡]	Deux Montagnes[‡]
38.047	57.56	1.73	74.295	21.65	22.03
38.022	58.26	1.76	74.11	21.67	22.14
38.032	58.29	1.76	74.155	21.68	
38.002	58.293	1.81	74.115	21.72	
37.927	58.34	1.815	74.005	21.985	
37.882	58.44	1.825	73.985	22.07	
37.892	58.465	1.83	73.975	22.085	
38.037	58.49	1.85	74.085	22.26	
38.027	58.515	1.87	74.155	22.355	
37.982	58.525	1.9	74.255	22.365	
38.007	58.55	1.93	74.135	22.375	
38.022	58.56	1.97	74.08	22.68	
38.042	58.685	1.975	74.11	22.79	
37.912	58.685	1.975	74.155	22.82	
37.932	58.74	2.005		22.86	
37.787	58.75	2.04		22.87	
37.827	58.755	2.085		22.88	
37.977	58.835	2.225		22.91	
37.832					

[*] Geodetic Survey of Canada Datum.

[†] Discharge (m^3/sec).

[‡] Great Lakes Datum.

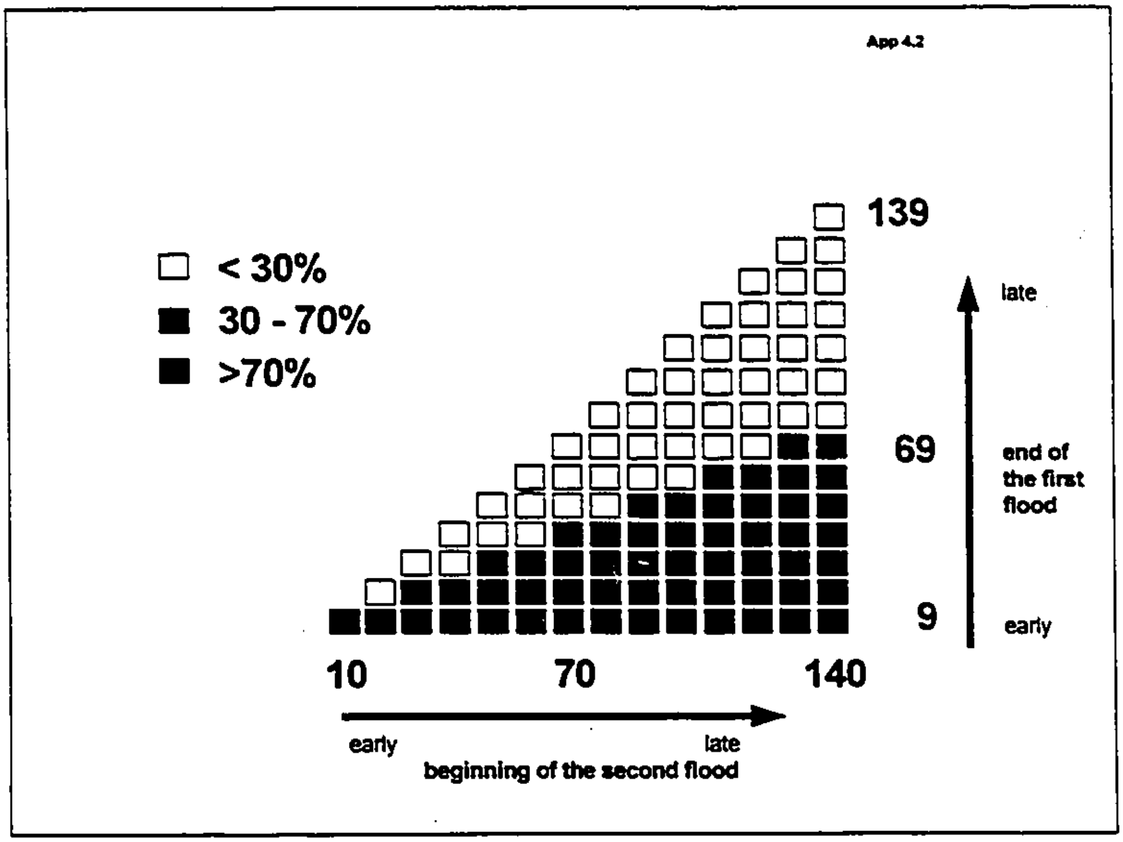
Appendix 4.1.b. Data from 62 transects at Lac St.-Louis site. Elevation refers to the lower limit of woody cover with respect to Great Lakes Datum. Exposure refers to the original classification of le Groupe Dryade (te = très élevée, e = élevée, m = moyenne, f = faible, n = nulle). Data extracted from le Groupe Dryade (1985).

Elevation (m)	Exposure
21.345	m
21.39	m
21.42	n
21.445	te
21.445	te
21.445	te
21.45	f
21.455	n
21.455	n
21.485	f
21.49	f
21.535	f
21.535	m
21.535	n
21.54	f
21.54	n
21.55	n
21.55	te
21.555	te
21.56	m
21.56	te
21.57	f
21.57	f
21.57	n
21.575	te
21.595	f
21.61	m
21.62	f
21.62	te
21.635	f
21.635	f
21.635	f
21.64	m
21.64	te
21.65	m
21.66	m

21.66	n
21.695	f
21.695	n
21.7	m
21.7	te
21.715	f
21.73	n
21.74	f
21.74	n
21.8	f
21.805	f
21.805	te
21.825	m
21.865	te
21.875	n
21.88	m
21.88	m
21.925	n
21.93	n
21.94	n
21.95	n
21.95	te
21.95	te
21.965	n
22.06	e
22.155	te

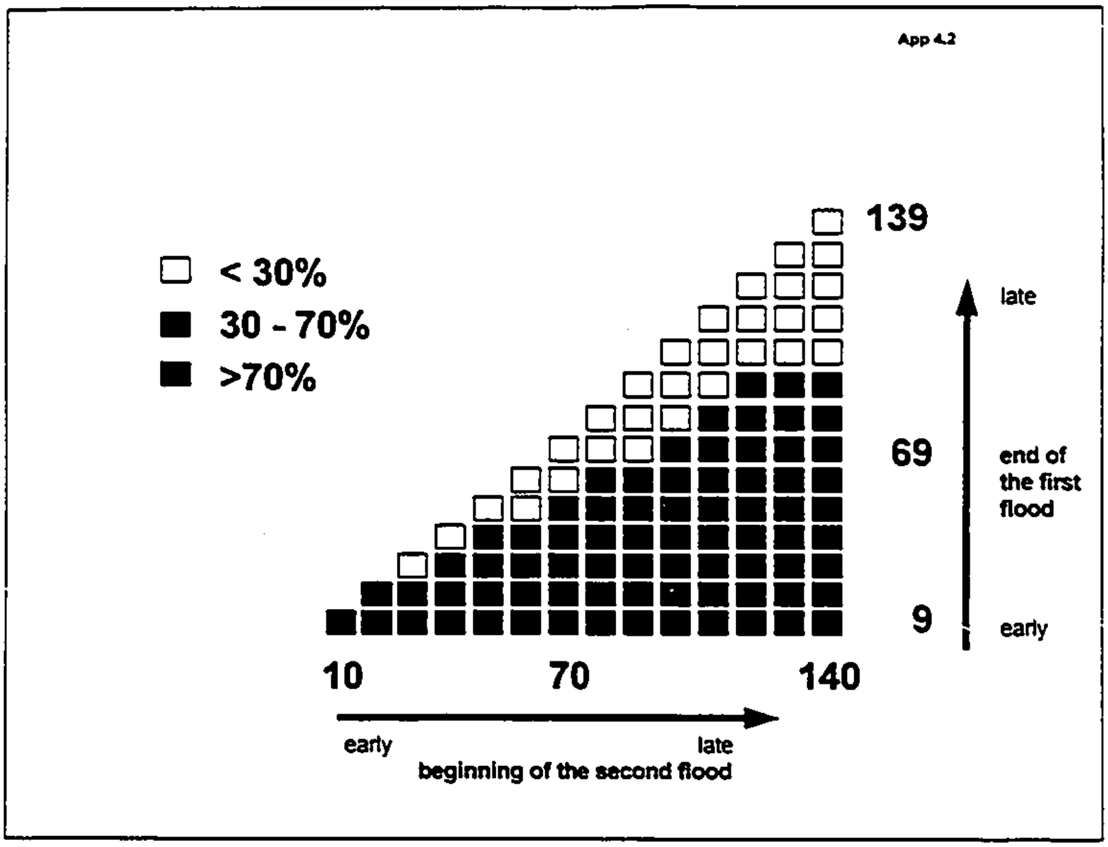
Appendix 4.2. Range of end of first flood (eff) and beginning of second flood (bsec) where the probability of occurrence of woody cover is between .3 and .7 for the (a) 7 year interval; (b) 18 year interval and (c) composite of the 7, 12 and 18 year intervals.

(a) 7 year interval.



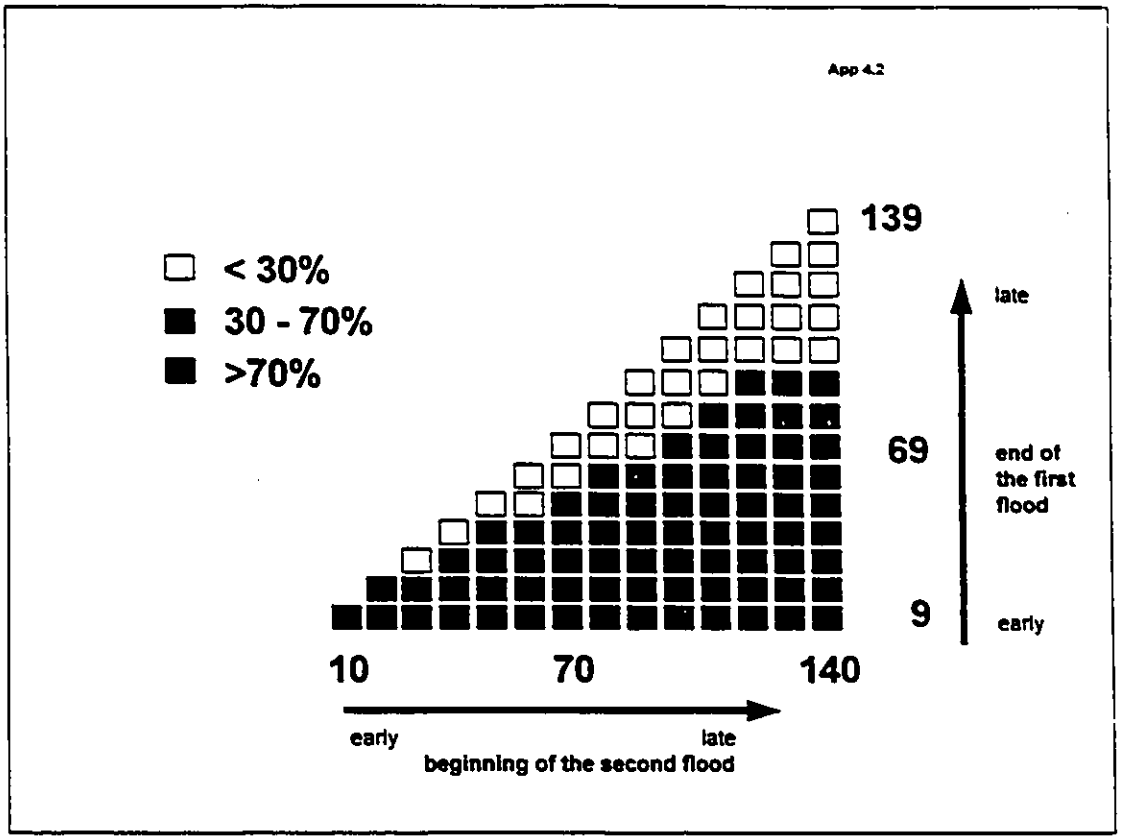
$\ln(p/(1-p)) = .11\ (bsec) - .21\ (eff)$

(b) 18 year interval.



ln(p/(1-p)) = .12 (bsec) - .17 (eff)

(c) composite of predictions.



Appendix 5.1. Duration of flooding at boundary of functional groups in 11 transects from Ottawa River wetlands. Values included are the lower boundary for herbids and plants with stem diameter of 1 - 2 mm; the upper boundary for aquatic, isoetid and leafless plants; and both boundaries for plants with stem diameter > 30 mm.

Site	Functional group	Elevation (m)	Fraction of the growing season flooded
Luskville	Aquatic		
	A	58.02	0.50
	B	58.19	0.38
	C	absent	
	D	57.82	0.76
	E	57.92	0.62
	F	58.16	0.39
	Herbid		
	A	57.79	0.79
	B	57.92	0.62
	C	58.43	0.27
	D	57.78	0.80
	E	57.77	0.82
	F	58.16	0.39
	Isoetid		
	A	58.54	0.22
	B	58.04	0.49
	C	58.78	0.13
	D	58.15	0.40
	E	58.3	0.32
	F	58.43	0.27
	Stem diameter > 30 mm		
	A	58.43	0.27
		57.7	0.91
	B	58.19	0.38
		58.11	0.43
	C	absent	
	D	58.15	0.40
		57.9	0.65
	E	57.9	0.65
		57.85	0.72
	F	57.39	1.00
		57.41	1.00
	Leafless		
	A	58.43	0.27

	B	58.1	0.43
	C	not dominant	
	D	58.15	0.40
	E	58.24	0.36
	F	58.24	0.36
	Stem diameter = 1 - 2 mm		
	A	not dominant	
	B	not dominant	
	C	not dominant	
	D	58.15	0.40
		58.1	0.43
	E	58.23	0.36
		58.19	0.38
	F	not dominant	
Fitzroy	Aquatic		
	A	57.75	0.58
	B	57.85	0.48
	C	57.8	0.53
	D	57.8	0.53
	E	57.8	0.53
	Herbid		
	A	57.7	0.63
	B	57.55	0.75
	C	57.75	0.58
	D	57.8	0.53
	E	57.7	0.63
	Isoetid		
	A	58	0.37
	B	58.2	0.28
	C	58.15	0.31
	D	58.05	0.34
	E	58.05	0.34
	Stem diameter > 30 mm		
	A	absent	
	B	57.4	0.76
		57.5	0.76
	C	58.4	0.20
		58.5	0.18
	D	58.15	0.31
		57.65	0.69
	E	absent	
	Leafless		

A	57.8	0.53
B	57.8	0.53
C	57.8	0.53
D	57.9	0.44
E	58.25	0.27
Stem diameter = 1-2 mm		
A	58	0.37
	57.7	0.63
B	not dominant	
C	not dominant	
D	not dominant	
E	not dominant	

Appendix 5.2. Substrate data for 11 transects for Ottawa River wetlands.

Site	Transect	Elevation	Loss on ignition (%)	Sand fraction (%)
Luskville	A	upper	4	89
		middle	7	89
		lower	5	79
	B	upper	7	82
		middle	8	68
		lower	4	89
	C	upper	3	86
		middle	1	87
		lower	1	96
	D	upper	6	67
		middle	5	88
		lower	4	75
	E	upper	3	93
		middle	8	82
		lower	2	87
	F	upper	4	79
		middle	1	83
		lower	1	90
Fitzroy	A	upper	6	86
		middle	7	71
		lower	-	-
	B	upper	14	85
		middle	-	-
		lower	10	82
	C	upper	10	84
		middle	8	83
		lower	9	76
	D	upper	20	77
		middle	23	70
		lower	8	83

E	upper	6	92
	middle	5	90
	lower	4	92