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Département d'anthropologie et d'écologie

FACULTE DES SCIENCES
Prof. J.-B. Lachavanne

Végétation aquatique et gradients environnementaux en zone alluviale péri-lacustre (lac de Neuchâtel, Suisse)

Thèse

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Jessica CASTELLA-MÜLLER

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que je me réjouis d’accompagner

dans la Vie et à la Vie, qui est si belle !

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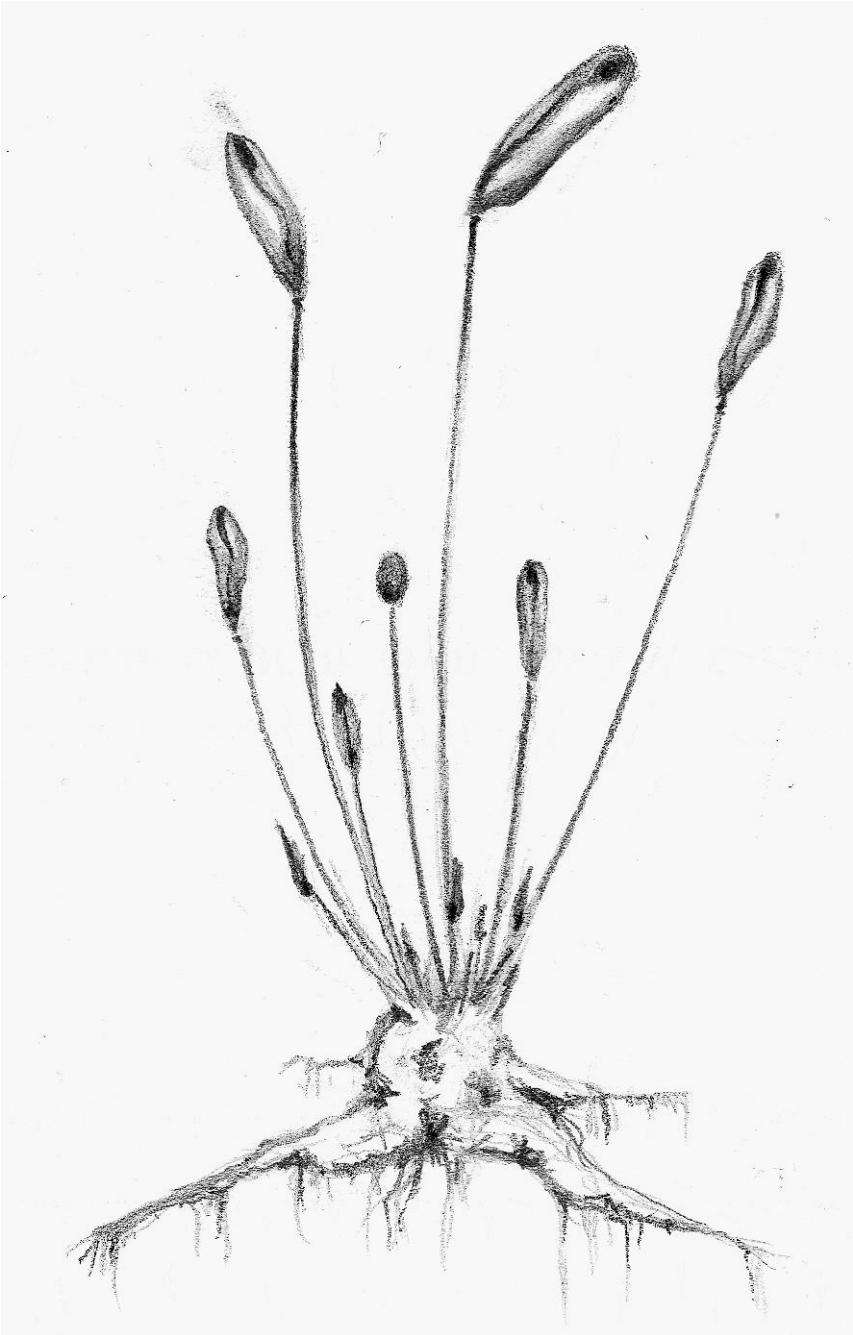
Introduction Générale



Les zones humides reçoivent une attention constante depuis le début des années 1980, époque à laquelle leur existence et leur valeur, en termes de ressources socio-économiques, est enfin reconnue. Le nombre important d'ouvrages publiés à leur sujet en témoigne (Good *et al*., 1978; Williams, 1990; Mitsch et Gosselink, 1993; Mitsch, 1994; Keddy, 2000). Les zones alluviales, qui se distinguent en zones alluviales péri-lacustres et fluviales en constituent une catégorie particulière.

L'agriculture (drainage), l'urbanisation des berges (construction de ports, d'industries, de zones résidentielles), l'endiguement, l'exploitation des fonds lacustres et la régulation du niveau de l'eau ont conduit à la disparition et à la dégradation de surfaces considérables de zones alluviales péri-lacustres (Whillans, 1982; Wilcox et Meeker, 1992; Crosbie et Chow-Fraser, 1999). En Europe, ces zones alluviales ont bénéficié très tôt des travaux remarquables effectués par Pieczyńska (1963, 1965, 1968, 1971, 1972, 1986, 1990) et Pieczyńska *et al*. (1988) sur l'hydrologie, la physico-chimie des eaux et des sédiments et certaines communautés vivantes (algues, macrophytes, macrofaune) de la zone eulittorale de lacs polonais. Ces recherches ont également porté sur l'étude de processus tels que la production primaire et la décomposition de la matière organique. Les grands lacs nord-américains (Etats-Unis et Canada), dont les zones alluviales ont perdu jusqu'à 75% (et souvent plus) de leur surface au cours des 175 dernières années (Whillans, 1982), font l'objet de programmes de gestion dès le début des années 1980. Les fluctuations du niveau de l'eau et la géomorphologie sont rapidement identifiés comme des facteurs déterminants dans la création et le maintien de ce type d'écosystèmes. De l'interaction entre la végétation et les variations du niveau de l'eau résulte i) la variation de la surface des zones alluviales péri-lacustres, ii) la diversité des formations végétales qui les colonisent et iii) l'importante diversité spécifique des espèces végétales au sein de ces différentes formations (Stuckey, 1975, Keddy et Reznicek, 1986). L'étude de divers groupes faunistiques (essentiellement oiseaux et poissons) en révèle l'importante richesse (Smith *et al*., 1991). Divers aspects du fonctionnement de ces écosystèmes sont également considérés ici, tels que la production primaire, la décomposition de la matière organique et le cycle des nutriments (Godshalk et Wetzel, 1978; Prentki *et al*., 1978). Plus récemment, les recherches sur les zones alluviales péri-lacustres des lacs nord-américains se sont étendues à l'échelle du bassin versant dans la perspective d'en déterminer l'importance dans les processus de dégradation des zones humides (Whigham *et al*., 1988; Crosbie et Chow-Fraser, 1999; Lougheed, 2001). La végétation suscite elle aussi une grande attention. Les principales études s'intéressent i) au phénomène de compétition entre les espèces végétales (Gaudet et Keddy, 1988; Shipley et Keddy, 1994; Gaudet et Keddy, 1995; Keddy *et al*., 1998), ii) à l'importance de la banque de graines contenue dans les sédiments et aux relations qui existent entre cette banque de graines et la végétation établie (van der Valk, 1981; Keddy et Reznicek, 1986; Wilson *et al*., 1993; Willis et Mitsch, 1995) et iii) aux traits et à la classification fonctionnelle des espèces végétales (Boutin et Keddy, 1993; Keddy et Weiher, 1995; Weiher et Keddy, 1995). La végétation a la particularité d'être fixe. Cette observation triviale implique cependant que les espèces végétales

doivent posséder la totalité des traits (caractéristiques morphologiques, physiologiques et phénologiques) nécessaires pour tolérer les conditions du site qu'elles occupent, et ce pendant plusieurs années (Keddy, 1999). Sous l'impulsion des travaux de Grime sur la végétation terrestre (Grime, 1974, 1979), la considération des traits des espèces s'est répandue comme une approche fonctionnelle prometteuse des communautés végétales, venant compléter l'approche phyto-sociologique descriptive classique. Les stratégies des espèces (combinaisons de traits) ont été intégrées par Keddy (1992) dans des procédures visant à prédire la composition spécifique des communautés végétales (Assembly rules) ou/et leur changement sous l'influence de conditions environnementales données (Response rules) (Keddy, 1992; Weiher et Keddy, 1999).

Il est frappant de constater que les auteurs ayant effectué des études sur les zones alluviales péri-lacustres ne s'intéressent, ni même ne mentionnent l'existence d'étangs au sein de ces écosystèmes. Pieczyńska (1972, 1990) et Pieczyńska et Zalewski (1997), rares (ou seuls ?) auteurs ayant intégré ces milieux dans leurs recherches, observent pourtant qu'ils se caractérisent par une physico-chimie particulière et abritent souvent, au sein de la zone alluviale péri-lacustre, la plus importante richesse et abondance de certains groupes de macrofaune.

Au contraire, ce type d'écosystème a été largement considéré dans l'étude des plaines alluviales fluviales, et reconnu comme partie intégrante des cette zone écotonale. Dans leur état originel, les zones alluviales fluviales apparaissent comme un réseau extrêmement riche et diversifié de milieux lotiques, semi-lotiques et lénitiques, permanents ou temporaires (Amoros et Roux, 1988, Amoros et Petts, 1993; Ward, 1998). L'importante hétérogénéité spatiale et temporelle qui caractérise ces écosystèmes résulte de l'action conjointe de phénomènes hydrologiques (crues, étiages), géomorphologiques (érosion, sédimentation, incision, exhaussement) et des successions écologiques à diverses échelles spatiales (Amoros et Roux 1988; Amoros et Petts, 1993; Bornette *et al*., 1998a; Amoros et Bornette, 2002; Buijse *et al*., 2002). Cette variété de conditions environnementales est potentiellement le support physique d'une importante diversité biotique (Tockner *et al*., 1998; Ward, 1998; Bornette *et al*., 1998a; Amoros, 2001; Amoros et Bornette, 2002). Au cours des deux derniers siècles, les zones alluviales fluviales ont connu elles aussi une très forte régression en Europe et en Amérique du Nord comme dans le reste du monde (Amoros et Roux, 1988; Petts *et al*., 1989; Dynesius et Nilsson, 1994; Anonyme, 1994). Le Haut-Rhône et le bas cours de l'Ain en France ne font pas exception et ont subi d'importantes transformations consécutives à la construction de barrages hydroélectriques et à l'endiguement des berges, ainsi qu'à l'incision du lit de la rivière. Ces plaines alluviales, et le réseau de plans d'eau qui les constituent, font l'objet de nombreuses recherches hydrologiques et géomorphologiques depuis les années 1980 (Juget *et al*., 1976; Bravard, 1982; Bravard, 1986; Bravard *et al*., 1986), de même que faunistiques (Castella *et al*., 1984, 1991; Copp, 1987; Statzner et al., 1994). La végétation aquatique y a reçu une attention particulière.

La composition et la richesse spécifique de ces milieux ont été étudiés, dans un premier temps, au travers d'une approche phyto-sociologique (Balocco-Castella, 1988; Henry *et al*., 1994; Bornette *et al*., 1996). Dans un deuxième temps, ces études ont été complétées par une approche plus fonctionnelle, basée sur la connaissance des traits des espèces recensées dans une perspective prédictive (Bornette *et al*., 1994; Barrat-Segretain et al., 1998, 1999; Barrat-Segretain and Bornette, 2000; Bornette *et al*., 2001; Combroux, 2001; Greulich *et al*., 2000, 2001). L'ensemble des approches menées dans ces deux secteurs ont conduit à une meilleure compréhension du fonctionnement des zones alluviales fluviales en général, de celles du Haut Rhône français et du bas cours de l'Ain en particulier. Elles ont également permis la mise en place d'un cadre conceptuel et théorique robuste nécessaire à l'identification des mesures de gestion (protection, conservation) plus efficaces.

Le présent travail vise tout d'abord à contribuer à une meilleure compréhension du fonctionnement des zones alluviales péri-lacustres, et de la Grande-Cariçaie en particulier. Plus grande zone alluviale péri-lacustre en Suisse, reconnue d'importance internationale par la Convention de Ramsar sur les zones humides (Ramsar Convention Bureau, 1971), la Grande-Cariçaie subit les conséquences de la régulation du niveau du lac de Neuchâtel. Les étangs, qui constituent des éléments particulièrement importants de cet écosystème en termes d'habitats et de biodiversité, connaissent la régression la plus sensible. Renevey (1981) indique en effet que 50% des surfaces d'eau libres ont disparus en 40 ans (entre 1937 et 1979). Grâce au Groupe d'Etude et de Gestion de la Grande-Cariçaie (GEG), cette zone alluviale bénéficie d'une cartographie précise de la végétation du bas-marais (Clerc, 1994), de même que d'un inventaire faunistique (Mülhauser, 1997) et d'une typologie des étangs (Mülhauser, 1996). Ces études fournissent des données très utiles sur ces écosystèmes, mais comme dans la plupart des travaux effectués sur ce type de milieu, i) les connaissances ne sont pas structurées au sein d'un cadre conceptuel et théorique bien établi et ii) les petits plans d'eau intérieurs demeurent encore peu étudiés.

Le présent travail a pour objectifs i) d'acquérir des connaissances sur des étangs de zones alluviales péri-lacustres, sous-représentés à la fois des études portant sur les petits plans d'eau et des études portant sur les zones alluviales péri-lacustes, et ii) d'apporter une dimension prédictive à l'étude de la végétation par l'intégration des traits des espèces, pour promouvoir à moyen terme une meilleure gestion de ces milieux. Dans ce but, quinze étangs de la Grande-Cariçaie ont été étudiés sur la base de relevés de végétation aquatique et d'analyses physico-chimiques de l'eau et des sédiments.

Il vise aussi à comparer des zones alluviales péri-lacustres et fluviales, puisque les étangs présents dans les premières s'apparentent, par divers aspects aux milieux semi-lotiques et lénitiques des secondes. A cette fin, des relevés de végétation aquatique, ainsi que des mesures physico-chimiques de l'eau ont été effectués dans dix plans d'eau de la plaine alluviale du cours inférieur de l'Ain (France).

L'étude des quinze étangs de la Grande-Cariçaie et des dix sites de l'Ain est présentée ici sous la forme de quatre articles successifs.

Le premier article décrit les caractéristiques physico-chimiques et sédimentaires des étangs de la Grande-Cariçaie, mesurées et analysées sur une période de deux ans, dans la perspective i) d'évaluer l'hétérogénéité spatiale et temporelle des conditions environnementales à diverses échelles au sein de la zones d'étude, ii) d'évaluer l'influence des connexions hydrologiques étangs-lac-eaux souterraines dans cette hétérogénéité spatio-temporelle et iii) de poser le cadre environnemental de référence nécessaire à l'interprétation des résultats relatifs à la végétation aquatique de ces étangs.

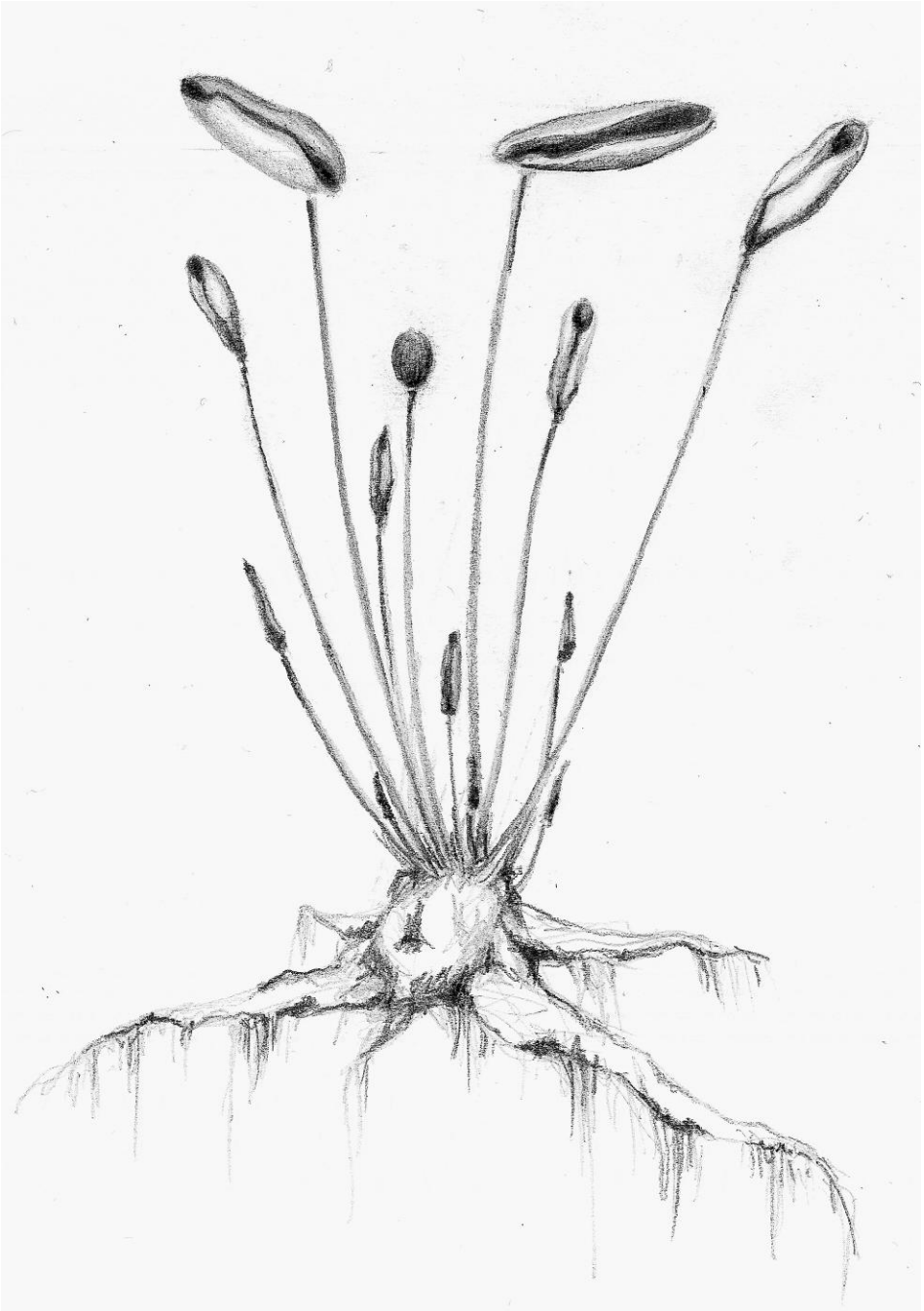
Le second article analyse la végétation aquatique de ces étangs en termes de richesse et de composition spécifiques et compare ces variables à diverses échelles spatiales. Il identifie également des groupements végétaux dont la répartition permet une mesure de l'hétérogénéité spatiale au sein des étangs.

Le troisième article présente une caractérisation fonctionnelle des communautés végétales des étangs de la Grande-Cariçaie par l'utilisation d'une base de données des traits des espèces échantillonnées. La mise en relation de la variabilité de la composition des traits et des conditions environnementales des étangs permet de tester dans le domaine péri-lacuste les prédictions effectuées dans le cadre des études menées sur les zones alluviales fluviales.

Le quatrième article intègre les données environnementales et floristiques des quinze étangs de la Grande-Cariçaie et celles des dix sites du bas cours de l'Ain, permettant une approche comparative des richesses et des compositions spécifiques, ainsi que des traits des espèces. Cet article présente également une approche comparative de la diversité des données utilisées pour décrire les communautés végétales (composition et richesse spécifiques, «uniqueness», composition et diversité des traits) et environnementales (moyennes *vs.* variabilité saisonnière) et cherche à comparer leur capacité respective à caractériser ces milieux.

Chapitre 2

Les Zones Humides



2.1 Définition des zones humides

Qu'est-ce, réellement, qu'une zone humide ? A cette question, qui introduit pourtant la majorité des ouvrages traitant de ce thème, aucun auteur ne saura donner de réponse simple ni unique (Mitsch et Gosselink, 1986; Finlayson et van der Valk, 1995; Keddy, 2000). La difficulté à définir précisément les limites scientifiques de ces zones découle sans doute de la position intermédiaire qu'elles occupent, entre terre et eau (Keddy, 2000). Keddy (2000) dira d'elles: «From outer space, our planet appears as a mosaic of blue and green – blue for water, green for plants. Wetlands are where green meets blue". Ce n'est qu'à partir des années 1980 que ces zones écotonales sont reconnues comme des unités à part entières, ayant des caractéristiques physiques, chimiques et biologiques spécifiques (van der Valk, 1981, Pieczyńska, 1990, Naiman et Décamps, 1990).

Toutes les zones humides ont en commun, 1) la présence permanente d'eau, à la surface ou à l'intérieur de la zone racinaire, 2) des sols aux caractéristiques uniques, saturés en eau, dans lesquels dominent le plus souvent des conditions anaérobies et 3) une végétation adaptée ou tolérante aux effets directs et indirects des inondations (Cowardin *et al*., 1979; Keddy, 2000). Ces trois caractéristiques ne constituent cependant qu'une petite base commune, face à la multitude de paramètres qui les différencient. Keddy (2000) écrit que «wetlands arise because there is water, but the particular kind of wetland, and the characteristics of its species or communities, will depend upon other environmental factors». Les zones humides se distinguent en effet de par la taille, le régime hydrologique (fréquence, époque et profondeur des inondations), le régime des perturbations (fréquence, intensité, durée et surface de la zone perturbée), la teneur en substances nutritives, le position dans le paysage (côtière ou intérieure) et le degré d'anthropogénisation. Le nombre de définitions reflète cette diversité de caractéristiques ainsi que celle des groupes d'intérêts concernés. Un scientifique ne définit sans doute pas une zone humide de la même manière selon qu'il est géologue, gestionnaire, sociologue ou biologiste. D'autre part, les définitions varient souvent en fonction des objectifs poursuivis. Deux d'entre elles sont néanmoins plus largement acceptées et citées que les autres: 1) celle du U.S. Fish and Wildlife Service (Cowardin *et al*. 1979), plus précise et restrictive que 2) celle adoptée dans le cadre de la Convention de Ramsar sur les zones humides d'importance internationale en 1971, qui inclut les rivières, les zones côtières et les massifs coralliens.

1) "Wetlands are lands transitional between terrestrial and aquatic systems where the water *tableau* is usually at or near the surface or the land is covered by shallow water…Wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes, (2) the substrate is predominantly undrained hydric soil, and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of each year" (Cowardin *et al*. 1979).

2) “Wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish, or salt including areas of marine water, the depth of which at low tide does not exceed six meters” (Ramsar Convention Bureau, 1971.

La difficulté à définir clairement et simplement les zones humides a eu comme conséquence la constitution tardive d’un cadre légal solide pour permettre des mesures de protection ou/et de compensation efficaces (Whigham, 1999).

2.2 Classification des zones humides

La classification des zones humides s’avère aussi ardue à établir que leur définition. Keddy (2000) et Cowardin et Golet (1995) s’accordent à dire qu’aucun système de classification unique ne peut capter, à l’échelle mondiale, la diversité des facteurs qui produisent les zones humides. Et pourtant les tentatives ne manquent pas. En effet, les classifications se basent selon les auteurs sur:

1) des critères «de position» dans le paysage (Tableau 2.1).

Tableau 2.1 Extrait de la classification des zones humides proposée par Cowardin *et al.* (1979) (in Keddy, 2000) sur la base, notamment, de leur situation géographique.

Estuarine	Subtidal	Rock bottom Unconsolidated bottom Aquatic bed Reef
	Intertidal	Aquatic bed Reef Streambed Rocky shore Unconsolidated shore Emergent wetland Scrub–shrub wetland Forested wetland
Riverine	Tidal	Rock bottom Unconsolidated bottom Aquatic bed Rocky shore Unconsolidate shore Emergent wetland
	Lower perennial	Rock bottom Unconsolidated bottom Aquatic bed Rocky shore Unconsolidated shore Emergent wetland
	Upper perennial	Rock bottom Unconsolidated bottom Aquatic bed Rocky shore Unconsolidated shore
	Intermittent	Streambed
Lacustrine	Limnetic	Rock bottom Unconsolidated bottom Aquatic bed

2) les régimes hydrologiques (variations du niveau de l'eau et durée de saturation en eau) associés aux apports en éléments nutritifs (Figure 2.1).

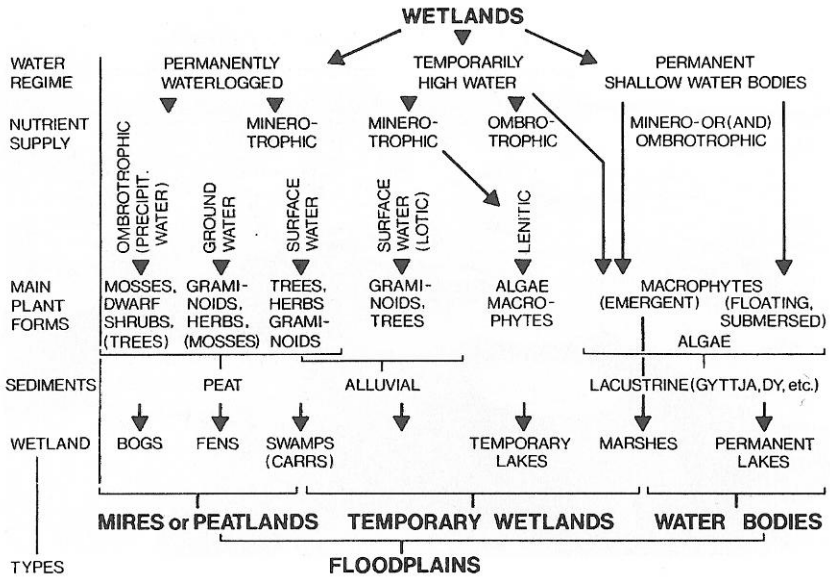


Figure 2.1 Identification de différents types de zones humides sur la base du régime hydrologique et de l'apport en substances nutritives (in Keddy (2000), d'après Gopal *et al*. 1990).

3) les contributions respectives de trois sources d'eau: précipitation, eau souterraine et eau de surface (Figure 2.2).

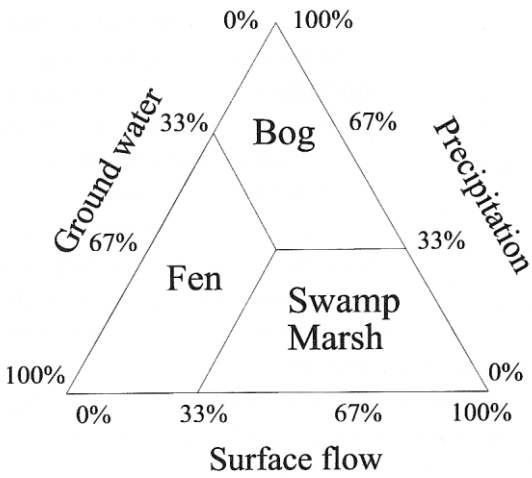


Figure 2.2 Identification de trois types de zones humides (fen, bog, swamp marsh) sur la base de la contribution respective de trois types d'alimentation en eau: eau souterraine, eau de surface et précipitations (in Keddy (2000), d'après Brinson (1993a, b).

4) les types dominants de végétation (Keddy, 2000):

   a. Swamp: communauté dominée par des arbres enracinés dans des sols inondés non tourbeux,
   b. Marsh: communauté dominée par des plantes herbacées émergentes enracinées dans des sols inondés non tourbeux,
   c. Bog: communauté dominée par des *Sphagnum*, des laîches et des arbustes d'éricacées, enracinés dans des sols épais tourbeux,
   d. Fen: communauté dominée par des laîches et des joncs enracinés dans un sol tourbeux peu épais et connaissant d'importantes fluctuations du niveau de l'eau,
   e. Wet meadow: communauté dominée par des plantes herbacées enracinées dans des sols inondés seulement occasionnellement,
   f. Shallow water: communauté dominée par des espèces strictement aquatiques dont la croissance s'effectue dans au moins 25cm d'eau.

La communication entre scientifiques est rendue d'autant plus difficile que les termes utilisés pour désigner les zones humides varient également avec les pays et les régions (Mitsch et Gosselink, 1993; Pieczyńska et Zalewski, 1997; Keddy, 2000) et sont même parfois utilisés de manière contradictoire (Mitsch et Gosselink, 1993). De plus, la correspondance des termes entre les différentes langues (notamment le français, l'allemand et l'anglais) est difficile à obtenir.

2.3 Fonctions des zones humides

La prise de conscience des fonctions remplies par les zones humides a certainement contribué à la reconnaissance de leur existence et de leur inestimable valeur pour l'homme. Selon Keddy (2000), les zones humides remplissent la plupart, si ce n'est l'intégralité, des fonctions attribuées par de Groots (1992) à la biosphère. Sur la base de Bardecki *et al*. (1989), Adamus *et al*. (1987) et Richardson (1995), il «résume» cependant à quinze les fonctions plus spécifiques aux zones humides: alimentation et exutoire de la nappe phréatique, régulation des crues, stabilisation des sédiments, rétention des sédiments, des substances toxiques et des substances nutritives, transformation des substances nutritives et du carbone, production de matière organique. Les zones humides offrent également des lieux de vie, de reproduction, de migrations et d'hivernage pour de nombreuses espèces animales. Finalement, elles constituent pour l'homme une mémoire historique, un lieu de loisirs, de détente et d'inspiration.

2.4 De l'émergence de l'écologie du paysage à une meilleure compréhension du fonctionnement des plaines alluviales

2.4.1 Avènement de l'écologie du paysage

L'avènement de l'écologie du paysage dans les années 1950 sous l'impulsion principale des géographes et des biologistes a permis une progression considérable dans la perception et la compréhension des écosystèmes. Troll (1939) définit l'écologie du paysage comme l'étude des relations physico-biologiques qui gouvernent les différentes unités spatiales d'une région. L'écologie, qui jusqu'à cette époque s'était essentiellement intéressée aux relations entre éléments biotiques et abiotiques à l'intérieur d'unités spatiales relativement homogènes, gagne de nouvelles perspectives en introduisant (et se concentrant sur) les relations entre les différentes unités spatiales (Forman et Godron, 1986). Une prise de conscience s'opère quant à la structure en mosaïque du paysage, à ses fonctions et à sa dynamique sous l'influence de paramètres naturels ou anthropiques (Forman, 1995). Le développement de l'écologie du paysage contribue très certainement à mettre en relief l'importance de la perte et de la fragmentation des habitats comme facteurs déterminants dans la disparition des espèces (Groombridge, 1992). En effet, les populations, tant animales que végétales, se voient éclater en de multiples «patchs» qui, s'ils sont inter-connectées, forment une unité fonctionnelle que Levins (1970) appelle «métapopulation». La survie à long terme de ces «métapopulations» dépend autant du taux d'extinction à l'intérieur des différents patchs (par ailleurs inversement proportionnel à la taille de ceux-ci (Fahrig et Merriam, 1985; Hanski, 1985), que du taux de migration des organismes entre patchs (Den Boer, 1981). La notion de connectivité prend ici toute son importance comme facteur primordial dans le maintien de la biodiversité. Deux types de connectivités sont généralement distingués:

1) la *connectivité spatiale* ou *connectance*, qui désigne les liens physiques existant entre des milieux de même type ou, dans le cas d'écosystèmes aquatiques, de *connexions* hydrologiques.
2) la *connectivité fonctionnelle* qui caractérise les échanges potentiels ou effectifs d'individus entre milieux distants d'un même type et qui prend en considération l'aptitude aux déplacements de l'espèce et son comportement. En effet, selon l'espèce considérée, des patchs connectés structurellement peuvent être déconnectés fonctionnellement, et vice et versa (With, 1997). La connectivité est une notion «espèce- et paysage- dépendante» (Wiens et Milne, 1989; Tischendorf et Fahrig, 2000). La migration des organismes n'est par ailleurs pas seulement influencée par la distance qui sépare les différents patchs mais aussi, pour certains auteurs (Boothby, 1997) surtout, par la nature de la matrice qui les sépare.

2.4.2 Application des principes de l'écologie du paysage à l'étude des plaines alluviales

Les plaines alluviales sont des zones humides intérieures, d'eau douces, qui se distinguent en deux types: les plaines alluviales péri-lacustres bordant les lacs, et les plaines alluviales fluviales, bordant les eaux courantes. Le terme «alluvial», «constitué par des alluvions», rappelle l'origine de ces zones, créées lors du dépôt des alluvions (limons, sables, graviers, galets) par un cours d'eau (ou un lac), quand la pente ou le débit sont devenus insuffisants. Ces zones humides sont souvent ponctuées de plans d'eau, dont l'origine et le mode de formation résultent du fonctionnement et de la dynamique intrinsèque des systèmes fluviaux et lacustres ou/et d'interventions humaines.

La dimension longitudinale du cours principal du fleuve fut pendant longtemps la seule dimension spatiale à être prise en considération dans l'étude de l'hydrosystème fluvial, comme par exemple dans le River Continuun Concept de Vannote *et al*. (1980). Cette dimension est la plus caractéristique puisqu'elle représente les flux amont-aval de matière, d'énergie et d'organismes et connecte les éléments de la plaine avec ceux du bassin versant. L'intégration des principes de l'écologie du paysage par Ward (1989), Petts et Foster (1990), Amoros et Petts (1993), Stanford et Ward (1993) a conduit à l'identification de deux dimensions spatiales supplémentaires, latérale et verticale, et ainsi à l'intégration de la plaine alluviale fluviale et de la zone hyporhéique dans l'étude des eaux courantes:

1) *dimension latérale*: l'augmentation du niveau de l'eau en période de crue permet la mise en connexion de la plaine alluviale (et de ses plans d'eau) avec la rivière. Ces périodes de remise en connexion permettent notamment aux poissons de quitter le cours principal et de gagner les plans d'eau de la plaine alluviale, protégés du courant et plus riches en nourriture, qu'ils utilisent comme frayères et nourricières (Figure 2.3, Ward, 1989). Ces périodes permettent également le déplacement, de la plaine alluviale vers le fleuve, de grandes quantités de matière organique (issues de la décomposition intense dans les plans d'eau), de plancton et de macrofaune benthique, constituant un apport substantiel de nourriture pour la faune de la rivière elle-même (Figure 2.3, Ward, 1989). Lors de la décrue, la plaine alluviale est à nouveau déconnectée de la rivière. Les processus autogènes y dominent alors les processus allogènes.
2) *dimension verticale*: cette dimension est certainement la plus méconnue et dont l'importance n'a été reconnue que récemment, puisqu'elle considère les échanges entre l'eau de surface et l'eau souterraine, dans une zone dite "hyporhéique". En plus d'abriter une faune très diversifiée (Gibert *et al*., 1981; Gibert *et al*., 1990; Marmonier *et al*., 1993) et souvent endémique (ce qui la rend particulièrement vulnérable), cette zone participe à l'oxygénation du lit de la rivière (Ward, 1998) et constitue un refuge pour la faune benthique en cas de crues ou de pollution.

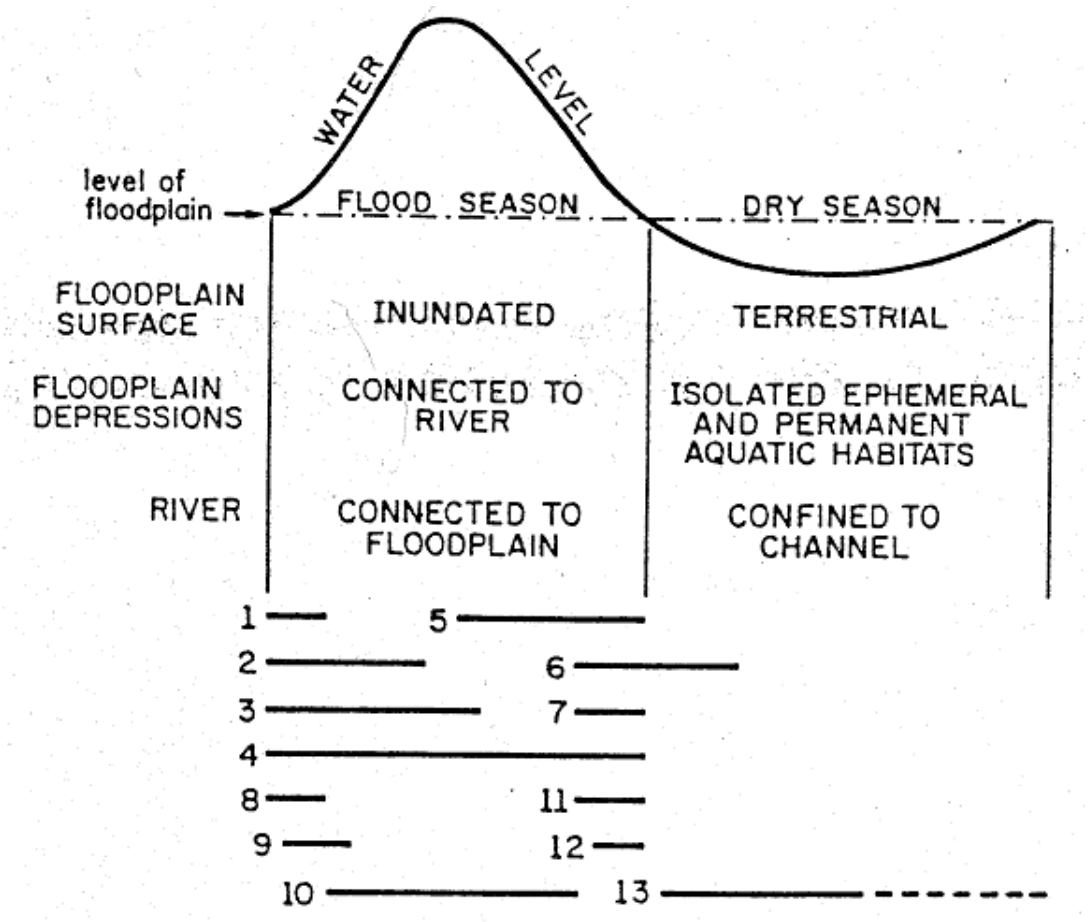


Figure 2.3 Schématisation des processus liés à la mise en connexion de la rivière avec sa plaine alluviale lors des épisodes de crue. Ces processus sont représentés par des barres numérotées qui illustrent, 1. L'exportation des nutriments de la plaine vers la rivière, 2. L'importation de nutriments dans la plaine par la rivière, 3. La croissance des hydrophtytes et des invertébrés aquatiques dans la plaine alluviale, 4. La période de décomposition dans la plaine alluviale, 5. L'exportation vers la rivière de la matière organique dissoute (DOM) et de la matière organique particulaire fine (FPOM), 6. La période de production maximale de plancton dans les dépressions de la plaine alluviale, 7. La dérive du plancton, du benthos et des hydrophytes vers la rivière, 8. L'entrée des poissons dans la plaine alluviale, 9. La période de fraie des poissons dans la plaine alluviale, 10. La période de croissance des poissons, 11. Le départ des poissons pour la rivière lors de la décrue 12. La prédation des poissons à la sortie de la plaine alluviale lors de 12. et 13. La mortalité importante des poissons prisonniers dans la plaine au cours de la saison sèche (Ward, 1989).

Aux dimensions spatiales présentées ci-dessus, s'est également ajoutée la dimension temporelle, qui se sub-divise fréquemment en variations:

- *intra-annuelles*: les épisodes de crue interviennent de manière saisonnière au cours d'une année,
- *inter-annuelles*: la fréquence, l'intensité et la durée des crues varient entre années,
- *décennales*: certaines rivières, comme l'Ain et le Rhône, connaissent des phénomènes tels que l'incision, ou au contraire l'exhaussement de leur lit. Ces processus ont pour conséquences de modifier les degrés de connexion entre le cours d'eau et sa plaine alluviale (Bornette *et al.*, 1996).

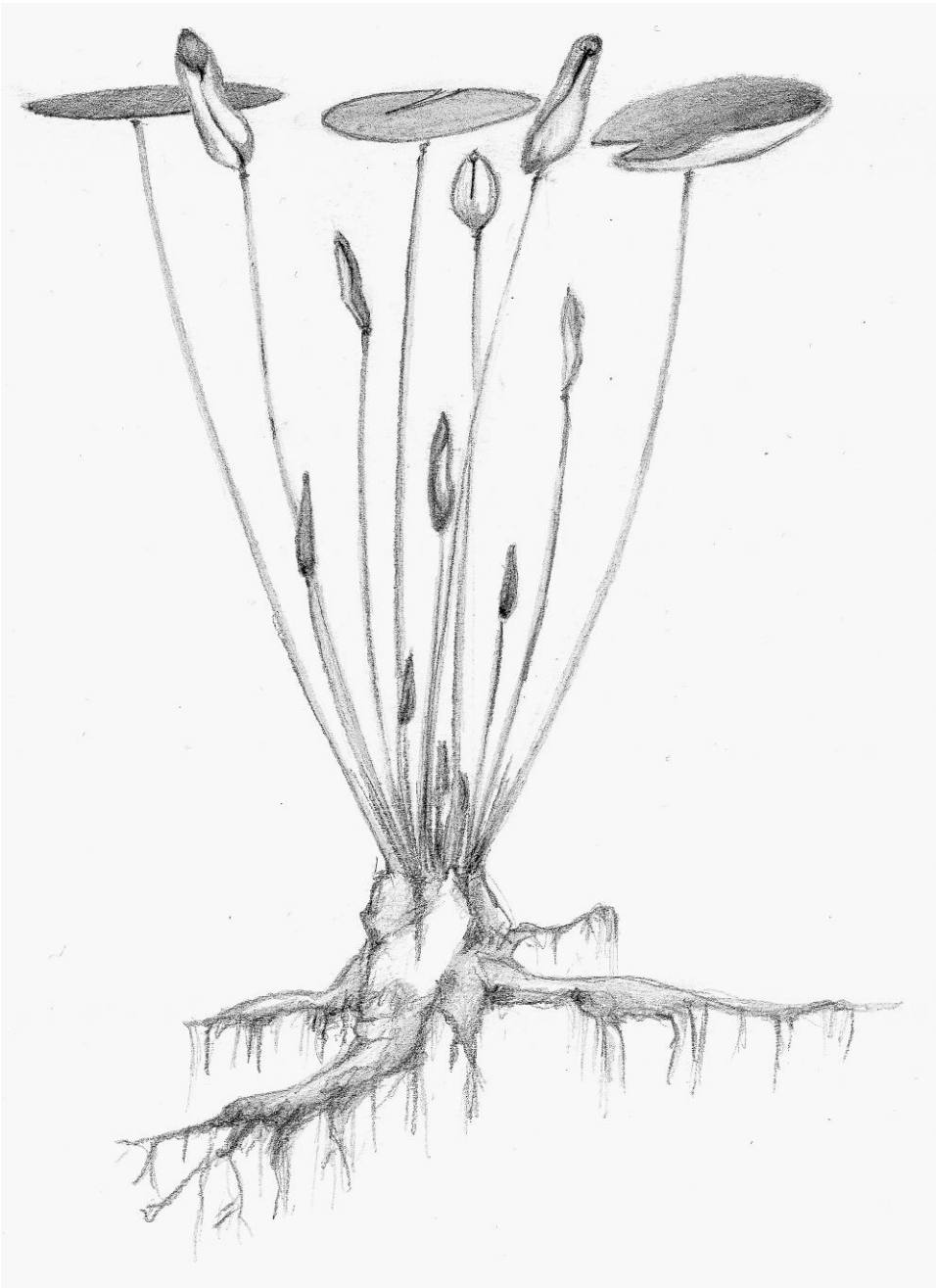
La compréhension du fonctionnement des plaines alluviales fluviales, plus particulièrement de la dynamique de création des milieux lotiques, semi-lotiques et lénitiques qui les ponctuent, a ainsi beaucoup bénéficié de l'étude des relations entre le cours principal du fleuve, sa plaine alluviale et le réseau hydrographique souterrain. Ces travaux ont également mis en évidence l'influence des différents types et degrés de connexions hydrologiques (connectance), dans les dimensions spatiales et temporelles vues plus haut, sur i) les conditions physico-chimiques et sédimentologiques des plans d'eau présents dans le plaine alluviale fluviale et ii) (par conséquence) sur les communautés végétales et animales qui les colonisent.

L'introduction générale a mis en évidence la quasi-absence de données sur les étangs des zones alluviales péri-lacustre, leurs fonctionnement et leurs caractéristiques. Pourtant, trois dimensions présentées ci-dessus dans le contexte des plaines alluviales fluviales peuvent également être appliquées aux zones alluviales péri-lacustres. Il s'agit des dimensions:

1) *latérale*, mettant en connexion le lac et les étangs en périodes de hautes eaux, ainsi que les étangs entre eux, permettant des échanges, principalement de matière (sédiments) et d'organismes.
2) *verticale*, permettant les échanges entre eaux de surface et eaux de la nappe,
3) *temporelle*, puisque le niveau du lac varie potentiellement de manière saisonnière, inter-annuelle (en amplitude et en durée) et décennale.

Chapitre 3

Les Macrophytes Aquatiques



Le présent chapitre n'a pas pour vocation de présenter une synthèse de l'écologie des macrophytes aquatiques. De nombreux ouvrages et articles (voir par exemple Sculthorpe, 1967; den Hartog et Brown, 1991; Spencer et Ksander, 1991, 1992, 1995; Cronk et Fennessy, 2001; Heegaard *et al*., 2001; Santamaría, 2002) traitent en effet, dans le détail, de l'influence des paramètres abiotiques (profondeur, variations du niveau de l'eau, température, teneur en oxygène dissous, teneur en substances nutritives, sédimentation, etc.) sur leur distribution, richesse, composition et abondance. Ce chapitre a comme objectifs i) de préciser le sens dans lequel le terme «macrophyte aquatique» a été utilisé dans le présent travail, ii) de brièvement rappeler l'importance de la végétation dans les écosystèmes aquatiques et iii) de faire état de l'approche fonctionnelle des communautés végétales aquatiques.

3.1. Définition

La végétation échantillonnée au cours de cette étude correspond aux macrophytes aquatiques tels qu'ils sont définis par Casper et Krausch (1980), c'est-à-dire comme «des plantes supérieures, dont la partie photosynthétique active est toujours, ou au moins pour quelques mois dans l'année, submergée ou flottante». En conséquence, ces auteurs intègrent également dans cette définition les hélophytes (plantes dont les racines et la base de la tige se trouvent presque constamment immergés mais dont les feuilles et les inflorescences s'élèvent au dessus de l'eau), les pleustohélophytes (plantes non enracinées, dont les parties végétatives et reproductives flottent sur la surface de l'eau) et les pseudohydrophytes (plantes supportant une immersion prolongée, se reproduisant végétativement, mais ne pouvant pas clore leur cycle de vie sous ces conditions).
En revanche, les espèces intégrées dans les analyses statistiques correspondent plus précisément aux espèces «strictement» aquatiques, codées hyd ou (hyd) (hydrophytes) par Casper et Krausch (1980). Cette définition répond à celle des hydrophytes de Willby *et al*.(2001): «all submerged and floating leaved vegetation». Les hélophytes et pseudohydrophytes ont ainsi été écartés. Bien que n'étant pas couvertes par Casper et Krausch (1980, 1981), les characées ont été considérées dans cette étude.

3.2 Rôles des macrophytes aquatiques

Les macrophytes aquatiques sont à la fois acteurs et témoins de nombreux processus écologiques au sein des écosystèmes. En tant qu'acteurs, ils influencent l'environnement physique des milieux qu'ils colonisent. Les conditions de lumière et de température, la concentration en oxygène dissous, ainsi que la vitesse du courant et la composition du substrat dépendent de la présence ou de l'absence d'herbiers de macrophytes aquatiques, ainsi que de leur densité et physionomie (Carpenter et Lodge, 1986; Carter *et al*., 1991; Madsen *et al*., 2001; Gulati et van Donk, 2002). Les macrophytes aquatiques participent également au cycle des nutriments, à la rétention et à la production de matière organique (Carpenter et

Lodge, 1986; Gulati et van Donk, 2002; Horvath, 2004). Ils fournissent des possibilités de refuges, d'habitats et de matériau de construction et constituent une source de nourriture pour de nombreux organismes (Juge et Lachavanne, 1998; Gulati et van Donk, 2002). Finalement, les macrophytes aquatiques structurent les milieux qu'ils occupent, tant dans leur dimension horizontale (répartition des herbiers dans le plan d'eau), que dans leur dimension verticale (occupation de la colonne d'eau par les individus). Ils contribuent ainsi à l'hétérogénéité spatiale au sein des plans d'eau, de manière différenciée en fonction de leur physionomie, puisque des espèces formant des gazons (meadow-forming) ou des canopées (canopy-forming) par exemple, n'ont pas la même influence sur le courant et la dynamique des sédiments (Madsen *et al*., 2001).

En tant que témoins, les macrophytes aquatiques répondent aux conditions environnementales dans lesquels ils se développent. Le caractère fixe de ces organismes en fait potentiellement de bons bioindicateurs, puisqu'ils intègrent les contraintes de l'environnement (courants, substances nutritives, et autres paramètres physico-chimiques) sur des périodes de temps prolongées (Haury et Peltre, 1993; Ali *et al*., 1999). Ils ont classiquement été utilisés pour établir des diagnostics de qualité des écosystèmes aquatiques et particulièrement du degré de trophie des eaux courantes et stagnantes (Haslam, 1982; Janauer, 1982; Lachavanne, 1985; Lachavanne *et al*., 1985; Carbiener *et al*., 1990; Haury et Peltre, 1993; Haury *et al*., 1996; Robach *et al*., 1996; Lehmann et Lachavanne, 1999).
Ali *et al*. (1999) émettent toutefois des réserves quant à la capacité des espèces (ou des assemblage d'espèces) de macrophytes aquatiques à révéler les changements de qualité trophique des eaux dans les rivières. Selon eux, la plasticité fonctionnelle de ces populations augmente considérablement la gamme des conditions trophiques à laquelle les espèces peuvent s'adapter et estiment, en conséquence, que les modèles basés sur la présence ou l'absence des macrophytes aquatiques ne sont pas suffisamment sensibles. Ces doutes sont partagés dans une certaine mesure par Haury et Peltre (1993), qui s'interrogent sur la place des espèces euryèces dans les indices macrophytes, d'une part et sur la «stabilité du pouvoir bioindicateur des espèces selon les éco-régions», d'autre part. Suite à l'application, dans des cours d'eau français, de quatre indices «macrophytes» proposés dans la littérature, ces mêmes auteurs soulignent un certain nombre de problèmes. Ils regrettent par exemple l'utilisation de macrophytes «indicateurs», sans que des relations statistiques aient été toujours clairement établies au préalable entre ces espèces et la qualité de l'eau. Preston (1995) et Demars et Harper (1998) évoquent d'ailleurs la difficulté à établir ces relations en raison i) de mesures physico-chimiques souvent trop ponctuelles, ii) de l'utilisation de paramètres physico-chimiques intégrant les effets d'autres paramètres (ex. de la conductivité qui mesure la concentration totale en élécrolytes et qui peut être élevée en raison de la salinité aussi bien que de l'alcalinité) et iii) de la variétés des facteurs environnementaux autres que les nutriments influençant la croissance des plantes aquatiques. Haury et Peltre (1993) reconnaissent également des problèmes liés non seulement à l'incomplétude ou

à la différence des listes d'espèces entre pays mais aussi à la difficulté de les comparer en raison d'incertitudes taxonomiques.

3.3 Approche fonctionnelle des communautés végétales

3.3.1 L'étude des traits: contribution fonctionnelle à l'étude des communautés végétales

Grime (1985), Kautsky (1988) ou encore Keddy (2000) estiment que l'approche phytosociologique des communautés végétales (description de la végétation par des listes d'espèces, leurs abondances et leurs associations) ne suffit plus quand il s'agit i) de mieux comprendre l'écologie des espèces, ii) de proposer des mesures de conservation et de gestion pertinentes et efficaces et iii) de prédire l'état des communautés végétales face à des changements d'origine naturelle ou anthropique. Par ailleurs, Wiegleb (1983), Haury et Peltre (1993) et Keddy (2000) (pour ne citer qu'eux) soulignent le fait que l'approche taxonomique pose des problèmes lorsqu'il s'agit de comparer les listes d'espèces provenant de pays, de régions ou de scientifiques différents, d'une part et de réutiliser du matériel échantillonné à d'autres époques, d'autre part. La prise de conscience de ces limites à conduit à un intérêt grandissant pour une approche plus fonctionnelle des communautés végétales. Au delà de leur composition floristique, celles-ci sont en effet définies par un ensemble de caractéristiques (ou traits) morphologiques, phénologiques et physiologiques. Murphy *et al*. (1990) désigne par le terme de «stratégie» l'ensemble des traits permettant aux populations végétales de s'établir, de se développer et de se reproduire, c'est-à-dire de s'adapter aux pressions environnementales agissant sur la communauté qu'elles occupent. L'acceptation du terme «stratégie» n'est cependant pas unanime et son utilisation reste controversée (Chapleau *et al*., 1988; Willby *et al*., 2000).

3.3.2 La pierre (tri-)angulaire de Grime

Pour Southwood (1977, 1988) les pressions environnementales qui agissent sur les communautés vivantes constituent le «templet on which evolution forges characteristic life-history strategies». Pour Keddy (1992), elles représentent des filtres qui éliminent successivement, aux différentes échelles spatiales et temporelles, les espèces n'ayant pas la combinaison de traits nécessaire à leur adaptation dans un habitat donné. Pour Grime (1974, 1977, 1979) et Grime *et al*. (1988), les pressions (ou filtres) exercées par l'environnement sur les communautés végétales se limitent à trois types:

- le *stress*, qui intègre l'ensemble des phénomènes conduisant à une réduction de la production photosynthétique, tels que des conditions sub-optimales d'eau, de lumière, de matières nutritives, de température, etc.,

- les *pertubations*, qui sont responsables d'une destruction partielle ou totale de la biomasse des plantes par l'activité d'herbivores, de pathogènes, des hommes ou de phénomènes naturels tels que les crues, l'action des vagues, etc.,
- la *compétition* avec les individus voisins pour la capture des mêmes ressources, et dont l'intensité dépend de l'intensité du *stress* et des *perturbations*.

En réponse à ces pressions environnementales, les espèces établies développent respectivement les stratégies «primaires» dites «stress-tolérante» (S), «pertubations-tolérante» (R) et compétitive (C), qui occupent chacune un angle différent du modèle triangulaire dont elles représentent les conditions extrêmes (Figure 3.1). L'intensité et la combinaison de ces contraintes varient cependant en fonction du temps et des habitats et conduisent le plus fréquemment les espèces à élaborer des stratégies dites «secondaires», combinaisons de deux, voire trois stratégies primaires (C-R, C-S, R-S, C-R-S, etc.) (Figure 3.1). Selon Grime, la survie des espèces n'est toutefois pas possible dans les situations de grandes intensités à la fois de stress et de perturbations.

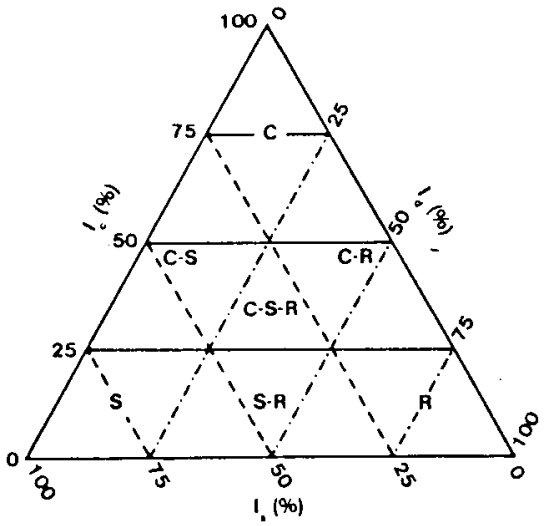


Figure 3.1 Modèle triangulaire de Grime *et al*. (1988) décrivant les différentes situations d'équilibre entre le stress, les perturbations et la compétition, ainsi que la position des stratégies primaires (S, R et C) et secondaires (C-S, C-R, S-R et C-S-R). I_c (à gauche) = importance relative de la compétition; I_d (à droite) = importance relative des perturbations; I_s (en bas) = importance relative du stress.

Le «modèle triangulaire» de Grime constitue un fondement théorique important pour les recherches sur les relations traits-conditions environnementales. En effet, i) il offre des prédictions quant aux traits susceptibles de caractériser les communautés végétales soumises à des intensités et à des combinaisons différentes de stress et de perturbations (Tableau 3.1) et ii) représente une des premières synthèses à grande échelle, avec celle de Frank *et al*. (1990), de données écologiques retranscrites sous

une forme codée. L'utilisation très répandue de cette source d'information, sous sa forme originale ou modifiée, démontre l'intérêt qu'elle suscite, de même que l'utilité et la nécessité d'une telle démarche, permettant potentiellement à différents groupes de personnes (biologistes ou gestionnaires p.ex.), parmi lesquelles des non spécialistes, de bénéficier de données qui sont le plus souvent connues des spécialistes seuls (Willby *et al.*, 2000).

Tableau 3.1 Présentation non exhaustive de caractéristiques morphologiques, phénologiques et physiologiques de plantes «competitives», «stress-tolerantes» et «perturbations-tolérantes» (selon Grime *et al.*, 1988). V = vegetative expansion; S = seasonal regeneration; W = numerous small, wind-dispersed seeds or spores; Bs = persistent bank of seeds or spores; Bj = persistent bank of juveniles.

Table 3.3 Some characteristics of competitive, stress-tolerant and ruderal plants. Characteristics shown in bold type have proved particularly useful in classifying plant strategies.

	Competitive	Stress-tolerant	Ruderal
(i) **Morphology**			
1. Life-forms	Herbs, shrubs, trees	Lichens, bryophytes, herbs, shrubs and trees	Herbs, bryophytes
2. Morphology of shoot	**High dense canopy of leaves. Extensive lateral spread above and below ground**	Extremely wide range of growth forms	**Small stature, limited lateral spread**
3. Leaf form	Robust, often mesophytic	**Often small or leathery, or needle-like**	Various, often mesophytic
4. Canopy	**Rapidly-ascending monolayer**	Often multilayered; if monolayer, not rapidly-ascending	Various
(ii) **Life-history**			
5. Longevity of established phase	Long or relatively short	**Long to very long**	**Very short**
6. Longevity of roots	Relatively short	**Long**	**Short**
7. Leaf phenology	**Well-defined peaks of leaf production coinciding with periods of maximum potential productivity**	**Evergreens, with various patterns of leaf production**	**Short phase of production in period of high potential productivity**
8. Phenology of flowering (or sporulation in ferns)	Flowers produced after (or more-rarely before) periods of maximum potential productivity	No general relationship between time of flowering and season	**Flowers produced early in the life-history**
9. Frequency of flowering	Established plants usually flower each year	**Intermittent flowering over a long life-history**	High frequency of flowering
10. Proportion of annual production devoted to seeds	Small	Small	**Large**
11. Perennation	Dormant buds and seeds	**Stress-tolerant leaves and roots**	Dormant seeds
12. Most commonly associated regenerative* strategies	V, S, W, B_s	V, W, B_j	S, W, B_s
(iii) **Physiology**			
13. Mean potential relative growth-rate	**High**	**Low**	**High**
14. Response to resource depletion	Rapid morphogenetic responses in the form and distribution of leaves and roots	Morphogenetic responses slow and small in magnitude	Rapid curtailment of vegetative growth, diversion of resources into flowering
15. Photosynthesis and uptake of mineral nutrients	Strongly seasonal coinciding with long continuous period of vegetative growth	Opportunistic, often uncoupled from vegetative growth	Opportunistic, coinciding with vegetative growth

3.3.3 Approche fonctionnelle des communautés de macrophytes aquatiques: état des connaissances

Le modèle triangulaire de Grime (1974, 1977) a essentiellement été développé dans le cadre de la végétation terrestre. Les espèces aquatiques n'ont certes pas été omises de la base de données qui lui est associée (Grime *et al*., 1988), mais elles ne représentent qu'une très faible proportion des espèces pour lesquelles les traits ont été codés. Cette base de données a cependant clairement inspiré l'élaboration de nouvelles bases, spécifiques aux macrophytes aquatiques, dont les plus importantes ont été publiées par Bornette *et al*. (1994) puis Willby *et al*. (2000). En outre, le modèle de Grime demeure une référence, même implicite, dans les discussions d'une grande majorité de travaux de recherche.

De nombreux auteurs ont cherché à tester la validité du modèle de Grime sur la végétation palustre et aquatique, y compris marine. Pour certains d'entre eux, le modèle s'applique parfaitement aux milieux aquatiques moyennant peu ou pas de modifications. Telle semble être l'opinion de Murphy *et al*. (1990), Greulich et Bornette (1999) ou encore Kautsky (1988). Cette dernière, dans le cadre d'une étude menée sur les macrophytes aquatiques en mer Baltique, identifie une stratégie supplémentaire («stunted»), correspondant à la présence de plantes malgré l'action conjointe de stress et de perturbations (non viable selon Grime), sans toutefois remettre en cause l'impossible survie des organismes en cas de conditions environnementales réellement extrêmes.
Pour d'autres auteurs en revanche, l'application du modèle de Grime au milieu aquatique semble plus problématique. Willby *et al*. (2000) estiment par exemple que l'étiquetage des plantes aquatiques selon les codes «C-S-R» de Grime est périlleux (alors qu'il est utilisé par Greulich et Bornette, 1999), dans la mesure où celles-ci ne représentent qu'une faible proportion des espèces utilisées pour l'élaboration du modèle. Rørslett (1989) soulignent également que les traits des macrophytes aquatiques sont tous stress- ou perturbation- tolérants dans le contexte plus général des stratégies des plantes. D'autre part, plusieurs de ces études conduisent à la création d'un nombre de groupements de traits bien plus important que le nombre existant de stratégies de Grime et concluent i) que seuls des niveaux de définitions plus fins sont pertinents dans le cadre de l'écologie et de la gestion appliquée (Willby *et al*., 2000) et ii) que la terminologie de Grime montre ses limites lorsqu'il s'agit de différencier des espèces aux stratégies similaires, c'est-à-dire représentant des «variantes» de stratégies primaires (Sabbatini et Murphy, 1996). Par ailleurs, Wiegleb et Brux (1991), sur la base de leurs études sur la morphologie et les stratégies de reproduction du genre *Potamogeton* L., soulignent la nécessité d'adapter le concept de stratégie face à des espèces clonales, à reproduction principalement végétative.

Il est vraisemblable que ces divergences résultent en partie des différentes utilisations et des différents degrés d'intégration des traits dans les études sur la végétation aquatique, comme en témoignent les

publications toujours plus nombreuses intégrant les notions de traits, de stratégies ou de groupes fonctionnels. Trois types d'approches peuvent être distingués:

- *Utilisation indirecte des traits des espèces*: dans le cadre d'une étude sur les canaux de drainage en Angleterre, Sabbatini et Murphy (1996) par exemple, mettent en relation les données de présence/absence et abondance/dominance de relevés phyto-sociologiques avec des paramètres physico-chimiques (facteurs de stress et index de perturbation) mesurés dans le milieu. L'intégration des traits n'intervient qu'à posteriori, lors de l'interprétation des résultats et de leur comparaison avec les stratégies C-S-R proposées par Grime. Selon ces auteurs la définition (au sens de la précision) des stratégies de Grime n'est pas suffisante lorsque les milieux étudiés montrent des conditions environnementales relativement homogènes et que les espèces appartiennent plus à des variantes d'un type de stratégie qu'à des stratégies bien différenciées. Ces résultats semblent toutefois en contradiction avec ceux de Greulich et Bornette (1999) (voir ci-dessous).

- *Utilisation directe des traits par l'emploi de bases de données*: Bornette *et al*. (1994) et Willby *et al*. (2000, 2001) par exemple, cherchent à mettre en évidence des relations non plus entre les espèces échantillonnées (présence/absence et/ou abondance/dominance) et leur milieu mais directement entre les traits de ces espèces et leur environnement. Les traits font alors partie intégrante de l'étape de l'analyse des données, sous la forme d'informations codées. Ce codage s'effectue le plus souvent sur la base de références bibliographiques, mais certains auteurs, comme Kautsky (1988) et Ali *et al*. (1999) utilisent essentiellement des données mesurées in situ.

  Ce type de recherches offre une approche globale tant par les gradients environnementaux considérés (types de milieux diversifiés et/ou échelles spatiales importantes) et le nombre d'espèces intégrées (quarante-deux à plus d'une centaine), que par le fait que les relations sont établies statistiquement. Toutefois, ces études n'identifient pas avec précision les liens entre des traits particuliers et des paramètres physico-chimiques ou environnementaux précis.

- *Utilisation directe des traits par mesures in situ ou en conditions expérimentales*: certaines études sont focalisées sur un nombre beaucoup plus restreint d'espèces, sur lesquelles des traits sont mesurés in situ ou en conditions expérimentales, non plus de manière ponctuelle mais sur des périodes prolongées (une à deux saisons de végétation). Ces travaux constituent une suite logique aux études morphologiques, physiologiques et phénologiques effectuées sur certains genres, comme celles de Pip (1987), Van Wijk (1988, 1989a, b,c), Van Wijk *et al*. (1988), Wiegleb et Brux (1991) et Preston (1995) sur le genre *Potamogeton*.

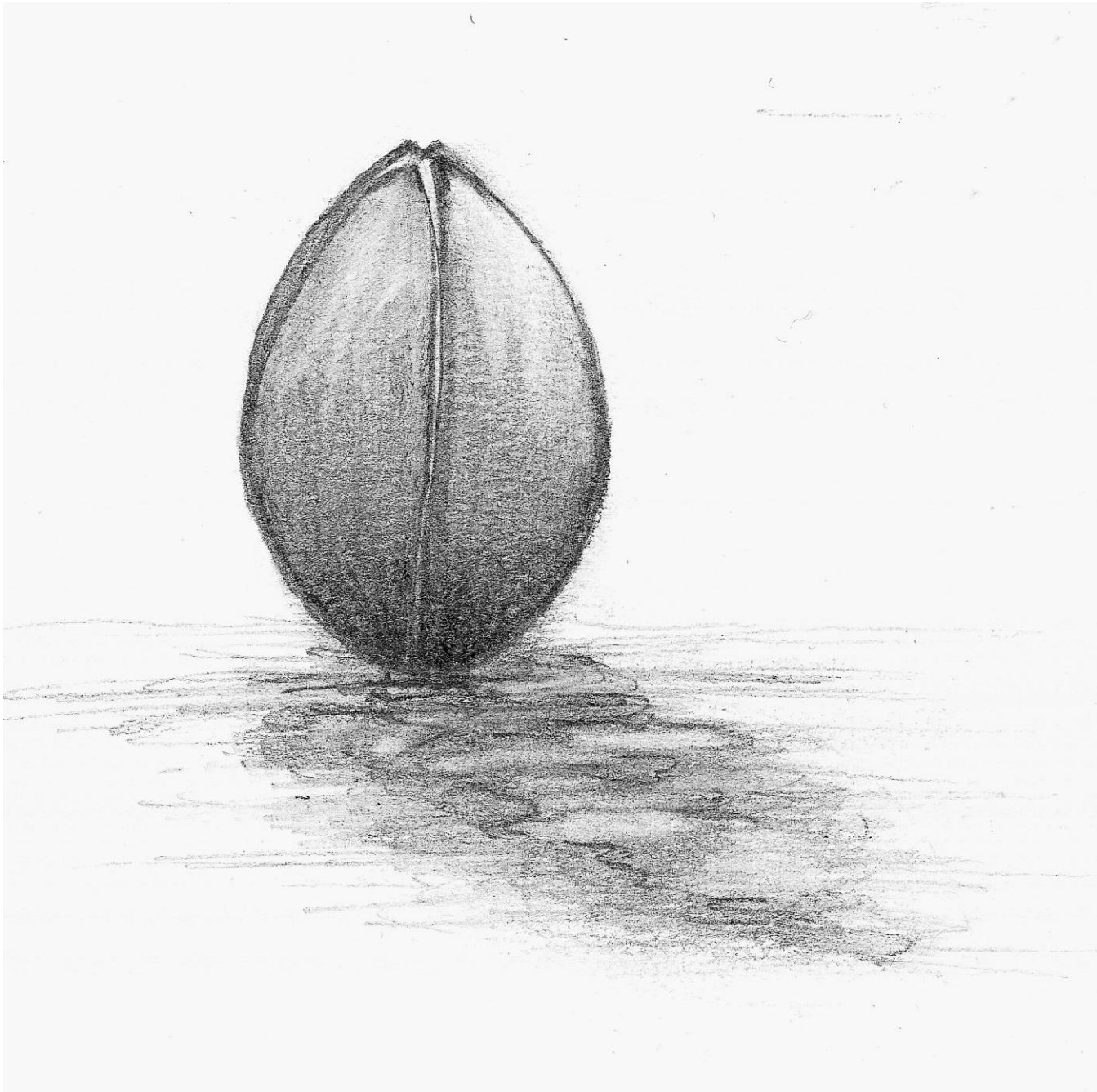
Ces recherches permettent une meilleure compréhension de l'écologie des espèces par une approche plus précise des relations entre certaines caractéristiques morphologiques ou physiologiques et des conditions de milieux mieux identifiées. Greulich et Bornette (1999), par exemple, mesurent in situ plusieurs traits des espèces *Hippuris vulgaris* L., *Groenlandia densa* (L.) Fourreau, *Luronium natans* L. et *Sparganium emersum* Rehmann, dans la perspective i) de hiérarchiser ces espèces en fonction de leur capacités compétitives, ii) de leur attribuer une stratégie selon la classification de Grime et iii) de tester l'hypothèse selon laquelle des milieux moyennement perturbés abritent des espèces ayant des stratégies différentes. Contrairement à Sabbatini et Murphy (1996) (voir ci-dessus), ces auteurs ne semblent pas rencontrer de problèmes avec le modèle de Grime, alors que leur site d'étude est spatialement retreint. La mesure directe des traits plutôt que leur utilisation sur des bases bibliographiques permet sans doute une plus grande précision dans l'attribution des stratégies.

Ce type d'approche directe permet également de mesurer la plasticité des espèces aquatiques. A l'issu d'une étude visant à tester l'hypothèse selon laquelle les plantes aquatiques pérennes vivant dans les milieux fréquemment perturbés attribuent une proportion plus importante de leur biomasse aux parties souterraines, comparativement aux plantes vivant en milieux moins perturbés, Barrat-Segretain (2001) constate que les espèces étudiées (*Groenlandia densa*, *Berula erecta* et *Myriophyllum spicatum*) montrent une importante variabilité intra-spécifique. Greulich *et al*. (2001), dans le cadre d'une recherche visant à mieux comprendre la distribution extrêmement limitée de *Luronium natans* dans les plaines alluviales du Rhône et de l'Ain constatent que cette espèce exhibe des formes de croissance très différentes (feuilles en rosette ou aux feuilles flottante) en fonction de la teneur en nutriments de l'eau.

La plasticité des espèces a des implications importantes dans leur capacité à s'adapter à différentes situations, de même qu'elle pose des problèmes i) lors du codage des traits dans une base de données (changement de classe de taille et de forme de croissance observés par Greulich *et al*. (2001) pour *Luronium natans*) et ii) lors de la classification dans les stratégies primaires de Grime (Barrat-Segretain, 2001). La mesure directe des traits permet vraisemblablement de s'affranchir en partie des discordances entre les données bibliographiques établies pour une région ou pour des conditions données et les valeurs réelles que les espèces peuvent présenter dans d'autres régions ou sous d'autres conditions environnementales.

Chapitre 4

Présentation des Sites d'Etude



4.1 Zone alluviale péri-lacustre de la «Grande-Cariçaie» (lac de Neuchâtel, Suisse)

Situé à 429.3 m d'altitude, le lac de Neuchâtel, de forme presque rectangulaire, couvre une superficie de 214km^2. Sa longueur et sa largeur maximales atteignent 38.3 et 5.7 km, respectivement. Le point le plus profond se situe à 153 m, pour une profondeur moyenne de 64 m (données tirées de Bapst, 1987).

4.1.1 La région des trois lacs

Le lac de Neuchâtel appartient, comme les lacs de Bienne et de Morat, aux lacs «subjurassiens», qui occupent une dépression au pied de l'arc intérieur du Jura. Une vaste zone humide, le Grand Marais et la plaine de l'Orbe, s'étendait entre ces trois lacs jusqu'à la fin du XIXème siècle.
La première Correction des eaux du Jura, entreprise dès 1868 en vue d'assainir ce vaste complexe alluvial et marécageux abaissa considérablement le niveau moyen des trois lacs en même temps qu'elle en augmenta l'amplitude des fluctuations. Pour le lac de Neuchâtel, cela signifia une diminution de son niveau moyen de 2.7 m et des fluctuations pouvant atteindre 3m (amplitude moyenne des variations 1.5m). 400 km^2 du Grand Marais furent ainsi asséchés entre 1868 et 1888 et partiellement destinés à l'agriculture. Cette vaste opération de drainage eu comme conséquence inattendue l'exondation sur la rive sud du lac de Neuchâtel, de la moitié de la beine lacustre, formée de l'accumulation de sédiments issus de l'érosion des falaises de molasse bordant le lac (Cornali, 1992). Cette zone de 20km^2 (1/5ème de 400km^2), s'étendant entre les coordonnées 539.880/181.950 et 568.100/205.550, allait devenir le plus grand marais de Suisse, la «Grande-Cariçaie».

4.1.2 La «Grande-Cariçaie»

La «Grande-Cariçaie», qui doit son nom à l'espèce dominante de cette zone humide, *Carex elata* Allioni, a servi de refuge pour de nombreuses espèces du Grand Marais. Un siècle de colonisation aura permis la diversification de cette zone en beine lacustre, roselières lacustres, cordons littoraux, étangs, roselières intérieures, prairie marécageuses (prairies à grandes et petites laîches, prairies à choins, prairies à canche bleue), forêts riveraines, et forêts de pente (Cornali, 1992).
Bien qu'énumérées ici de façon linéaire, ces formations végétales constituent sur le terrain une mosaïque complexe, dans laquelle les éléments sont représentés dans des proportions différentes: les étangs n'occupent en effet que 20ha de la rive sud, au contraire des roselières, lacustres et intérieures qui en occupent 200, des prairies à grandes laîches, 400 et des prairies à petites laîches, 180. Marais non-boisés (éléments cités précédemment) et boisés (forêts riveraines) représentent une surface équivalente d'environ 780ha.

La «Grande-Cariçaie» en général, les étangs, les roselières intérieures et les prairies marécageuses en particulier, abritent de très nombreuses espèces devenues rares au niveau national, en conséquence de la disparition des zones humides sur tout le territoire helvétique. La richesse de cette zone alluviale lacustre ne tient pas seulement à la diversité de ses milieux et à celles des espèces animales et végétales qu'ils abritent. Elle tient également à sa superficie, exceptionnelle pour la Suisse, et à son arrière-pays rural, constitué de nombreux éléments naturels et semi-naturels (Cornali, 1992). La proximité de ces différents éléments constitue une «unité fonctionnelle» de valeur (Cornali, 1992), permettant le maintien d'espèces ayant de grandes exigences en termes de territoire encore peu dégradés et favorisant les échanges biologiques entre les différents éléments du paysage.
A l'heure actuelle, la «Grande-Cariçaie» est considérée comme bas-marais et paysage marécageux d'importance nationale et comme réserve d'oiseaux d'eau et d'oiseaux migrateurs d'importance internationale (Ramsar, 1971).Ces titres de noblesses n'empêchent pas de lourdes menaces de peser sur ce patrimoine naturel.

4.1.3 Menaces pesant sur la «Grande-Cariçaie»

La «Grande-Cariçaie» perd environ 10ha de sa surface par an depuis sa création, il y a un peu plus d'un siècle. Par ordre «décroissant d'importance», les raisons en sont l'urbanisation, l'atterrissement et l'érosion.
Comme toutes les zones humides, la «Grande-Cariçaie» est soumise au processus naturel qu'est l'atterrissement, qui conduit à des formations végétales successivement plus sèches et finalement forestières. Deux processus d'origine anthropique ont cependant stimulé cette dynamique naturelle. L'eutrophisation des eaux du lac de Neuchâtel d'une part, favorisant le développement d'une biomasse végétale importante dont l'accumulation participe à l'élévation du marais. La stabilisation excessive des niveaux du lac lors de la deuxième Correction des eaux du Jura (1965-1973) d'autre part, empêchant le rajeunissement ou la création de nouvelles zones humides par l'absence (ou la très nette diminution) des débordements du lac.
Les problèmes d'érosion affectent la rive sud du lac de Neuchâtel surtout dans sa partie ouest, exposée au vents dominants que sont la bise et le vent. Ils sont responsables de la disparition d'un quart du marais depuis la première Correction des eaux du Jura (Chervet et Huber, 1990, 1993). Clerc (1996) a pu mettre en évidence une érosion moindre ou nulle dans les zones colonisées par la roselière lacustre. Sans solutions rapides pour freiner, voire même arrêter et compenser les surfaces déjà disparues, le marais aura probablement disparu dans un siècle. Actuellement, divers ouvrages (épis perpendiculaires à la rive et brise-lames au large de la beine) sont à l'essai dans les zones les plus affectées par ce phénomène (Durand *et al*., 2002).

Conscients de l'importance de cette zone humide au niveau national et international, et conscients de l'importance des menaces qui pèsent sur son intégrité, la Ligue Suisse pour la Protection de la Nature et le WWF (LSPN/WWF, 1981) ont déterminé un plan de protection de la rive sud-est du lac de Neuchâtel dont les objectifs comprennent:

- la conservation de l'intégrité des zones naturelles en l'état, dans leurs qualités et leurs dimensions, en portant une attention particulière au marais non boisé et plus spécifiquement aux étangs et aux roselières,
- le ralentissement de l'atterrissement par faucardage, débroussaillage, création d'étangs et régulation adéquate du lac,
- la stabilisation de la surface urbanisée,
- la surveillance scientifique.

Ce dernier point est particulièrement important. L'acquisition de données sur la physico-chimie, la faune et la flore, ainsi que le suivi des mesures de gestion en cours permettent une meilleure compréhension du fonctionnement de ces écosystèmes et aideront à la définition d'objectifs futurs de protection et de restauration des milieux. Depuis sa création en 1982, le Groupe d'Etude et de Gestion de la «Grande-Cariçaie» (GEG) mène des études sur l'impact du fauchage sur la vitesse de succession des communautés végétales (Le Nédic, 2002), sur la dynamique du roseau (*Phragmites australis*) (Güsewell et Klötzli, 1998; Gander, 2003), de même qu'il établit des inventaires faunistiques et floristiques, et cartographie les formations végétales de la zone (Clerc, 1994; Clerc, 1996; Mulhauser, 1996, 1997). Concernant les étangs à proprement parler et la végétation aquatique en particulier, les études sont peu nombreuses (mais voir Oïhénart *et al*., 1988; Mulhauser, 1996; Antoine, 2002; Antoine *et al*., 2004).

Le choix de la présente étude s'est précisément porté sur les étangs, milieux comptant parmi les plus riches de la rive sud mais aussi parmi les plus menacés. Le suivi de quinze d'entre eux sur une période prolongée cherche à compléter les données existantes, tant du point de vue de la physico-chimie de l'eau et des sédiments que de celui de la végétation. Les étangs étudiés, ainsi que les stratégies d'échantillonnages seront présentés dans les parties «Materials and Methods» des articles constituant les chapitres 5 à 8.

4.2 Zone alluviale fluviale de la Basse plaine de l'Ain (France)

4.2.1 Pourquoi ce choix ?

Dans une perspective d'application et de validation de concepts théoriques, l'étude comparée entre deux types de zones alluviales, lacustre et fluviale, en termes de dynamique et donc de fonctionnement, peut être intéressante. Le choix de la zone alluviale de la Basse plaine de l'Ain comme site d'étude comparatif fluvial s'est effectué en fonction des critères suivants:

- le fonctionnement géomorphologiqe et hydrologique de cette zone est très bien étudié (Bravard, 1986; Marston *et al*., 1995; Piégay *et al*., 2000). Bravard (1986) souligne en effet l'importance de la connaissances des processus géomorphologiques pour la compréhension des paramètres écologiques.
- la végétation et la faune ont fait l'objet d'études extensives depuis le début des années 1980 (Castella et Amoros, 1986; Balocco-Castella, 1988; Castella, 1987; Castella *et al*., 1991). Ces études se poursuivent encore aujourd'hui (Bornette *et al*., 1998b; Bornette *et al*., 2001; Antoine, 2002) et offrent une vision synchronique et diachronique des processus en cours dans cette zone.
- les espèces aquatiques et semi-aquatique recensées au cours de ces études sont des espèces cosmopolites ou sub-cosmopolites (Pautou et Girel, 1986). Elles ne sont donc pas en limite d'aire de distribution par rapport au site d'étude suisse. Par ailleurs, les deux sites d'études peuvent être considérés comme appartenant à la même aire biogéographique.

4.2.2 Brève description du site de la Basse plaine de l'Ain

La rivière Ain dans son cours aval, c'est-à-dire peu avant sa confluence avec le Rhône, est caractérisée par une pente forte (entre 1.2 et 1.8 pour mille (Bravard, 1986)) et un débit moyen de 123 m^3/sec. Ses crues sont fréquentes et violentes, en raison de son parcours encaissé (Bravard, 1986). Elles lui confèrent un cours extrêmement dynamique, dans lequel les milieux, et donc les communautés biotiques qu'ils abritent, sont en constant remaniement (Amoros *et al*. 1986).

A l'hétérogénéité spatiale qui résulte des phénomènes hydrologiques et géomorphologiques du cours actuel s'ajoute l'hétérogénéité héritée du fonctionnement passé de la rivière. En effet, le XX^{éme} siècle a marqué une transition entre un style géomorphologique tressé et un méandrage (Bravard, 1986). Selon ce même auteur, cette transition résulterait de la réduction de la recharge du cours en éléments grossiers causée par:

- le reboisement naturel et donc la stabilisation de certaines zones en amont,

- la construction de barrages qui réduisent la fréquence et l'intensité des crues (augmentation de la stabilité), et jouent le rôle de bassin de rétention,
- la multiplication des ouvrages (ponts routiers, autoroutiers et ferroviaires) qui canalisent la rivière sur de longues distances, l'empêchant de divaguer et la contraignant à creuser son lit.

La réduction de la charge et l'accentuation de la pente augmentent l'énergie de la rivière qui n'a d'autre choix pour la dissiper que de creuser son lit et de méandrer. Les conséquences de ce changement de fonctionnement sur la dynamique de régénération des milieux et leur organisation en mosaïque sont encore difficiles à évaluer. Les premières observations laissaient penser à une complexification de l'écosystème (Bravard, 1986).

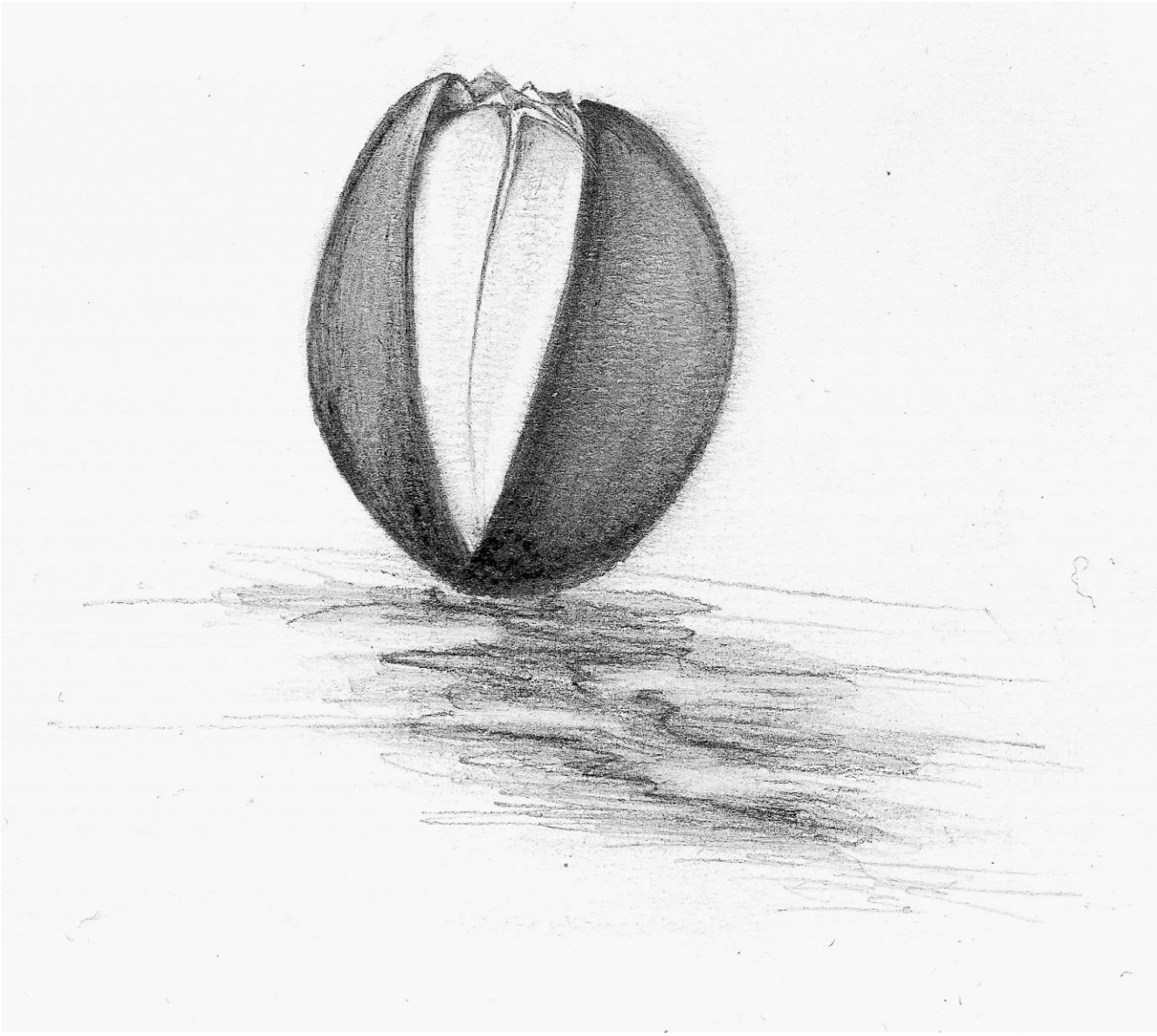
Finalement, la rivière Ain se caractérise par l'incision rapide de son cours, et l'effondrement de la nappe phréatique qui en résulte, entraînant une isolation accélérée des plans d'eau de la plaine alluviale, par rapport au cours principal et l'intensification des processus d'atterrissement, comme ce fut observé par Castella et Amoros (1986), Amoros *et al*. (1986) et Bornette *et al*. (1996).

L'hétérogénéité des conditions environnementales, qui résulte des processus hydrologiques et géomorphologiques passés et présents (anciens méandres d'origine, d'âge et de degré de connectivité différents) est le support d'une diversité biologiques élevée, qui peut, dans le cas de la végétation aquatique être perçue à trois échelles spatiales successives:
- celle de la plaine alluviale dans son ensemble,
- celle des anciens méandres (appelé localement lônes),
- celle des mésohabitats (Amoros, 2001).

Dix lônes de la Basse plaine de l'Ain ont fait l'objet d'un suivi de la physico-chimie de l'eau et des sédiments et de relevés de végétation aquatique selon des protocoles proches voir identiques, à ceux utilisés dans la Grande-Cariçaie. L'acquisition de ces données s'est faite dans la perspective de comparer des plans d'eau de plaines alluviales péri-lacustre et fluviale, du point de vue de leur fonctionnement, de leur richesse et diversité taxonomique végétale ainsi que des stratégies élaborées par les espèces végétales pour répondre aux conditions environnementales.

Chapitre 5

Spatial and temporal variation in habitat characteristics among pools within a lake fringe wetland (Lake Neuchâtel, Switzerland)



5.1 Introduction

During the last decades of the 20th century, Europe suffered a dramatic decrease in the number of freshwater pools (Duigan and Jones, 1997; Gledhill, 1998; Bressi and Stoch, 1998). The main reasons for this decrease are urban development, agricultural intensification, river regulation (for alluvial water bodies) or simply neglect and absence of management. This rapid disappearance of pools has led to an increased awareness of their crucial importance in the maintenance of biodiversity in the European landscape. Pools are more and more identified as hotspots of species diversity (Oertli *et al*. 2000), harbouring important numbers of species of aquatic plants and animals , which together comprise a substantial proportion of a country's species pool (Duigan and Jones, 1997; Guest, 1997). For instance, in Britain 55% of the vascular wetland plant species of the country were recorded during a recent survey of 377 pools, i.e. 177 species of vascular species and 5 charophytes (Williams *et al*. 1998). The high conservation value of pools results not only from the high species diversity they support but also from the fact that a significant proportion of those species are endangered (Biggs *et al*., 1994; Guest, 1997; Gledhill, 1998). In the existing literature, reference is made to pools of various types and in a variety of locations, including farmland ponds, village ponds, marl-pits, drainage pools, urban pools etc, but few or no studies seem to deal with pools enclosed within lacustrine wetlands. The reason may be the absence of limits between inundated reed-beds and open water zones in wetlands, where pools are often not identified as such in the continuum of water-depth gradients observed (Duever, 1990). Yet, the surface of these open water zones experiences the same drastic decrease as their "isolated" (i.e. pools that are not part of a larger wetland) counterparts (Mulhauser, 1996). And the species diversity supported by these pools is similarly important.

One focus of the study reported on here has been the role of the connections, or the absence of connection, between pools in a lake-fringing wetland and the lake itself. The present text aims i) at describing physical and chemical characteristics of the water and sediment of the 15 pools studied and ii) at producing a baseline environmental data for use in further studies of their biota. All of the pools studied are enclaves within one large, lake-fringing wetland. Particular attention is given here to the interaction between pool location and fluctuation in pool physicochemical character.

5.2 Materials and Methods

5.2.1 Study Site

The study site is the largest fringing wetland in Switzerland (mean altitude: 429.3 m), the "Grande-Cariçaie", recognised as of international significance by the Ramsar Convention. The origin of this 40 km-long wetland dates from the first phase of modification of the hydrological system of the Swiss Jura catchment (1869-1888): 2000 ha of bare soils were exposed as a consequence of a 2.7 m lowering

of Lake Neuchâtel's water level. Nowadays, and despite severe problems of erosion on the lake-ward side and terrestrialisation on the land-ward side, the wetland which developed on the exposed lake shore is made up of inundated and non-inundated reed beds, sedge beds, sand dunes and pools, coexisting in a complex mosaic of habitats. The origins of the waters feeding the wetland are many and varied. Since water-level fluctuations in the lake became regulated in the 1970's, the direct influence of the lake has become limited to a 50-meter wide band, which can be further reduced in width by the presence of sand dunes. Water-level fluctuations do not now exceed 1m. Levels are maximal in spring (May-June), decrease during summer and are minimal in winter. When distance from the lake increases or when sand dunes disconnect the wetland from the lake, the relative importance of groundwater influence increases. In addition to lake surface water and groundwater, water from two other origins may contribute to the water reaching pools within the wetland. In those sectors of the lake margin where the wetland is restricted to a narrow strip between the lake and cliffs, water input can occur through surface water runoff from the cliffs. Finally, streams reaching the lake from its hinterland (most often agricultural) constitute a fourth substantial water input in some sectors. The climate of the region is temperate. Meteorological data, obtained for the three years of study (1996 to 1998), indicate a mean temperature of 0.03 °C in January and 17.8 °C in July, accompanied by mean precipitations of 295 mm in January and 1078 mm in July.

Fifteen pools at four different locations (sectors) were selected for the purpose of this study: Champ-Pittet (pools CP1 to CP4), la Maladaire (pools MA1 to MA6), Châbles-Perron (pools CH1 and CH2) and Font (pools FO1 to FO3). The location of the pools, along the southern shore of Lake Neuchâtel, is shown in Figure 5.1. Except for CP and MA3, these pools are all man-made. Some of these pools are connected to one another, while others are not: a connection exists from CP1 through CP2 and CP3 to CP4, as between CH1 and CH2 and FO2 and FO3. Moreover, the pools exhibit different degrees of connection to the lake (at mean lake water level): CP1, CP2 and CH2 are directly connected to it, through a channel. The connection of CP3 and CP4 to the lake operates through their connection to CP2 and CP1. The other pools are separated from the lake by a more or less developed sand dune, which is flooded only during high lake water levels. Pools MA1 and MA2 were considerably affected by the input of a small stream at the beginning of this study, but its influence subsequently decreased and became irregular.

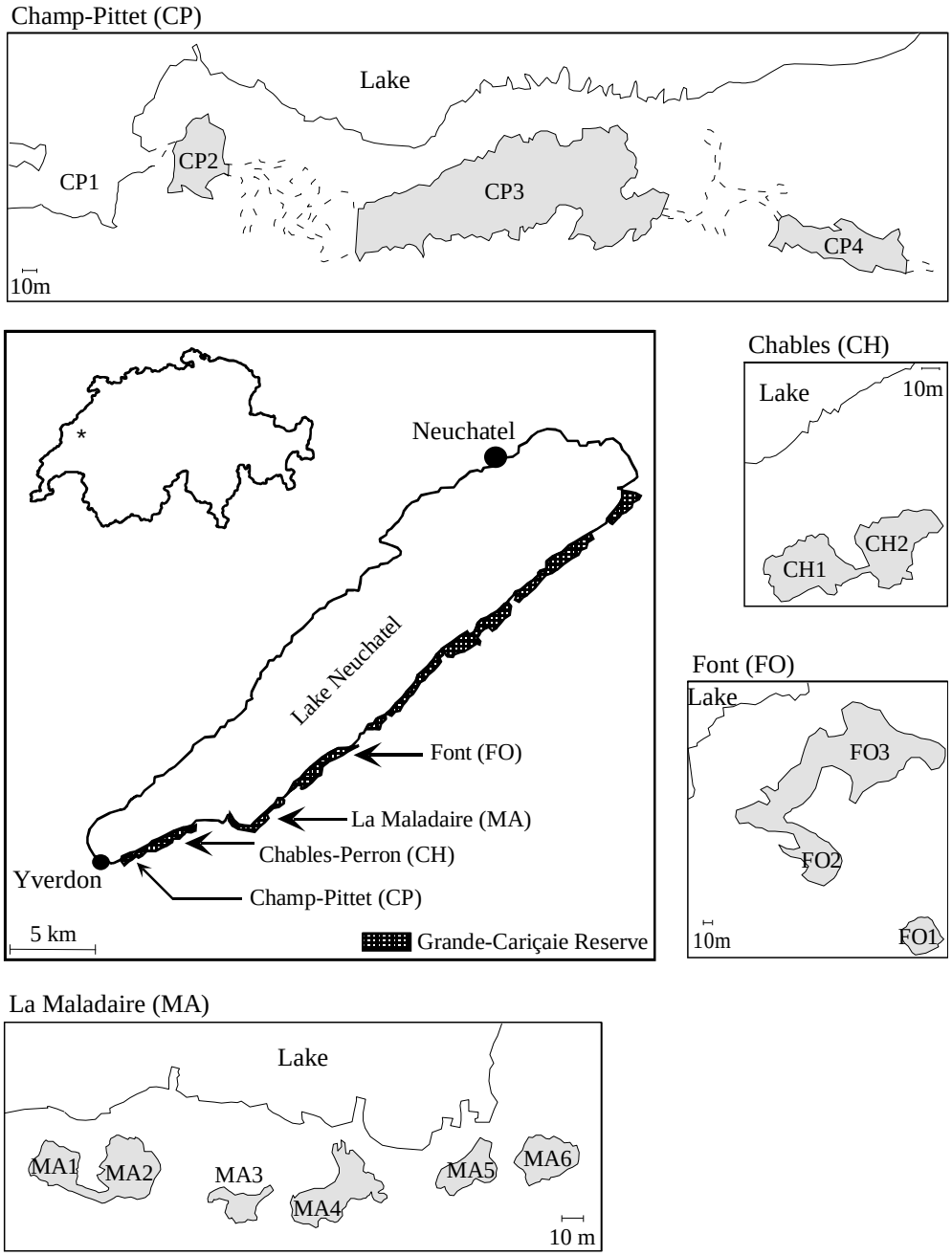


Figure 5.1 The "Grande-Cariçaie" fringing wetland on the southern shore of Lake Neuchâtel (Switzerland) and the location of the four pool sets.

5.2.2 Sampling regime

5.2.2.1 Water physico-chemistry

Conductivity, pH, dissolved oxygen and temperature were measured in the field, using WTW probes (LF 320 conductivity-meter, pH 320 pH-meter and Oxi 320 oxi-meter, respectively). Water transparency and pool water level were recorded simultaneously, with a Snellen tube and fixed gauges, respectively. Transparency will be further considered as the deviation to the overall mean transparency. Water level measurements were standardised to the level recorded at a common date for all pools (21st of January 1998).

Pools CP and MA were monitored from March 1996 to January 1998 (14 samples), whereas CH and FO were monitored from January 1997 to June 1998 (10 samples). Field measurements and samples were taken in the open water and not in the helophyte belt of the pools.

Continuous water temperature monitoring was carried out by means of temperature loggers (Tiny Talk ™), during two periods: from mid June to mid November 1997 (in all pools except CP1 and CH1), from mid November 1998 to mid May 1999 (in all pools except CP1). Data for the second period in pools CP3 and FO2 were unusable, because of loss of and defects in loggers, respectively. The data (generally recorded at a 3-hour time interval) were averaged per fortnight and subsequently expressed for each pool as the deviation between the pool fortnight average and the fortnight average of all pools. This calculation was based upon a subset of 11 pools for which complete time series were available. Hence, the seasonal temperature pattern of each pool was described in terms of a distance to the fortnight average.

Ammonia, nitrites, nitrates, ortho-phosphates, total phosphorus, total and calcium hardness and silica content were measured on five occasions (quarterly), between January 1997 and January 1998. Pools FO1, FO2 and FO3 were not instrumented on the first date (January 1997). Ammonia, nitrate and nitrite concentrations were determined using the salicylate, cadmium reduction and diazotisation methods, respectively. Ortho-phosphate concentrations were measured by the persulfate acid digestion method. Total and calcium hardness were determined by the EDTA method. Silica concentrations were measured using the Heteropoly Blue method or the silicomolybdate method, depending on the concentration range.

5.2.2.2 Sediment characteristics

Bottom sediment samples were taken in all pools during the winter of 1997, for grain size analysis (Coulter LS-100) and organic matter content (loss on ignition). For some pools, complementary data were taken during the winters of 1996 and 1998. Five sediment cores (diameter 5 cm) were taken from each pool, except the largest (CP3), where 8 cores were taken. The top 5 cm of each core was analysed (Rostan *et al*., 1987). Concerning the granulometry, only the percentage of particles under 63 µm and the median of the particle size distribution were considered for further analyses.

Sedimentation rate was assessed in each pool by means of sediment traps (1 litre parallelepipedic containers, height: 15.6 cm, aperture area: 64 cm^2). Five sediment traps were installed in each pool (8 in the larger CP3), but some traps were not recovered. Each trap was installed such that its base was in contact with the pond sediment. In the very shallow pool MA3, the traps were installed deeper in the sediment. Sediment deposition was recorded from April 1996 to May 1999, thus covering three "winter" (~ September to March) and three "summer" (~ March to September) periods. However, not all pools were sampled for sediment deposition over that entire period. A minimum of one-year's data (one summer and one winter period) are available for each pool. The traps were emptied every four to seven months and their content dried at 60° degrees to constant mass and weighed. "Sedimentation rate" data are expressed as kg dry weight/month/m^2. In order to compensate for differences in residence time of the traps between periods, the trap sediment weight was divided by the number of fortnights spent in the pool (and multiplied by 2 in order to have monthly values). In addition to this "sedimentation rate" measure and as for bottom sediment samples, grain size distribution and organic matter content were also determined.

5.2.3 Data analysis

Water and sediment data underwent the same statistical treatments. The Kruskal-Wallis test (called hereafter KW test) was used to test differences between sectoral groups of pools, individual pools or dates (Sokal and Rohlf, 1995). In a second step, the Wilcoxon test was carried to refine the KW results and identify differences between pairs of pools or dates. All calculations were computed with the S-Plus 2000 software (Anonymous, 1998).

A covariance matrix Principal Component Analysis (PCA) was used to ordinate the 11 pools on the basis of their fortnight temperature deviations. The PCA was carried out with the ADE-4 software (Thioulouse *et al*., 1997).

5.3 Results

5.3.1 Water physico-chemistry

Annex 1 contains the median, quartiles, minimum and maximum values of the water physico-chemistry parameters.

5.3.1.1 Water level fluctuations

5.3.1.1.1 *Lake*

Lake water levels showed general similarity between years (Figure 5.2) in that they increased during spring, were maximal in June-July and minimal in winter. The mean water level was 25 cm higher

during the first half of 1995 than in 1996 and the greatest differences reached 40 cm (e.g. between February 1995 and February 1996). Moreover, the minimum and maximum values indicate that the range of fluctuation was highest in 1995 (94 cm) and lowest in 1998, when it hardly exceeded 50 cm. In 1996 and 1997, fluctuations approached 70 cm. Weekly water level fluctuations over the same four-year period (1995- 1998) averaged 7 cm, with 9 cm in 1995 and 6 cm in 1998. An exceptional week was recorded in January, 1995, when the fluctuation reached 60 cm.

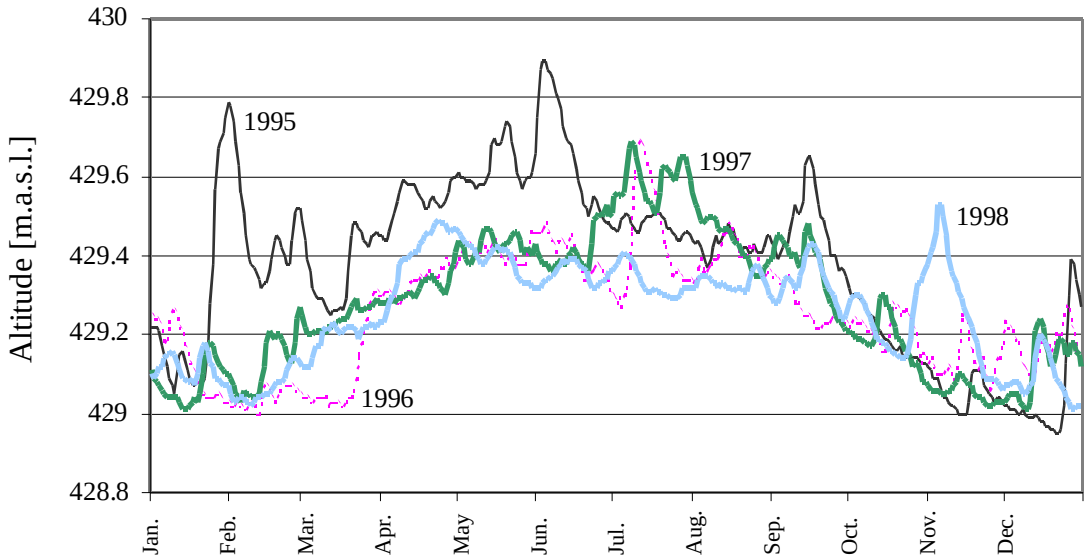


Figure 5.2 Lake water level fluctuations in Lake Neuchâtel, between 1995 and 1998.

5.3.1.1.2 *Pools*

The KW tests evidenced significant differences in median values of pool water levels between sectoral groups as well as between individual pools ($p < 0.01$ in both cases). Of the four sectoral groups of pools, the CP pools were characterised by the greatest water level fluctuations (Figure 5.3, Annex 1).

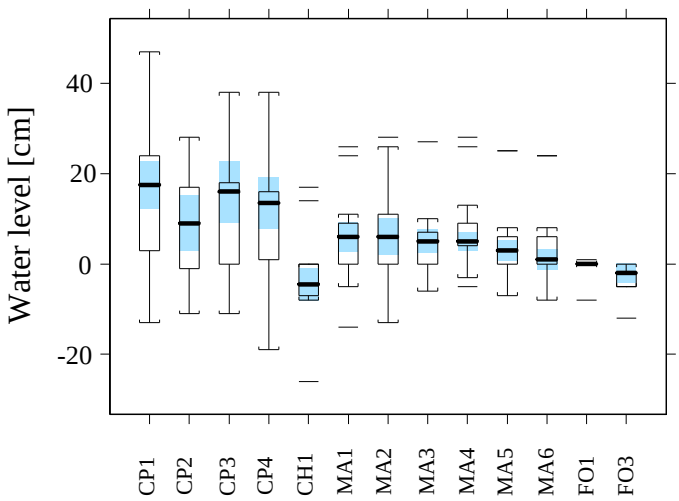


Figure 5.3 Water level (cm) expressed for each pool as the deviation to the level recorded on January the 21st and 22nd. The vertical boxes represent the inter-quartile range (Q25 – Q75) around the pool median (horizontal black line). Upper and lower whiskers are drawn to the nearest value not beyond Q75+1.5 (Q75-Q25) and Q25-1.5 (Q75-Q25). Shaded area is a 95% confidence interval around the median.

5.3.1.1.3 *Lake-pool water level relationships*

Lake and pool water level fluctuations showed a significant positive linear relationship (r^2 = 0.58, p = 0) when the regression was calculated between the lake and the pool water levels for the entire set of pools. This relationship increased for CP and MA when these sectoral groups of pools were considered separately. It was higher for the CP pools (r^2 = 0.8, p = 0) than for MA (r^2 = 0.71, p = 0), which was confirmed by the regressions performed on the pools taken individually (Table 5.1). Pool CH1 displayed only a weaker relationship with the lake, while water levels in pools FO1 and FO3 showed no relationship with the lake at all (Table 5.1).

Table 5.1 Coefficient of determination of pool water level regressed upon lake water level and the associated significance level (p).

Pond	n	r^2	p-value
CP2	22	0.86	<0.001
CP3	20	0.80	<0.001
CP4	19	0.85	<0.001
CH1	10	0.65	<0.01
MA1	19	0.72	<0.001
MA2	19	0.65	<0.001
MA3	18	0.69	<0.001
MA4	17	0.82	<0.001
MA5	17	0.76	<0.001
MA6	17	0.73	<0.001
FO1	6	0.02	0.77
FO3	5	0.73	0.07

5.3.1.2 Water temperature

The ordination of the 11 pools on the basis of their fortnight temperature deviations showed that the temperature differences between pools were maximal in February and August. Four types of pool could be distinguished: i) "summer-warm" pools (FO1, FO3), with summer averages above +3°C of the pool average, ii) "winter-warm" pools (MA4), with winter averages above +2°C of the pool average, iii) "winter-cool" pools (CP2, CP4, MA3, CH2, to which CP3 and FO2 could be added on the basis of more fragmentary data), with winter averages below –1°C of the pool average, and average summer temperatures, iv) "summer cool-to-average" pools (MA1, MA2, MA5, MA6), with summer averages between +0.5 and –2,5 °C of the pool average, and average winter temperature. Actual temperature time series are given for one pool per type in Figure 5.4. In February and August, differences between the median temperatures of these four pools were all significant (Figure 5.5). The representation of water temperature fluctuations over the first fortnight of August and of February (the months showing greatest contrast) revealed marked differences in daily variations between pools. Differences were maximal in August (Figures 5.6a, 5.6b and 5.6c) and reduced in February (Figures 5.6d and 5.6e).

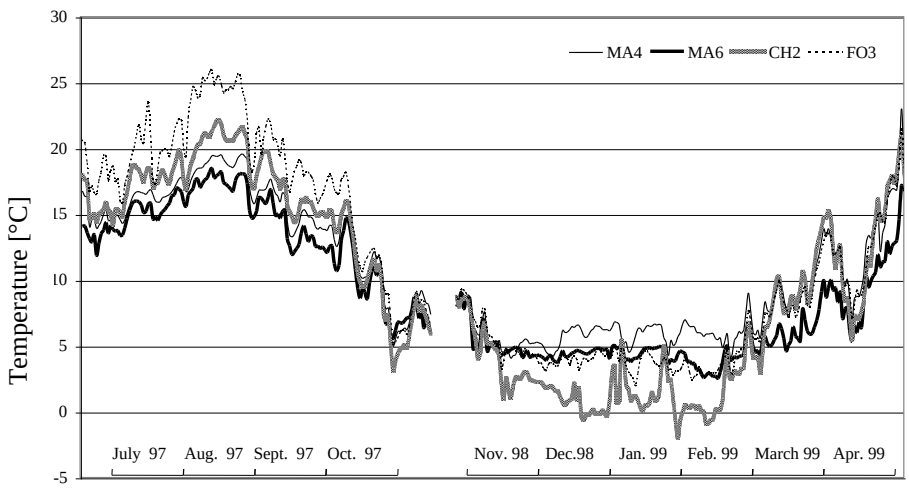


Figure 5.4 Water temperature time series for MA4 (winter warm pool-type), CH2 (winter cool pool-type), FO3 (summer warm pool-type) and MA6 (summer cool to average pool-type).

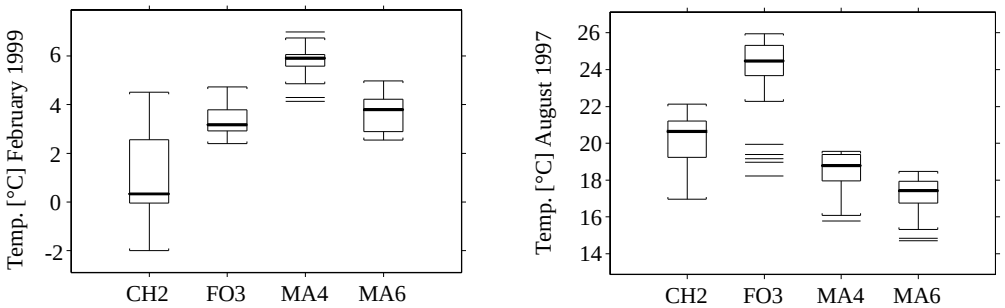


Figure 5.5 Differences in water temperature for pools CH2, MA4, FO3 and MA6 in winter (February 1999) and summer (August 1997). The vertical boxes represent the inter-quartile range (Q25 – Q75) around the pool median (horizontal black line). Upper and lower whiskers are drawn to the nearest value not beyond Q75+1.5 (Q75-Q25) and Q25-1.5 (Q75-Q25).

5.3.1.3 Transparency

The KW tests, performed on the deviation from the mean transparency values per date, attested to the existence of significant differences between individual pools ($p = 0$) but not between the four sectoral groups of pools ($p = 0.51$). In contrast to the other pools, MA1, MA2, FO3 and CP3 experienced transparencies usually under the mean (Figure 5.7). The substantial inter-quartile ranges observed in CP and FO, compared to MA and CH, suggest the existence in these pools of important temporal variations. Regressions of transparency on lake water levels revealed no relationship, whatever combinations of pools were considered (all pools, pool sets or pools taken individually).

5.3.1.4 Dissolved oxygen and pH

KW tests evidenced significant differences between sectoral groups of pools, and between individual pools, for pH ($p = 0.0004$ and $p = 0.0001$, respectively), but only between-pool differences for dissolved oxygen ($p = 0.098$ and $p = 0$, respectively). The minima and maxima (Figure 5.8a and 5.8c and Annex 1) indicated that pools CP and MA experienced more extreme conditions of dissolved oxygen and pH (0.3 to 22.8 mg l^{-1} O_2) than did pools CH and FO (2.9 to 13.4 mg l^{-1} O_2). The most obvious pattern was a decreasing gradient within the CP sectoral group of pools, from alkaline, well-oxygenated lake waters in CP1 (median pH = 8.5; dissolved oxygen = 12 mg l^{-1}) to the more neutral, less oxygenated CP4 water at the other end (median pH = 7.6; dissolved oxygen = 4.6 mg l^{-1}) (Figures 5.8b and 5.8d). Fluctuations in both parameters (inter-quartile ranges) showed the exact reverse trend and increased from CP1 to CP4 (Table 5.1 and Figures 5.8b and 5.8d).

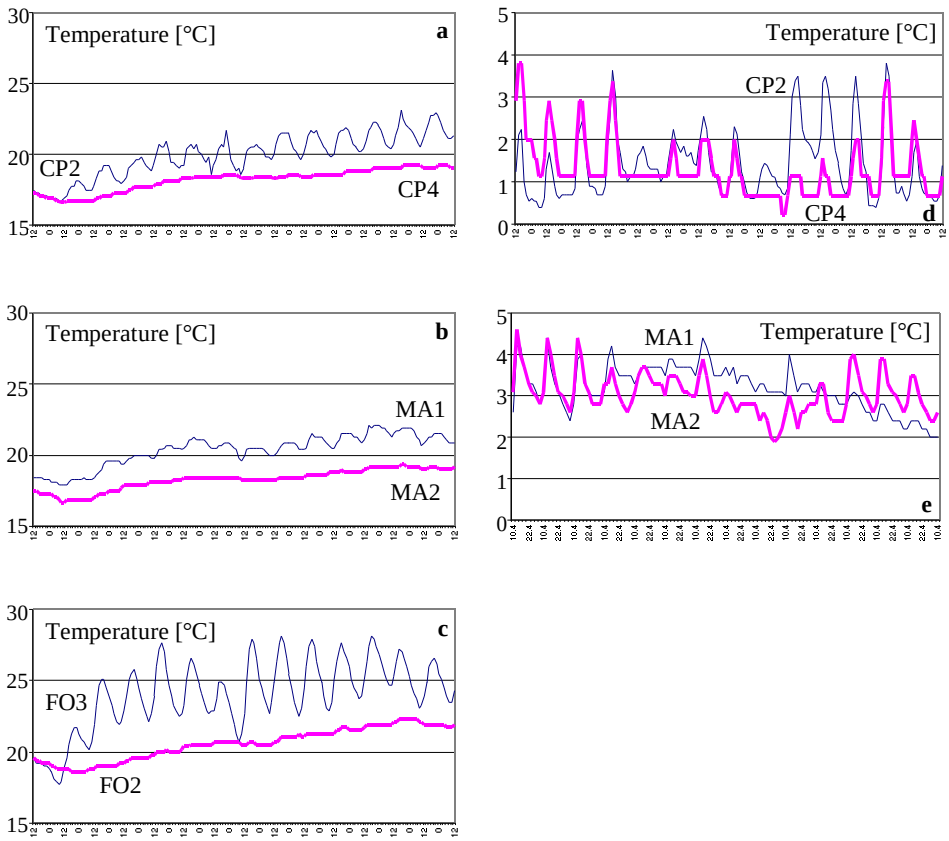


Figure 5.6 Water temperature time series of the first fortnight of August 1997 (a, b, c) and February 1998 (d, e) in pairs of pools belonging to a same sector.

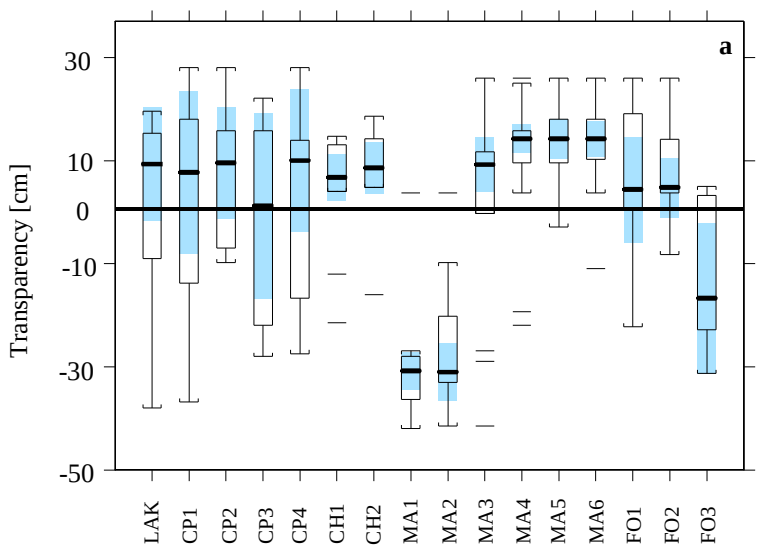


Figure 5.7 Water transparency [cm] expressed as the deviation to the mean transparency of all pools at the given date. Shaded area is a 95% confidence interval around the median.

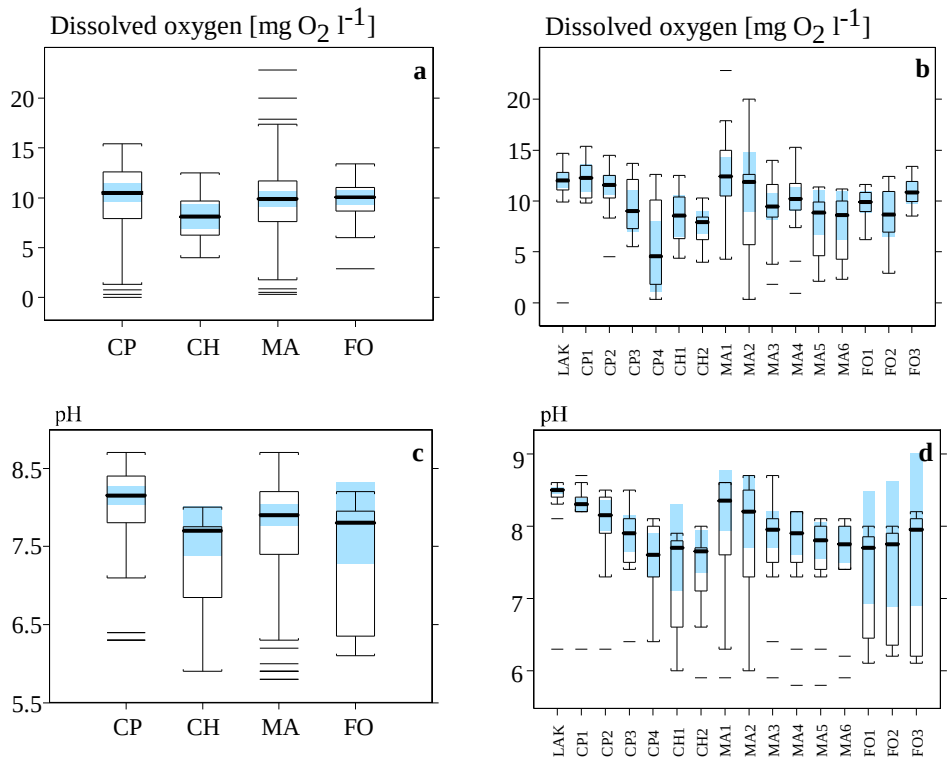


Figure 5.8 Box-plots of dissolved oxygen (a and b) and pH (c and d), for the pool sets (a and c) and the pools (b and d). The vertical boxes represent the inter-quartile range (Q25 – Q75) around the pool median (horizontal black line). Upper and lower whiskers are drawn to the nearest value not beyond Q75+1.5 (Q75-Q25) and Q25-1.5 (Q75-Q25). Shaded area is a 95% confidence interval around the median.

5.3.1.5 Mineralisation parameters

Conductivity varied significantly between sectoral groups of pools and between individual pools ($p < 0.01$ in both cases). The CP group of pools displayed the lowest conductivity (median = 422 µS cm^{-1}) and MA the highest (578 µS cm^{-1}) (Figure 5.9a). There was a marked conductivity gradient from CP1, the conductivity of which was closer to that of the lake (median = 318 µS cm^{-1}) to CP4, whose values were closer to those of the MA pools (median = 514 µS/cm) (Figure 5.9b). The incursion of lake water to the pools was expected to decrease the pool's conductivity. But, except for CP2 ($r^2 = 0.36$, $p = 0.03$), there was no significant relationship between lake water level and water conductivity in the pools. Calcic hardness and silica showed differences between sectoral pool groups and individual pools similar to those exhibited by conductivity, and the differences between sectors and pools were significant as well. Medians were highest in the MA pools and lowest in CP (Figures 5.9c and 5.9e) and they increased from pool CP1 to pool CP4 (Figures 5.9d and 5.9f).

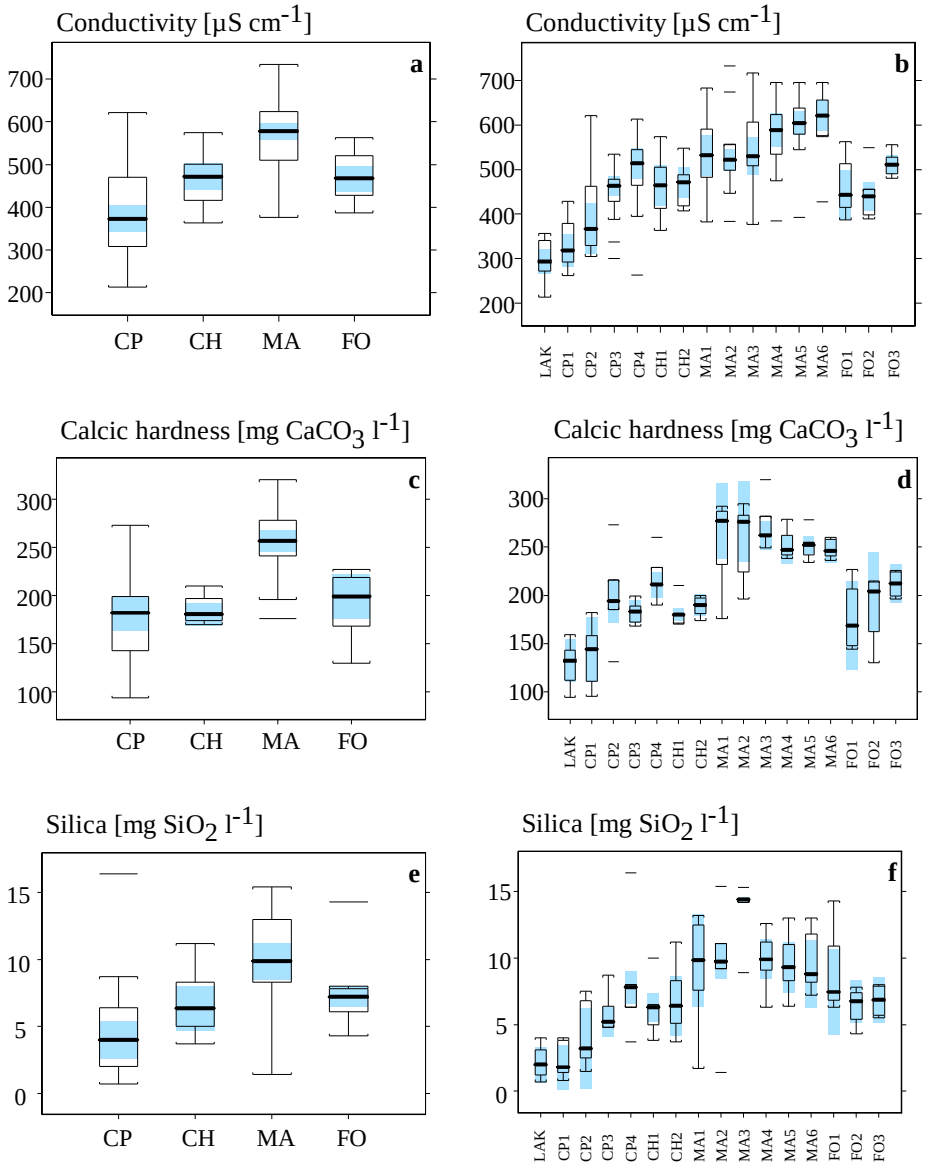


Figure 5.9 Box-plots of conductivity, calcic hardness and silica, for pool sets (a, c, e) and pools (b, d, f), respectively. The vertical boxes represent the inter-quartile range (Q25 – Q75) around the pool median (horizontal black line). Upper and lower whiskers are drawn to the nearest value not beyond Q75+1.5 (Q75-Q25) and Q25-1.5 (Q75-Q25). Shaded area is a 95% confidence interval around the median.

5.3.1.6 Nutrients

Most nutrient variables did differ significantly between sectoral groups of pools or between individual pools (Annex 1). Within the pools of the MA sector, MA1 and MA2 had higher total phosphorus and lower nitrite and nitrate concentrations, as compared to MA4, MA5 and MA6, which exhibited the reverse trend (Figures 5.10b, 10c and 5.10 and Annex 1).

The latter three pools however were characterised by more important seasonal fluctuations. Nitrate concentrations, for instance, were highest during the cold months (January and November 1997 and

January 1998) and could reach (e.g. in MA4) 17 times the lowest pool value (minimum in MA4 = 0.2 mg l^{-1} and maximum in MA4 = 3.3 mg l^{-1}). Ammonia displayed exceptionally high concentrations and seasonal fluctuations in pools MA1 and MA2, during which values varied by 68 and 40 times, respectively (highest values in January and November 1997) (Figure 5.10a and Annex 1). Within the CP group, CP1 and CP2 experienced higher and seasonally more stable nitrite concentrations than CP3 and CP4 (Figure 5.10b and Annex 1). Nitrate concentrations were highest in CP1 (median = 1 mg l^{-1}; minimum = 0.5 mg l^{-1} and maximum = 1.7 mg l^{-1}), but CP2 experienced more extreme fluctuations (minimum = 0.25 mg l^{-1}; maximum = 2.2 mg l^{-1}).

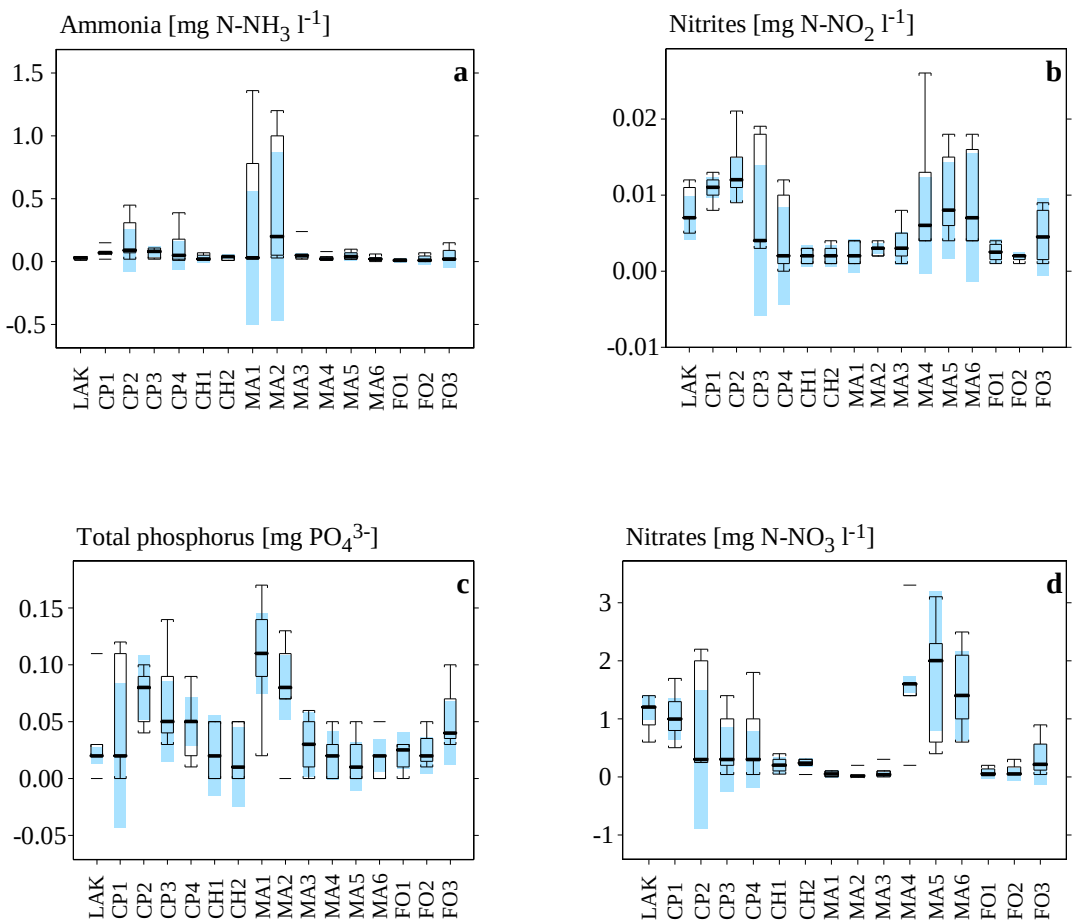


Figure 5.10 Box-plots of ammonia (a), nitrites (b), total phosphorus (c) and nitrates (d) concentrations in the lake and the pools. The vertical boxes represent the inter-quartile range (Q25 – Q75) around the pool median (horizontal black line). Upper and lower whiskers are drawn to the nearest value not beyond Q75+1.5 (Q75-Q25) and Q25-1.5 (Q75-Q25). Shaded area is a 95% confidence interval around the median.

5.3.2 Sediment characteristics

5.3.2.1 Bottom sediments

5.3.2.1.1 *Organic matter content*

Pools MA1 between 1996 and 1997, and between 1996 and 1998 ($p<0.01$ in both cases) and MA3 between 1996 and 1997 ($p<0.05$) exhibited significant differences in organic matter content between sampling years (Figure 5.11a). These temporal differences, however, did not veil the significant between-sector and between-pool differences. Thus, the pools of the CP sector were characterised by a gradient of increasing sediment organic matter content from CP1 (median = 1.6 %) to CP4 (median = 35 %) (Figure 5.11a and Annex 2). In the CH sector, pools CH1 and CH2 displayed very similar medians but very different spatial heterogeneity manifested by the inter-quartile ranges (Figure 5.11a and Annex 2).

5.3.2.1.2 *Sediment particle size*

The percentage of fine particles (under 63 µm) decreased significantly with time (Wilcoxon test) in pools CP3 between 1996 and 1997, and between 1996 and 1998 ($p<0.01$ in both cases), CP4 between 1996 and 1997, and between 1996 and 1998 ($p<0.01$ in both cases), MA5 between 1996 and 1997 ($p<0.05$) and MA6 between 1996 and 1997 ($p<0.05$), while it significantly increased in pools MA1 ($p = 0.037$ between 1996 and 1998) and MA2 ($p = 0.01$ between 1996 and 1997 and 1996 and 1998) (Figure 5.11b). In all cases significant differences involved 1996, that appeared distinct, in comparison with 1997 and 1998. In addition to these temporal variations, pool groups and individual pools revealed significant spatial differences (Figure 5.11b and Annex 2). For instance, pools CH1 and CH2, although inter-connected, displayed marked differences in median values and inter-quartile ranges. Pools MA1 and MA2 showed exceptionally high percentages of particles under 63 µm, as compared to all other pools.

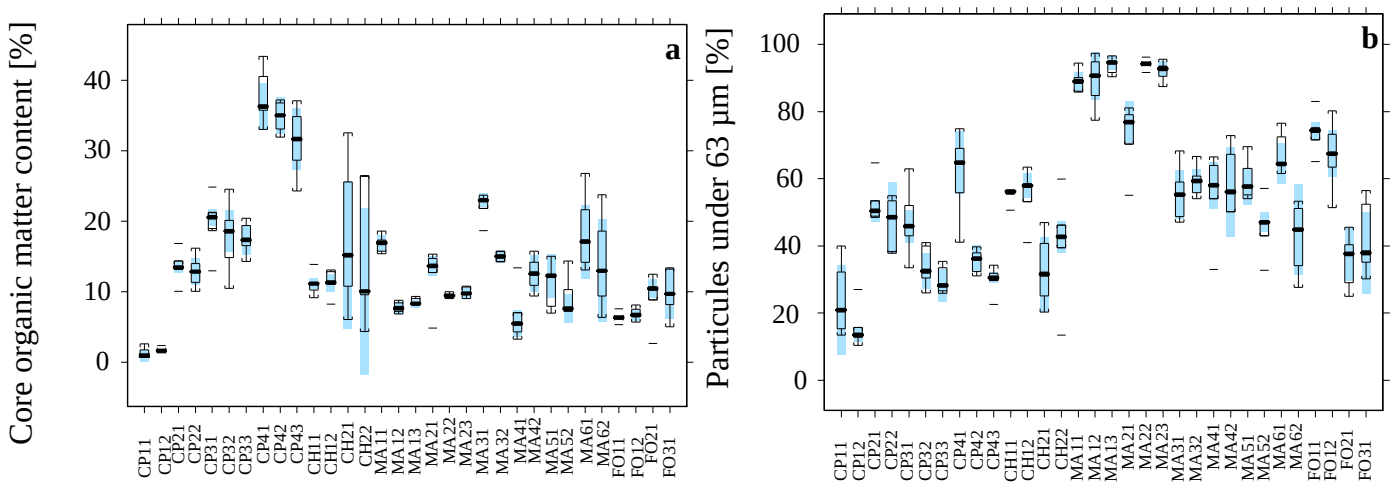


Figure 5.11 Box-plots of bottom organic matter content (a) and percentage of particles under 63 µm (b) in the pools. The numbers 1, 2 and 3 placed after the pool's code designate the sampling years of 1996, 1997 and 1998, respectively. The vertical boxes represent the inter-quartile range (Q25 – Q75) around the pool median (horizontal black line). Upper and lower whiskers are drawn to the nearest value not beyond Q75+1.5 (Q75-Q25) and Q25-1.5 (Q75-Q25). Shaded area is a 95% confidence interval around the median.

5.3.2.2 Trapped sediments

5.3.2.2.1 *Sedimentation rate*

Wilcoxon tests identified significant differences in sedimentation rate in pools CP2, MA4, MA5 and MA6 between summer and winter, but usually not between consecutive summers or consecutive winters (Figures 5.12a, 5.12i, 5.12j and 5.12k). In the sector of the CP pools, the seasonal fluctuations were marked in CP2 (Figure 5.12a), and lessening in CP3 and CP4 (Figures 5.12b and 5.12c). Except in pools MA1 and MA2, sedimentation rates were higher during the summer periods than during the winter. Four groupings of pools could be identified on the basis of their total yearly sedimentation rate (i.e. summer and winter) (Figure 5.13). The pools FO1, CH1 and CH2 experienced the lowest sedimentation rates (below or equal to 0.6 kg dry weight/m^2/month), whereas MA1 and MA2 occupied the other extreme, with sedimentation rates higher than 20 kg dry weight/m^2/month. In the intermediate positions, pools CP4, MA4, MA5, MA6 and FO2 were characterised by sedimentation rates between 0.8 and 1.9 kg dry weight/m^2/month, while in CP1, CP2, CP3, MA3 and FO3, they varied between 3.4 and 6.1 kg dry weight/m^2/month. The high sedimentation rates in pools MA1 and MA2 were largely the result of a thunderstorm event during the first trapping period (Figure 5.12f and 5.12g, see s1). The sedimentation rate in MA2 during s1 was almost 6 times higher than the

sedimentation rate in the same pool during s2 (Figure 5.12g) and more than 20 times higher than the sedimentation rate in MA5 during s1 (Figure 5.12j).

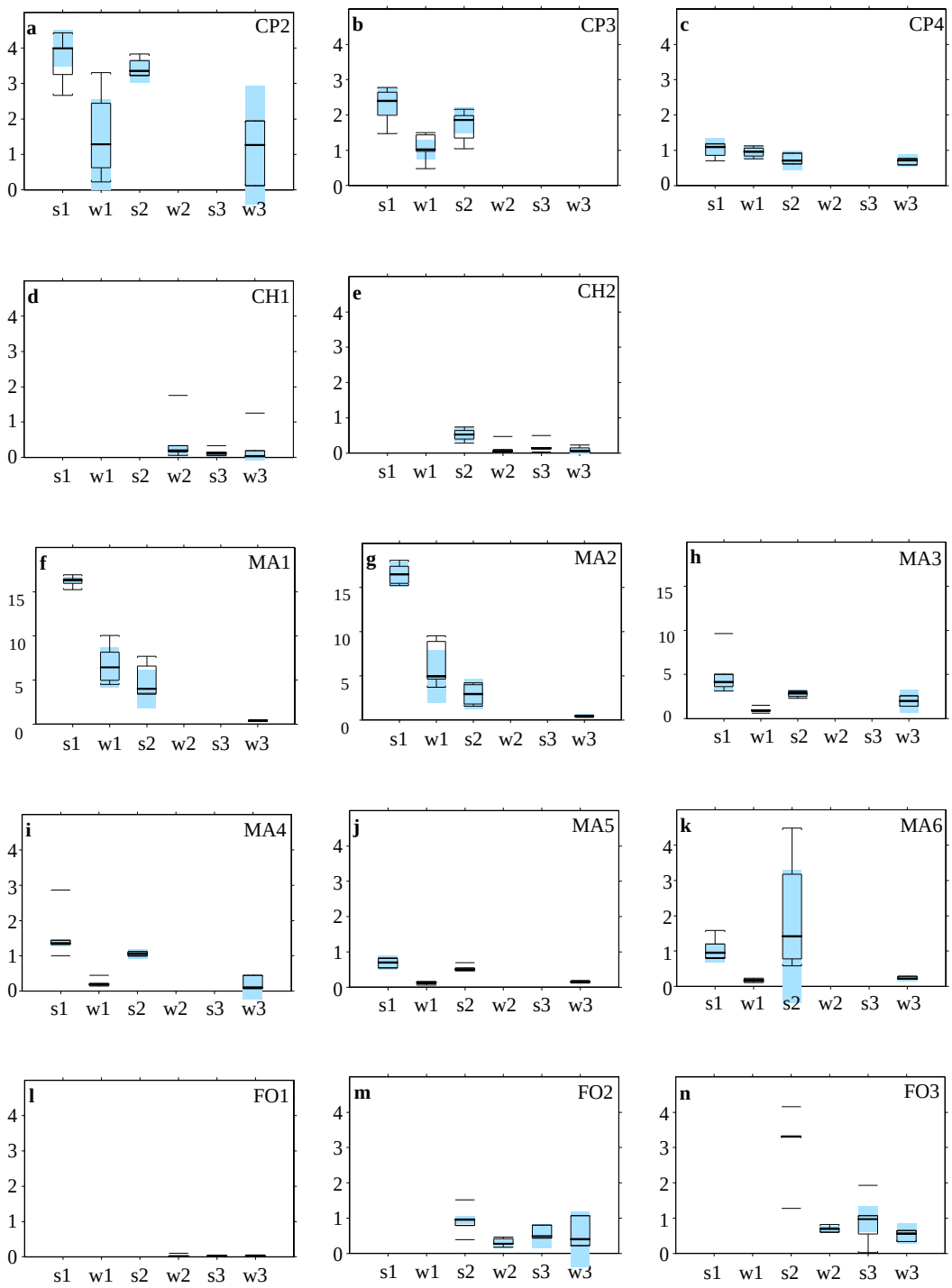


Figure 5.12 Box-plots of sedimentation rates [kg dry weight m^{-2} $month^{-1}$] in the pools. "s": summer periods (from March to September), "w": winter periods (from September to March). 1 = 1995, 2 = 1996, 3 = 1997. The vertical boxes represent the inter-quartile range (Q25 – Q75) around the pool median (horizontal black line). Upper and lower whiskers are drawn to the nearest value not beyond Q75+1.5 (Q75-Q25) and Q25-1.5 (Q75-Q25). Shaded area is a 95% confidence interval around the median.

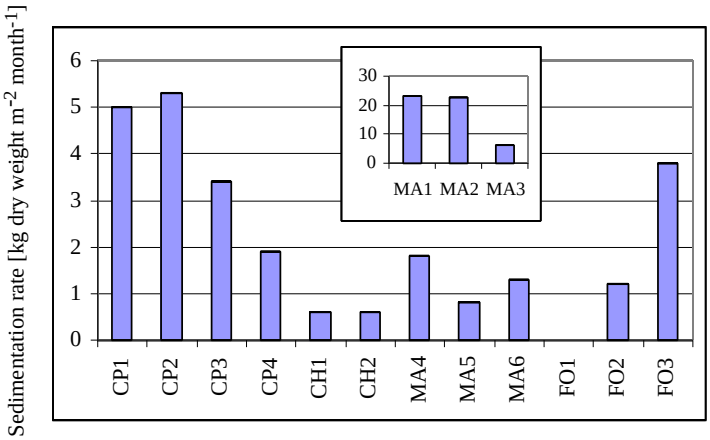


Figure 5.13 Yearly sedimentation rates in the pools, expressed as the sum of winter and summer values for one year.

5.3.2.2.2 *Organic matter content*

The range of values for organic matter content of the trapped sediment was similar to that measured in the bottom sediment (5.4 % to 55 % vs. 0.7 to 43.4 %). The Wilcoxon tests highlighted significant differences between sampling periods in all pools except for CP4, CH1, CH2, FO1 and FO3 (Figure 5.14). Seasonal trends were more difficult to draw out than for sedimentation rate. They appeared however to be opposite to those observed for the sedimentation rate, i.e. organic matter content in traps was generally highest in winter and lowest in summer (see, e.g. Figure 5.14k). As a consequence of these seasonal variations, the values presented in Figure 5.15 correspond to mean values of the summer- and winter sampling periods. As with organic matter content of core samples, percentages increased from pool CP2 to CP4 (Annex 2). A second gradient, not identified with core organic matter, was also observed between MA1 and MA6. The results obtained for MA3, MA4 and FO1 have to be considered with caution, because of the small number of values available for some sampling periods.

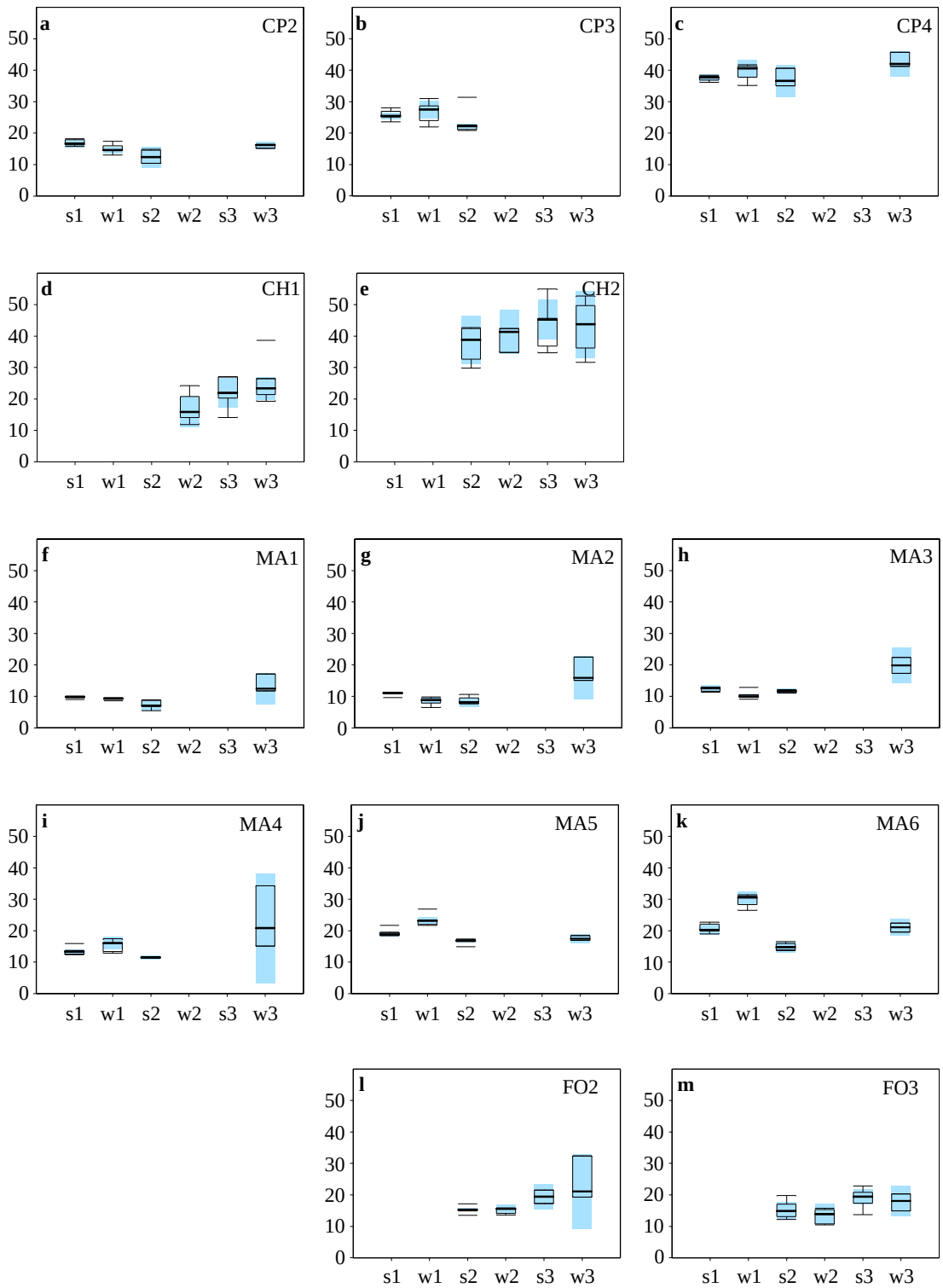


Figure 5.14 Box-plots of organic matter content [%] of the trapped sediment. "s": summer- (from March to September) and "w" winter (from September to March) periods. 1 = 1995, 2 = 1996, 3 = 1997. The vertical boxes represent the inter-quartile range (Q25 – Q75) around the pool median (horizontal black line). Upper and lower whiskers are drawn to the nearest value not beyond Q75+1.5 (Q75-Q25) and Q25-1.5 (Q75-Q25). Shaded area is a 95% confidence interval around the median.

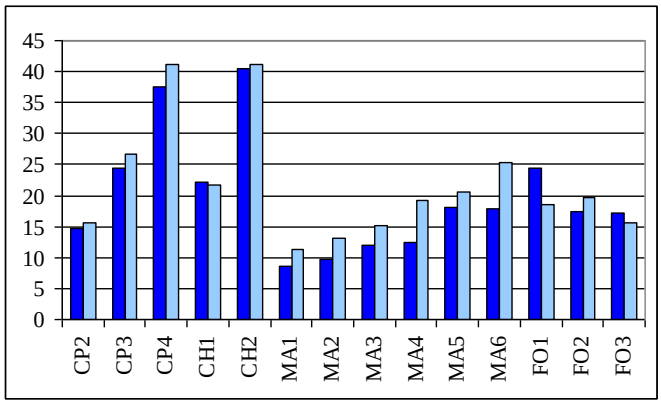


Figure 5.15 Organic matter content of the trapped sediment [%]. Dark columns represent mean values of the summer sampling periods, while pale-coloured columns represent mean values of the winter sampling periods.

5.4 Discussion

Pools are often depicted as discrete entities difficult to categorise (Úlehlová and Pribil, 1978; Balvay, 1984; Friday, 1987; Soranno *et al*., 1999; Linton and Goulder, 2000; Oertli *et al*. 2000). Evidences presented in this study largely support this general perception, as the variety of physico-chemical conditions represented in this limited subset of 15 pools is important, and reflected by significant differences between both sectoral groups of pools, and individual pools, in nearly all environmental variables considered. The proximity of other aquatic ecosystems and water sources (lake, stream, groundwater) and their various degrees of connection between with the pools, provide clues to the understanding of this heterogeneity in physical and chemical conditions, at the scale of the region (entire set of pools) and of the sectors.

Annual water level fluctuations in Lake Neuchâtel (max 1m) are close to some observed in North American Great Lakes, which have also been subject to regulation (Cole and Weigmann, 1983; Lyon *et al*., 1986; Keough *et al*., 1999; Shay *et al*., 1999). They are nevertheless weak in comparison to other regulated lakes or reservoirs, where variations of up to 26 meters have been recorded (Smith *et al*., 1987; Murphy *et al*, 1990; Ali *et al*, 1995). Several authors even consider water level fluctuations lower than one metre as negligible (Chamber and McComb, 1994; Murphy *et al*., 1990). Weekly water level fluctuations, regarded as equally important by Smith *et al*. (1987), were also insignificant (7 cm), in comparison to variations these authors reported in Scottish lochs. Thus, the differences in water level fluctuations observed between the pools studied here, even if statistically significant, only represent a small range of values at the more stable extreme of the potential gradient in standing freshwater bodies. Despite the reduced range of fluctuations in Lake Neuchâtel, our results have shown co-variation between lake and pool water levels, that was higher in the pools of the CP sector,

that are connected to the lake (as outlined by Buttler *et al*. 1995), than in the pools of MA, CH1 or FO, lake-isolated by a sand dune. Co-variation between lake and pool water levels, in the absence of direct connection (as in the case of MA), has also been reported by Shay *et al*. (1999). In their study, marsh water levels were perfectly correlated to mean lake water levels in the presence of a connection, while the correlation still existed but to a lesser extend in its absence. The influence of the lake in this latter case might involve indirect groundwater connections.

The analysis of conductivity, used in the present study as a tracer of water origin and witness to the influence of the various water supplies, brought confirmation and precision to the lake-pool-groundwater relationships suggested above. Because of the direct connection between pool CP2 and the lake, and because of the inter-connection between pools CP2, CP3 and CP4, conductivity in these pools was expected to be closer to that of the lake (average = 301 µS/cm), than to groundwater conductivity, which varies between 400 and 3000 µS/cm, depending on the depth of the water table (Buttler, 1987). Decreasing lake influence from CP1 to CP4 was accompanied by increasing conductivity. In comparison, the absence of direct connection between, e.g., the MA pools and the lake, was suspected to result in higher groundwater influence, which was confirmed by higher conductivity values. In pools MA4, MA5 and MA6, high conductivity was also associated with significant nitrate concentrations. An association between values for these two parameters was observed by Bornette and Amoros (1991), Bornette and Large (1995) and Bornette *et al*. (1998a), in cut-off channels of the Ain and Rhône Rivers, and indicated, in their cases also, groundwater feeding and pollution of the groundwater through agricultural activities. The intermediate conductivity measured in the pools of Châbles-Perron (CH) may illustrate a combination of water origins, lake water on one side and runoff water from the surrounding cliffs on the other side, and corroborates Buttler *et al*. (1995), who mentioned an important role of the cliffs in the functioning of the Châbles pools, in periods of heavy rainfall.

The range of conductivity values measured in the pools of the "Grande-Cariçaie" is comparable to that measured by Friday (1987), in 16 pools scattered in a region of similar surface area. It is also comparable to values measured on a cut-off channel of the Rhône River, between the river-connected site (246 µS/cm) and the non-connected-site under groundwater influence (517 µS/cm) (Juget *et al*. 1979). Finally, it is more important than the range of values observed by Balvay (1984), in 75 pools of the Dombes region (France) or by Gacia *et al*. (1994), in 116 Pyrenean lakes.

The above-mentioned consideration of lake-pool water level co-variations and conductivity values suggests the existence of a gradient from more "allogenic" water bodies, that are directly influenced by the lake and therefore mainly driven by external forces, such as wave action or mineral sediment deposition, to more "autogenic" water bodies, where external influences are weaker and local processes (e.g. plant biomass production and decomposition) dominate.

In river floodplain studies, the position of the cut-off channels along the allogeny-autogeny gradient, i.e. along the connectivity gradient with the river, can be assessed by the sediment organic matter

content (Rostan *et al*. 1987; Cellot *et al*. 1994; Tockner and Bretschko, 1996; Tockner *et al*. 1999; Bornette *et al*. 2001), which increases as connectivity (allogeny) decreases. Variation observed here in sediment organic matter content in the pools in a fringing wetland seems to lead to similar conclusions as illustrated in the CP sector pools, where sediment organic matter content increased from the CP1-connected site to the CP4 "protected" site. The range of values along the CP1-CP4 gradient (0.7 to 43.3%) is comparable to those mentioned by Weisner *et al*. (1997) in two Swedish lakes (0 and 50 and 12.3 and 44 percent, respectively), by Mann and Wetzel (2000) in a small lotic wetland (2 to 38%) and by Rostan *et al*. (1987) in a set of cut-off channels (braided channels and former meanders) in the alluvial floodplain of the Rhône River (2 to 44%).

Pools positioned along this autogeny-allogeny gradient tend to be characterised by a suite of more or less inter-related water physico-chemical and sedimentological parameters that vary along the gradient. The CP sector pools studied here, provide an example of this allogenic-autogenic gradient. The more allogenic pools (CP1 and CP2) experienced both higher sedimentation rates and greater sedimentation rate fluctuations between seasons than the more autogenic pools (CP3 and CP4), where sedimentation rates were much lower and temporally stable. The seasonal difference in sedimentation rates (higher during the summer- than the winter sampling periods) might find an explanation in the lake water level, which was higher during the March-September- than during the September-March period. When the whole set of pools is considered, the degree of connection may also account for the differences in sedimentation rates. Pools CH1, CH2 and FO1, most distant from the lake, experienced the lowest sedimentation rates, when compared with CP1 and CP2, as presented above. At intermediate distance from the lake, or separated from it by a sand dune, MA6, FO2 or FO3, experienced intermediate sedimentation rates. Pools MA1 and MA2, connected to a small stream, illustrate potential undesirable effects of a direct connection. The high sedimentation rate in MA3, in the absence of any direct connection with either the lake or the stream, results probably from overflow from MA2 during the storm event. In the case of very shallow pools, such as FO3, re-suspension processes by wind or rain may certainly play an important role. The sedimentation rates measured in the studied pools are comparable to those of Nõges *et al*. (1999), in a shallow lake in Estonia (0.78 to 21 $kg/m^2/month$, mean value 5 $kg/m^2/month$), which also exhibited substantial spatial and seasonal differences. Both studies seem to indicate increasing sedimentation rates towards autumn.

The decreasing water level fluctuations and sedimentation rates, observed in pools CP1 to CP4, favour the colonisation of the more autogenic pools by larger and more competitive aquatic plant species, which in turn sustain organic matter production. In addition, decreasing wave action reduces turbulence and consequently dissolved oxygen concentrations in the water. The decrease in dissolved oxygen concentration from CP1 (concentrations always higher than 6 mg l^{-1}) to CP4 (concentration dropping under the limits of fish survival) may thus result from the combined effect of a decrease in water turbulence and the presence of vegetation. A similar pattern was observed in pools MA1 and MA2, while they were connected to the stream (concentrations always above 10 mg l^{-1}), compared to

the other non-connected pools of MA, which experienced important decreases in summer. This trend, however, ceased when the stream was diverted and stopped supplying MA1 and MA2. Values then dropped to generally below 5 mg l^{-1} in summer, in all pools. Pools FO3 and CH2, which are the most lake-influenced pools in their respective sectors, displayed higher dissolved oxygen concentrations than the other pools, usually above 10 mg l^{-1} and 6 mg l^{-1} respectively.

As reported elsewhere (Bapst, 1987; Chapman, 1992) the patterns of pH closely coincided with those of dissolved oxygen discussed above. As expected from chemical reactions, pH values were lower in autumn, because of intense decomposition activity producing large amounts of CO_2 and resulting in a shift of the equilibrium from a clear basic situation toward acidity. In summer, during intense photosynthetic activity and important CO_2 consumption, pH was expected to be higher. This was however not the observed situation, probably because measurements were carried out in the morning when maximum oxygen saturation was not reached.

The between-pool differences in water temperature seem more closely related to groundwater influences and to the presence of aquatic vegetation. Groundwater supply reduces seasonal temperature fluctuations, as in pools MA4 and MA6, that were cooler in summer and warmer in winter, and provide more stable habitats conditions year-round. The presence of vegetation buffers summer daily fluctuations that were striking in those pools deprived of aquatic vegetation (as CP2, MA1 and FO3), while they were nearly non-existent in entirely colonised pools (as CP4, MA2 and FO2). Rose and Crumpton (1996) similarly observed lower temperature, and lower amplitude temperature variations, within stands of vegetation vs. open water sites.

Nutrient load is also closely related to the degree of connectivity between pools and lake, as again illustrated in the CP sector pools. In agreement with Buttler (1987), who suggested using the nitrates as a tracer of lake water origin (mean $N\text{-}NO_3^-$ in the lake = 1.06 mg l^{-1}), CP1 and CP2 had higher nitrate concentrations than CP3 and CP4. However, the lake is not the unique source of nitrates, because elevated concentrations in MA5 and MA6 were the result of groundwater feeding, following contamination through agricultural soil leaching (see above). Moreover, as with temperature, there is a strong biological component. Seasonal fluctuations in nitrate concentrations related to biological activity provoked variations from 1 to 45 times the initial concentration, as was also reported by Auderset Joye (1993) or Úlehlová and Pribil (1978). They were also higher than those reported by Úlehlová and Pribil (1978) in Norwegian and Polish ponds, but corresponded better to situations observed in Czechoslovak fishponds considered as highly eutrophicated. The range of nitrate values encountered in the ponds (0.1 to 3.3 mgl^{-1}) also appeared as large in regard to Balvay's (1984) (0 to 0.61 mgl^{-1}), Friday's (1987) (0.1 to 2 mgl^{-1}) and Murphy *et al.*'s (1990) (0.2 to 1.4 mgl^{-1}) observations. In floodplain water bodies Barrat-Segretain (1996) encountered a much wider range of nitrate values (1.32 and 8.54.mgl^{-1}).

The high ammonia concentrations in pools MA1 and MA2 were probably consequent upon nitrogen inputs from the small stream (3.5-7.2 mg $NO_3\text{-}Nl^{-1}$), which induced an important development of

algae. In January and November 1997, low water level, ice cover and very low dissolved oxygen concentration led to anoxic conditions, during which the decomposition of the algal mats produced high ammonia levels. High ammonia concentrations combined to high pH values can shift the NH_4^+/NH_4OH equilibrium towards NH_4OH, which is very toxic to fish. Many young fish were indeed found dead during the periods of high ammonia concentrations. LaBaugh (1989) also reported important ammonia concentration as a result of decomposition under ice cover and Auderset Joye (1993) corroborated these results with the observation of peaks of ammonia in autumn, and to a lesser extent in March-April, following organic matter decomposition. In waters considered as unpolluted, ammonia concentrations average 0.2 mgl^{-1} but can reach 2-3 mgl^{-1} (Chapman, 1992). This corresponds to what has been observed in the present study, even in the most "polluted" MA1 and MA2 pools. However, in respect of the findings of Worrall *et al* (1997) and Balvay (1984) the values observed in pools MA1 and MA2 represent an important degree of pollution of the system. The other pools, on the contrary, offer unpolluted conditions from the ammonia point of view, as no values were above 0.45 mgl^{-1}.

Analysis of the water physico-chemistry and sedimentological data of a set of 15 pools in the "Grande-Cariçaie" lacustrine fringing wetland demonstrates the existence of a high diversity of habitat conditions, at the scale of a small landscape feature. This diversity of habitat conditions might provide an environmental explanation for the "individualistic" character of pools in their species richness and composition, corroborating Jeffries (1997) in his observation that "the diversity of pond life arises from the diversity of causes rather than truly random or chaotic processes".

It is very tempting to draw a parallel between the lake fringe wetland studied and river floodplain ecosystems, which are widely recognised diversity hotspots (Bornette *et al*., 1998a; Ward *et al*., 1999). In both cases, indeed, this diversity results from spatial heterogeneity (Tockner *et al*., 1998; Ward *et al*., 1999) generated by various types of physical connections between ecosystems (Bornette *et al*., 1998a). In both cases also, the structure and processes of the sub-systems (cut-off channels or pools) seem to be determined by the interaction of these subsystems with each other and with adjacent ecosystems (Schiemer, 1995; Ward and Stanford, 1995). Finally, in both cases, menace arises from the disruption in connectivity caused by water level regulation and thus reduction in flooding frequency and/or intensity. However, disruption in lacustrine wetlands may be "only" lateral (lake-pools) or vertical (pools-groundwater) and not longitudinal as in rivers. It may lead, through the absence of rejuvenation processes, to a shift, from a complex mosaic of the riparian landforms and associated aquatic and semi-aquatic communities, towards an increased geographical and temporal uniformity.

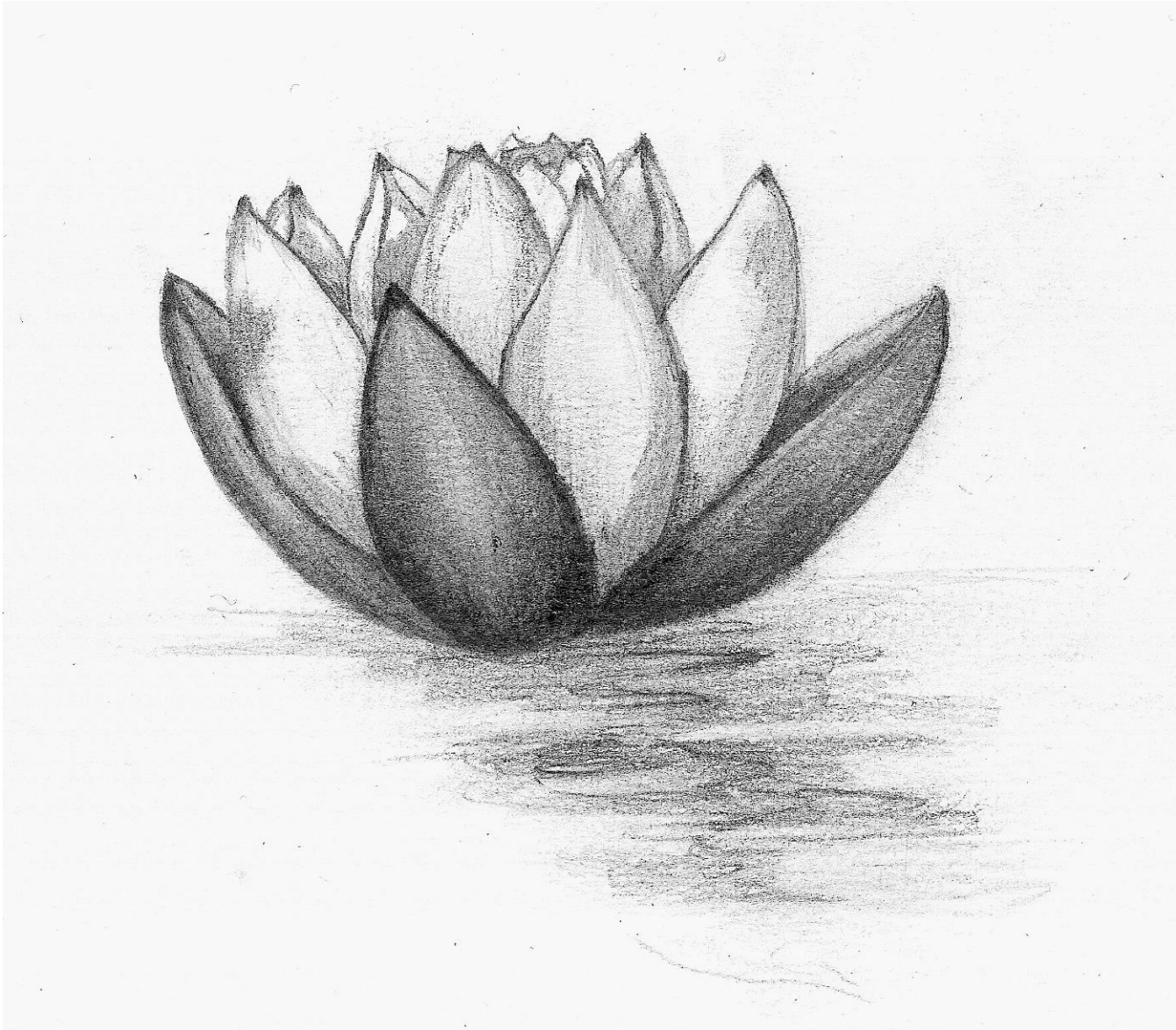
As a substitute for restoration of water level fluctuation, management measures include attempts to artificially maintain high diversity of habitat conditions, through creation of new water bodies in wetland such as the “Grande-Cariçaie”. Knowledge of the relationships between pools and adjacent water-sources (lake, streams, groundwater, other pools, surface run-off) and of their reciprocal

influences, could clearly be helpful in identifying sites appropriate for pool creation. A first step would be description of the physico-chemical heterogeneity of the target area, leading to compilation of an environmental database. Such a database would provide a good basis for predicting relationships between potential pool sites and their biotic components. This knowledge will further help decision taking about how far from the lake pools might most appropriately be established, what might be the optimal distance between one pool and the next, which type of water supply is preferable, depth, type of banks, etc, depending on the type of water body predicted to develop, in terms of fauna and/or flora, speed of terrestrialisation, etc.

Attention has been focussed in this study on the mean (median) characteristics of sectoral groups of pools and individual pools, as well as upon their variability. Inter-quartile or min-max ranges observed suggest the existence of within-pool heterogeneity, which might also be related to the type and degree of connectivity. Consideration of only average values may hide precious information on spatial and temporal variability. Study of the relationships between within-pool heterogeneity, type of connection and degree of connectivity, could be expected to provide further insights into the functioning of such fringing-wetland pools.

Chapitre 6

Aquatic macrophytes in a Western European lake-fringe wetland (Lake Neuchâtel, Switzerland)



6.1 Introduction

Most of the literature devoted to aquatic ecosystems is concerned with running waters or lakes. The work of Biggs *et al*. (1994), Boothby (1997, 1998), Boothby and Hull (1997), Friday (1987), Jeffries (1991, 1998), Oertli *et al*. (2002) and others shows that pools have not been forgotten, but they have been neglected, at least until recently, and most frequently studies have dealt with isolated pools, i.e. pools in agricultural or forested landscapes, marl-pits, drainage ponds, etc. Pools punctuating lacustrine wetlands seem to have received little attention, although they must now be regarded as severely threatened, as are rivers cut-off channels in riverine floodplains. Two factors contributing to this neglect can be identified. Firstly, because of the imprecise boundaries existing between reed-beds and open water zones, pools are often not identified as such, in this water-depth gradient continuum (Duever, 1990). Secondly, "general rules describing patterns of pond-life are surprisingly difficult to pin down" (Jeffries, 1997). This incapacity to delineate clear patterns for decision-makers may be interpreted by potential "pond creators" as implying that "ponds have no value". In the US, pond creation represents the most widely spread mitigation measure in “freshwater emergent marshes”, as a result of which the wetland landscapes tend to homogenise and lose biodiversity (Bedford, 1999).

The Grande-Cariçaie wetland fringes the southern shore of Lake Neuchâtel (Switzerland). As in the case of other rare remnants of its kind in Western Europe, it faces the threats and degradations associated with lake water level regulation. Rejuvenation processes (through lake flooding) are impeded and terrestrialisation on the land-ward side accelerates. On the lake-ward side, the “Grande-Cariçaie” faces severe problems of erosion, which contribute to pool loss: less than one percent of the pristine open water surfaces of 1888 remained in 1982 (Mulhauser, 1996). To counteract terrestrialisation and the lack of hydraulic dynamics in this wetland, effort has been invested in the re-creation of a network of pools.

Fifteen pools enclosed within the "Grande-Cariçaie" were selected for study of their water chemistry and sediment characteristics. The results demonstrate the existence of a diversity of environmental conditions at various spatial scales (within pools, between pools and between sectors), related to the diversity of water sources (chapter 5 in this thesis). Here data are presented on the aquatic vegetation of the same set of pools.

Aquatic vegetation (like terrestrial vegetation) is of overwhelming importance in the life-cycle of a variety of organisms. It offers habitat or refuge possibilities (Dawson *et al*. 1999), food or building resources, and contributes to biodiversity through its presence, as well as through the life it supports. It is also implicated in the functioning of ecosystems, through nutrient cycling (Reddy *et al*. 1989; Barko *et al*., 1991; Saunders and Kalff, 2001), organic matter production (Godshalk and Wetzel, 1978a,b), oxygen production (Rose and Crumpton, 1996) and its influence on sedimentation processes (Sand-Jensen, 1998; Benoy and Kalff, 1999).

Aquatic vegetation has been comprehensively studied in cut-off channels of the Ain and Rhône Rivers (France), where species richness and composition, as well as species traits, were analysed in relation to water and sediment physico-chemistry, along a connectivity-disturbance gradient (Balocco-Castella, 1988; Bornette and Amoros, 1991; Bornette *et al*., 1994b, 1996 and 1998a; Barrat-Segretain *et al*., 1999; Barrat-Segretain, 2001). The availability of data on the aquatic vegetation of riverine floodplain pools (see also Tockner *et al*., 1999), isolated pools (Oertli *et al*., 2002), and pools in lake fringing wetland (this study) makes it possible to investigate if the species richness of these various pool types comparable.

In the more restricted context of the 15 pools examined in this study, we were interested in 1) identifying vegetation groups through ordination and clustering methods, to infer one measure of spatial heterogeneity, 2) identifying relationships between aquatic vegetation and environmental conditions and 3) considering implications of these findings to conservation and management of these ecosystems. The present study is focussed on strictly aquatic macrophyte species, i.e. hydrophytes as defined by Casper and Krausch (1980) or Willby *et al* (2001) and on charophytes.

6.2 Materials and Methods

6.2.1 Study site

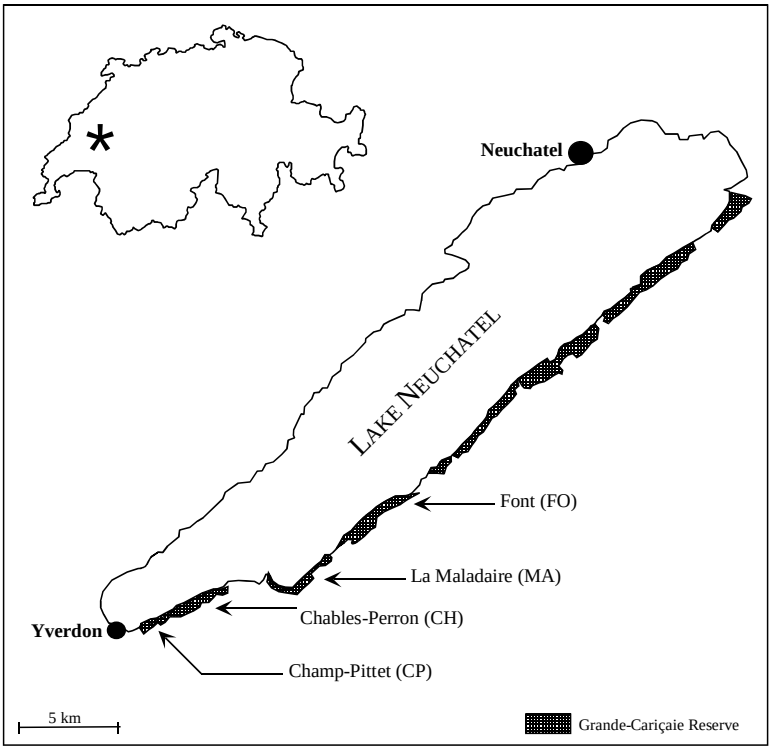


Figure 6.1 The "Grande-Cariçaie" fringing wetland on the southern shore of Lake Neuchâtel (Switzerland) and the location of the four pool sets.

The "Grande-Cariçaie" wetland (mean altitude: 429.3 m asl) fringes the whole southern shore of Lake Neuchâtel, Switzerland, and is recognised as being of international significance by the Ramsar Convention. The origin of this 40 km-long wetland dates from the first phase of modification of the hydrological system of the Swiss Jura catchment (1869-1888): 2000 ha of bare soils were exposed as a consequence of a 2.7m lowering of Lake Neuchâtel's water level. Nowadays, after one century of existence, the wetland comprises a complex mosaic of vegetation types, which are dependent upon the water-level: inundated and non-inundated reed-beds mixed with sand dunes, pools, small and tall sedge beds and alluvial forests. The fifteen pools selected here for the environmental and vegetation studies are grouped into four pool sets (or “sectors”): Champ-Pittet (CP1 to CP4), la Maladaire (MA1 to MA6), Châbles-Perron (CH1, CH2) and Font (FO1 to FO3), which are all, except those of CP and MA3, man-made. The geographic location of the pools along the southern shore of Lake Neuchâtel is shown in Figure 6.1. Some of these pools are connected to one another, while others are not: a connection exists from CP1 through to CP4, between CH1 and CH2, FO2 and FO3. Moreover, direct (through a channel) or indirect (through the reed beds) connections exist between some of these pools (CP1, CP2, CH2, and FO3) and the lake, at normal lake water levels. Other pools (MA) are isolated

from the lake by a sand dune and connection with the lake happens only during high lake water levels. Table 6.1 summarises for the 15 pools the age, surface area, depth and some water chemistry parameters.

Table 6.1 Data on the age (number of years in 1998), surface area (sa), avergae depth (avdepth), temperature (expressed by min and max values), average dissolved oxygen (avO_2), average nitrate concentration, average sediment organic matter content (avom) and average proportion of sediment particles under 63 µm. The number of samples used for calculations is given on the right of the concerned parameters (n). Based on sampling programms between March 1996 and June 1998.

	age	**sa**	**avdepth**		**$temp_{min}$**	**$temp_{max}$**	**avO_2**	**avcond**		**$avnno_3$**		**avom**	**av63**	
	(year)[in 1998]	(m^2)	(cm)	**n**	(°C)	(°C)	(mg l^{-1})	(uS/cm^{-1})	**n**	(mg l^{-1})	**n**	(%)	(%)	**n**
CP1	>110	3000	72	**25**	4	24.5	12.1	333	**14**	1.06	**5**	2.6	23.4	**10**
CP2	110	1000	54	**28**	1.1	24.5	11	412	**14**	1.01	**5**	13.2	49.9	**10**
CP3	110	9600	64	**38**	0.2	23.7	9.3	442	**14**	0.588	**5**	18.5	38.1	**21**
CP4	110	1800	48	**33**	0.2	20.3	5.5	497	**14**	0.688	**5**	34.6	42.1	**15**
CH1	6	1625	77	**27**	2.6	23	8.6	464	**10**	0.21	**5**	11.2	54.9	**10**
CH2	110	1000	55	**26**	3	21.9	7.4	468	**10**	0.216	**5**	16.7	36.6	**10**
MA1	6	260	38	**29**	2.1	24.5	12.7	539	**14**	0.052	**5**	11.1	90.5	**15**
MA2	13	480	42	**29**	2.2	19.3	9.8	532	**14**	0.048	**5**	10.6	86.2	**15**
MA3	110	360	13	**29**	3.8	21.5	9.3	556	**14**	0.096	**5**	18.5	57.5	**10**
MA4	12	690	45	**29**	2.9	19	9.6	571	**14**	1.62	**5**	9.3	56.7	**9**
MA5	12	320	40	**28**	2.7	20.6	7.6	597	**14**	1.68	**5**	10.2	52.7	**10**
MA6	12	310	42	**28**	2.6	20	7.6	613	**14**	1.52	**5**	16.5	56.6	**9**
FO1	10	648	29	**24**	2.1	23	9.7	462	**8**	0.083	**5**	6.7	70.5	**10**
FO2	10	2138	82	**24**	1.8	22	8.6	441	**8**	0.11	**5**	9.0	35.5	**5**
FO3	5	5021	39	**24**	0.2	26.9	10.9	512	**8**	0.343	**5**	9.9	42.4	**5**

6.2.2 Sampling regime

6.2.2.1 Water physico-chemistry

Conductivity, dissolved oxygen and temperature were measured in the field using WTW probes (WTW Cond LF 320 and WTW Oxi 320; WTW GmbH, Weilheim, Germany). Pools CP and MA were monitored from March 1996 to January 1998 (14 samples), whereas pools CH and FO were monitored from January 1997 to June 1998 (10 samples). Nitrates were measured on five occasions (quartely), between January 1997 and January 1998. Pools FO1, FO2 and FO3 were not covered during January 1997. Nitrate concentrations were determined using the cadmium reduction method. Field measurements and samples were taken in the open water and not in the helophyte belt of the pools.

6.2.2.2 Sediment characteristics

Bottom sediment samples were taken, in all pools during the winter of 1997, for grain size analysis (Coulter LS-100) and organic matter content (loss on ignition). For some pools, complementary data were taken during the winters of 1996 and 1998. Five sediment cores (diameter 5 cm) were taken in each pool, except the largest (CP3) were 8 cores were taken. The top 5 cm of each core was analysed (Rostan *et al*., 1987). Concerning grain size, only the percentage of particles under 63 µm was considered for further analyses.

6.2.2.3 Vegetation

Plant species composition and cover were recorded using a modified Braun-Blanquet coverage index 1: < 5%; 2:] 5-25%]; 3:]25-50%]; 4:]50-75%]; 5: > 75%. All pools were sampled during the summer of 1997, while some of them were visited during the summers of 1996 and/or 1998 as well. Depending on pool surface area, plots of 50 x 50 cm were distributed every 5 to 10 m along transects perpendicular to the longest axis of the pools, and separated from each other by 10 - 20 m. The present study is focussed on strictly aquatic macrophyte species (i.e. hydrophytes), as defined by Casper and Krausch (1980) and Preston (1995) and on charophytes. The nomenclature followed Lauber and Wagner (2001), except for charophytes (Corillion, 1975). Species recorded outside the plots, as well as hybrids, were excluded from analysis, except in comparison of observed with estimated species richness (see below).

6.2.3 Data analysis

6.2.3.1 Species richness

Species richness is the simplest way to describe diversity (Magguran, 1988). In the present study, species richness was measured at four spatial scales: the plots, the pools, the sectoral groups of pools and the region (i.e. all pools combined). In order to standardise species richness measurements at the scale of the pool and to account for the difference in plot numbers per pool (Burnham and Overton, 1979), the first- (Jack1) and second-order (Jack2) Jackknife estimators were calculated using the EstimateS software (Colwell, 2001).

Jack1 = $S_{obs} + Q_1 (m-1/m)$

Jack2 = $S_{obs} + [(Q_1(2m-3)/m)-(Q_2(m-2)^2/m(m-1))]$

where S_{obs} = total number of species observed in all samples pooled, Q_1 = number of species that occur in one sample, Q_2 = number of species that occur in two samples and m = total number of samples.

The species richness per plot was taken as our α-level diversity. Literature offers several formulae, to calculate β diversity as a ratio between the cumulated richness of a set of sampling units, and their individual richness (α level) (Whittaker, 1977; Harrison *et al*., 1992; Tockner *et al*., 1999). β diversity representing the accumulation of α diversity leading to the total pool species richness, we chose to express β diversity simply as the cumulated richness of all plots within one pool. The simple biplot ordinating all pools along their α and β diversity scores was chosen as a graphic way to express the relationship between these two levels of species diversity. At the higher spatial scale, the accumulation of β diversity of the 15 pools led to the species richness at the scale of the region (γ diversity). This simple and transparent procedure allows an objective comparison of the α and β components of the γ diversity.

6.2.3.2 Ordination and Clustering

After removal of 1) the empty plots and 2) the species present in only one or in only two plots, the plot x species floristic matrix was ordinated through a Correspondence Analysis (CA) (Legendre and Legendre, 1998).

A cluster analysis by Ward's method (Ward, 1963), which grouped sampling plots according to the similarity of their hydrophyte assemblages, was carried out using the factorial scores of the sites in the CA, as a summary of the vegetation data. Following Roux (1991), the contribution ($CV_{(j,p)}$) of each species (j) to each cluster (p) was calculated as:

$$(CV_{(j,p)}) = (Z_{pj} - Z_j)^2 / \ \Sigma_j (Z_{pj} - Z_j)^2$$

with Z_{pj} = average of species j in cluster p

Z_j = overall average of species j

A Simpson diversity index (S.I.) was calculated per pool, to quantify the pool's spatial heterogeneity in terms of the proportion of plots belonging to each vegetation group. The area represented by empty plots was considered as a category in the calculation of the Simpson Index. S.I. = $1-\Sigma pi^2$ with pi: proportion of plots belonging to cluster (i) in the pool.

The ADE-4 programme library (Thioulouse *et al*., 1997) was employed for multivariate data analyses and production of associated graphs. Clustering was performed with the S-Plus software (Anonymous, 1999).

6.2.3.3 Vegetation-environment relationships

Vegetation-environment relationships were described by means of two complementary approaches using 1) simple linear regressions (univariate approach) and 2) co-inertia analysis (multivariate approach). Regressions were performed between richness indices and state variables on the pool x year

data set. The richness indices comprised mean richness per plot (= quadrat) (mQR), maximum richness per plot (maxQR), pool richness (PR) and number of vegetation groups per pool (Gr6).

Co-inertia analysis (Dolédec and Chessel, 1994) looked for common trends between the mean abundance of species per pool and the mean values of state variables per pool. The vegetation matrix was computed through a COA and the variable data set through a correlation matrix PCA prior to co-inertia analysis. The co-inertia analysis was tested for significance with a Monte-Carlo permutation test.

The environmental variables were the average value of sediment organic matter content (avom), proportion of sediment particles under 63µm (av63), conductivity (avcond), dissolved oxygen (avO_2), pH (avpH), nitrate concentration (avnno3) and temperature (avtemp). Pool species richness (ln) was also regressed against pool surface area (ln).

Regressions were computed with the S-Plus software (Anonymous, 1999), while the co-inertia was performed using ADE-4 (Thioulouse *et al*., 1997).

6.3 Results

The sampling of the 15 pools over three successive summer periods provided data from 997 plots and yielded a total richness of 29 hydrophyte species. The species list, mean abundance per plot and Jackknife estimations are presented in Annex 3.

6.3.1 Species richness

Pool species richness ranged between 0 and 10, and reached 11 in pool CH2, when all dates were considered. Sectoral species richness ranged from 5 in pool group MA to 16 in pool group CP, with CH and FO having intermediate values (13). Important between-date differences in pool species richness were also observed, as, e.g., in pools FO1 and CH2.

The observed pool species richness was significantly and positively related to the Jack1 ($R^2 = 0.95$, $p = 0$) and Jack2 ($R^2 = 0.87$, $p = 4x10^{-15}$) estimators, indicating no major bias associated with differences in sampling efforts. The addition to the observed pool species richness of the outsider species (i.e. recorded outside the plots) led also to a near correspondence of the observed with the Jackknife estimates. As a consequence, only observed pool species richness is employed here in further calculations.

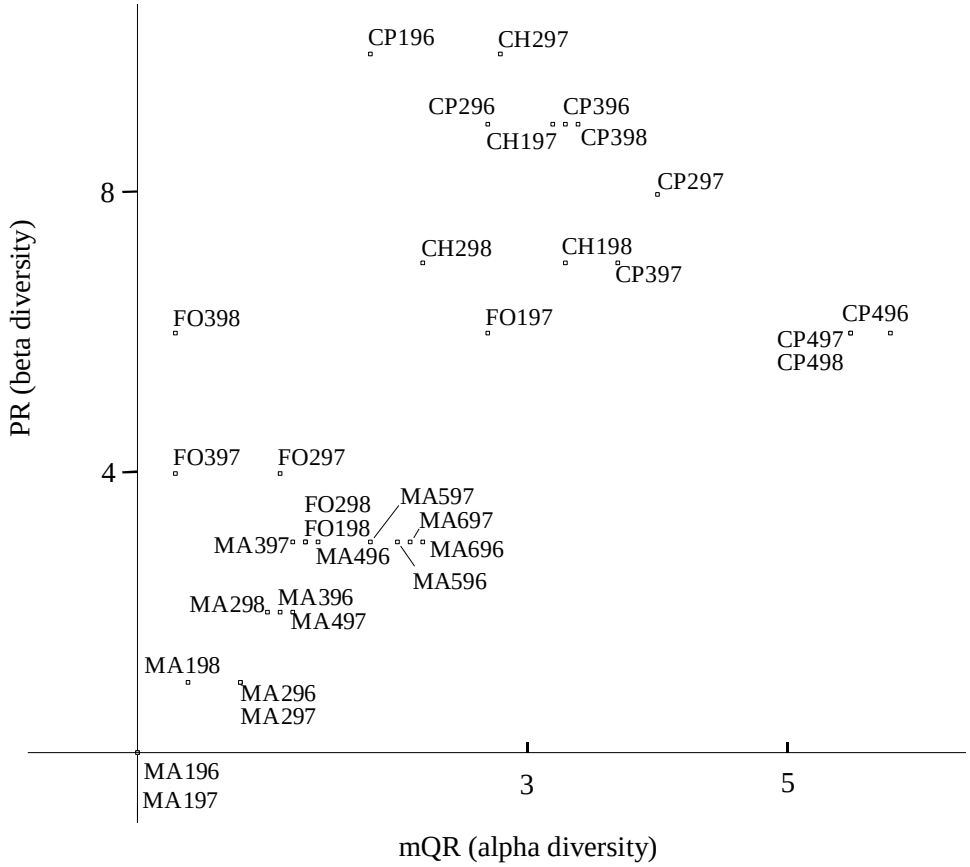


Figure 6.2. Relationship between the α diversity, expressed as the mean plot richness (mQR) and the β diversity, expressed as the pool species richness (PR).

Figure 6.2 illustrates the relationship between the α (mean richness per plot) and the β (pool species richness) diversities of the pools, at the scales of the region (entire set of pools), as well as within and among sectors. Pools could be divided into three groups. The MA sector was characterised by low values of both mean species richness per plot (below 2) and pool species richness (below 4). The FO sector group was characterised by low to median mean species richness per plot (below 3) and median values of pool species richness (between 4 and 6). Finally, the CP and CH pools displayed medium to high mean species richness per plot (between 2 and 6) and high pool species richness (above 6). Plot species richness (x-axis on Figure 6.2) was significantly different between all pairs of sectoral groups (Wilcoxon test, $p < 0.01$). Pool species richness (y-axis on Figure 6.2) was significantly different between all pairs of sectoral groups (Wilcoxon tests, $p \leq 0.01$), except between CP and CH.

6.3.2 Macrophyte communities

The MA sector pools were dominated by three species with different growth forms: *Nymphea alba* L. (anchored with floating leaves) (mean plot coverage above 2.5), *Potamogeton plantagineus* Roem & Schult. (anchored with submerged leaves) (mean plot coverage usually above 1) and, to a lesser extent,

Utricularia gr. *vulgaris* (free-floating) (Annex 3). Pool MA1 was "colonised" by only one macrophyte species during the study period, *Lemna minor* L..Pool MA2 remained entirely covered by *N. alba* alone. Two of the three pools comprising the FO sector were intensively colonised and dominated by one to two species: *Myriophyllum spicatum* L. in pool FO2 (mean plot abundance higher than 3) and *Chara hispida* L. and *Potamogeton gramineus* L. in pool FO1 (mean plot abundance generally higher than 1). The newly created FO3 pool was only poorly colonised, i.e. none of the seven species sampled over 1997 and 1998 had mean abundance higher than 0.1 (Annex 3). In the CP sector pools a transition operated from pool CP1, where a high number of low abundance species of submerged growth form coexisted (e.g. *Chara contraria* Braun ex Kützing, *Elodea canadensis* Michx, *Potamogeton* gr. *pusillus*, *Potamogeton pectinatus* L.) to pool CP4, colonised by a lower number of high abundance, all floating-leaved species (e.g. *L. minor*, *Riccia fluitans* and *N. alba*.) (Annex 3). Finally, the Châbles pools exhibited the highest number of *Potamogeton* (*P. gramineus*, *Potamogeton. natans* L., *P.*gr. *pusillus*. and *P. plantagineus*), *Chara* (*C. hispida* and *C. globularis* Thuillier) and *Utricularia* (U. gr. *vulgaris*, *U. intermedia* Hayne, *U. ochroleuca* R.W.Hartm. and *U. minor* L.) species and dominance by one or few species was less obvious (Annex 3). Two species only were common to all sectors, *N. alba* and *U.* gr. *vulgaris*, while 63% of the species present in the CP pools were restricted to this sector, vs. 38% in CH, 24% in FO and 0% in MA.

Table 6.2 Groups of hydrophytes identified on the basis of the factorial scores of the sites in the CA. "f": frequency of the species in the groups of plots; "c"contribution of the species to the identification of the group. Only the species having positive contributions are shown.

		CERDE	CHACO	CHAHI	HYDVU	LEMOR	LEMTA	LEMTR	MYSPI	MYRVE	NUPLU	NYMAL	POTGR	POTPU	POTNA	POTPL	RICFL	UTRVU	UTRIN	UTRMI	ZANPA
Gr1	f			0.13	0.57							0.04	0.7						0.65	0.39	
Gr1	c				2								6						32	1	
Gr2	f			0.03		0				0.09		0.98	0.11	0.01	0.12	0.21		0.16	0.01	0.01	
Gr2	c											47				2					
Gr3	f		0.8						0.05					0.8							
Gr3	c		19											9							
Gr4	f			0.88	0.02					0.32		0.27	0.53	0.08	0.37			0.02	0.08	0.08	
Gr4	c			57						2			2		3						
Gr5	f					0.01			1			0.14						0.03			
Gr5	c								60												
Gr6	f	0.02				0.65	0.85	0.75	0	0.01	0.08	0.53		0.03	0.01		0.65	0.55			0.01
Gr6	c					12	34	21									17	9			

6.3.3 Vegetation clustering and spatial heterogeneity

Six groups of plots were derived from the classification procedure. They were very distinct, in that none of the species (except *P. gramineus*) contributed to the identification of more than one group. Groups 1 to 5 were strongly characterised by one species of very high relative contribution value (e.g. *U.* gr. *intermedia* in Gr.1, *N. alba* in Gr.2 or *C. hispida* in Gr.4) (Table 6.2), while group 6 was characterised by several species (Table 6.2).

Some groups were dominated by submerged (Gr5) or, on the contrary, free-floating species (Gr6), while in others (Gr1, Gr2, Gr4) several growth forms co-existed, offering a higher architectural heterogeneity.

Table 6.3 Frequency of the six vegetation groups in each pool expressed as the proportion of plots belonging to each group. EQ: “empty plots”. S.I.: Simpson diversity index calculated from these proportions.

	CP196	CP296	CP297	CP396	CP397	CP398	CP496	CP497	CP498	CH197	CH198	CH297	CH298	MA198	MA296	MA297	MA298	MA396	MA397	MA496	MA497	MA596	MA597	MA696	MA697	FO197	FO198	FO297	FO298	FO397	FO398
Gr1												4														60	26				
Gr2										56	23	88	91		78	81	88	100	94	100	100	90	100	95	85						3
Gr3	64	6																													
Gr4										44	77		6													36	52				
Gr5																												97	94	9	18
Gr6	21	76	92	100	74	95	100	100	100			8		40			8					10		5	15			3	3	16	24
EQ	15	18	8	0	26	5	0	0	0	0	0	0	3	60	22	19	4	0	6	0	0	0	0	0	0	4	22	0	3	75	55
S.I.	0.52	0.38	0.15	0	0.38	0.1	0	0	0	0.49	0.36	0.22	0.17	0.48	0.34	0.3	0.21	0	0.11	0	0	0.18	0	0.1	0.26	0.51	0.61	0.05	0.12	0.41	0.6

The number of vegetation groups per pool ranged between 2 and 5, vegetation-free zones being here considered as a "group" (Table 6.3). The CH and FO sectoral groups of pools displayed a significantly higher number of vegetation groups than did CP and MA (Wilcoxon test, $p < 0.05$). Differences were largely non-significant between CH and FO, and CP and MA. The proportion of plots occupied by a given vegetation group differed between pools (e.g. Gr.6 in CP4, vs. MA5 or FO3) as well as between sectors (e.g. Gr6 occupied 11 pools in all sectors, while Gr3, was present in 2 pools -and one sector- only). The proportion of empty plots varied between 0 and around 20%, but could reach more than 50% (see MA198, FO397 and FO398). The Simpson index, calculated on the proportion of plots occupied by the different vegetation groups, ranged from 0 (very homogeneous) to 0.6 (more heterogeneous) within the entire set of pools, but significant differences were evidenced only between MA and FO (Wilcoxon test, $p = 0.05$). Within sector differences were obvious, as illustrated by CP1 (S.I. = 0.52) and CP4 (S.I. = 0) or FO1 (S.I. = 0.51 and 0.61) and FO2 (S.I. = 0.05 and 0.12).

6.3.4 Vegetation-environment relationships

6.3.4.1 Linear regressions

Species richness indices were correlated to several parameters of both sediment (avom and av63) and water chemistry (avcond and avO_2), while the number of vegetation groups per pool (Gr6), pH (avpH) and temperature (avtemp) displayed no significant relationship. Mean and maximum plot richness (Figure 6.3a and 6.3b) were significantly and positively correlated to sediment organic matter ($r^2 = 0.5$, $p = 7.7 \times 10^{-6}$; $r^2 = 0.19$, $p = 0.016$). After the removal of CP496, CP497 and CP498, characterised by the highest levels of sediment organic matter content recorded, both relationships became non-significant ($r^2 = 0.09$, $p = 0.1$; $r^2 = 0.07$, $p = 0.2$). We did, however, consider these points as representative of one end of the organic matter gradient rather than as artefacts. The negative correlation between mean plot richness and avO_2 ($r^2 = 0.3$, $p = 0.002$) (Figure 6.3c) also became non-significant after the removal of CP496 and CP497 ($r^2 = 0.12$, $p = 0.08$). Mean plot richness was significantly and negatively correlated to the quantity of fine particles, av63 ($r^2 = 0.29$, $p = 0.002$, Figure 6.3d), while maximum plot richness was significantly and negatively correlated to av63 ($r^2 = 0.49$, $p = 0.00001$, Figure 6.3e) and cond ($r^2 = 0.2$, $p = 0.01$, Figure 6.3f). In both cases involving av63, pool CP4 displayed the highest values of plot richnesses and lowest values of av63, contrasting with pools MA1 and MA2, characterised by particularly high percentage of fine sediment.

At the scale of the pool, pool species richness was negatively correlated with both av63 ($r^2 = 0.52$, $p = 5.5 \times 10^{-6}$, Figure 6.3g) and cond ($r^2 = 0.4$, $p = 0.0002$, Figure 6.3h). A strong positive relationships ($r^2 = 0.48$, $p = 7.3 \times 10^{-6}$) was highlighted between pool species richness and pool surface area.

6.3.4.2.Co-inertia analysis

The co-inertia analysis revealed a highly significant ($p = 0.014$) co-structure between the state variable PCA and the species abundance COA (Figure 6.4). The species (Figure 6.4a) and variable (Figures 6.4b) factorial planes showed a continuous distribution of the species along water conductivity- (F1) and sediment organic matter content (F2) gradients. On the right side of the plane, high conductivity pools (MA) were characterised by *N. alba* and *Potamogeton plantagineus*. They contrasted maximally with CP1 (lowest conductivity), colonised by *C. contraria*, *E. canadensis* and *P. pectinatus*. Along axis F2 the transition operated from pool CP4 (34% of sediment organic matter content), characterised by *Lemna* and *Riccia* species (but *N. alba* was also very well repesented), to pool FO1 (under 7% of organic matter content), inhabitated by *Hydrocotyle vulgaris* L., *U. intermedia*, as well as *C. hispida*, *U. minor* and *P. gramineus*. In Figure 6.4c, the length of the arrow described the agreement between the pool's position as given by the state variables (circles) and by the species distribution (arrow tips). In MA1 and MA2, extreme values of fine sediment (63av) caused the divergence of their ordination in terms of environmental variables.

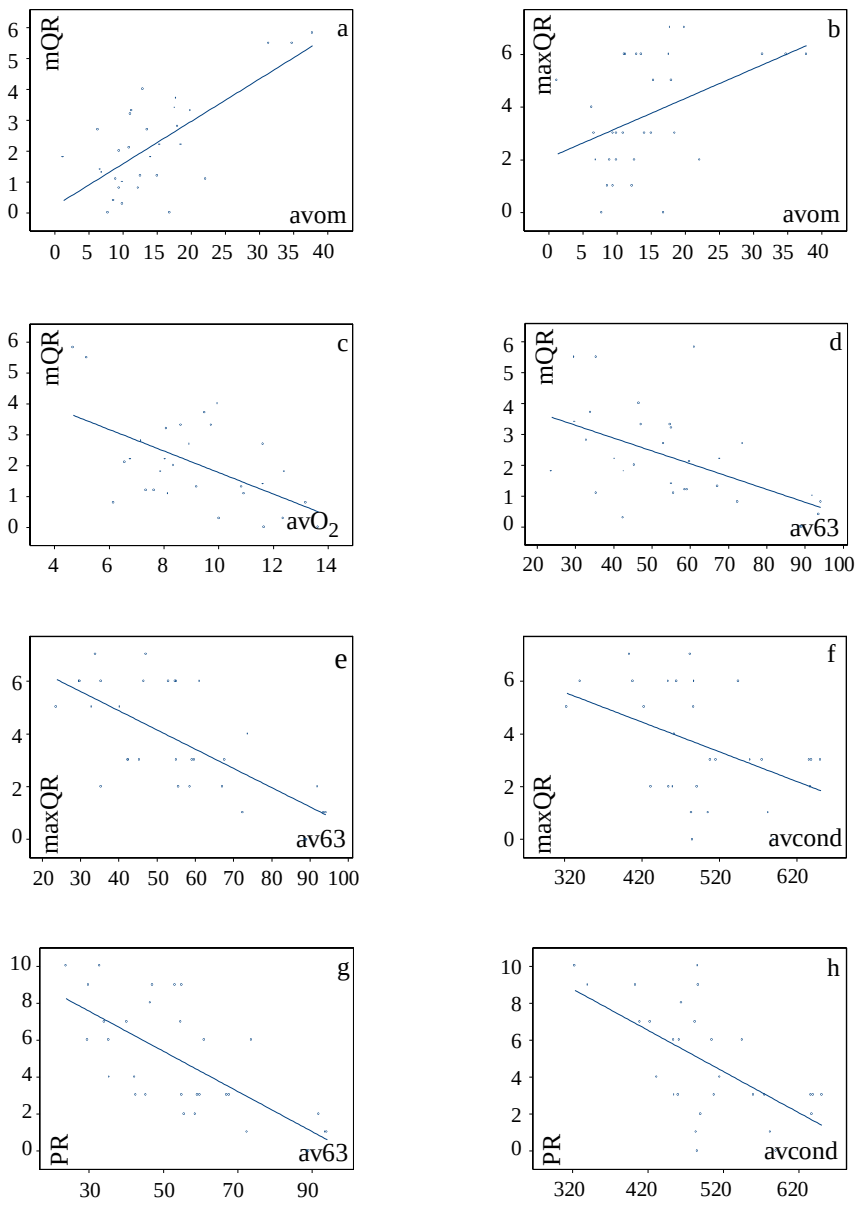


Figure 6.3 Species richness indices (mQR: mean plot richness; maxQR: maximum plot richness; PR: pool richness) in relation to physico-chemistry parameters of water (avO_2: average dissolved oxygen in water [mg O_2 l^{-1}]; avcond: average conductivity [µS cm^{-1}]) and sediments (av63: average proportion of sediment particles under 63mµ [%]; avom: average sediment organic matter content [%]).

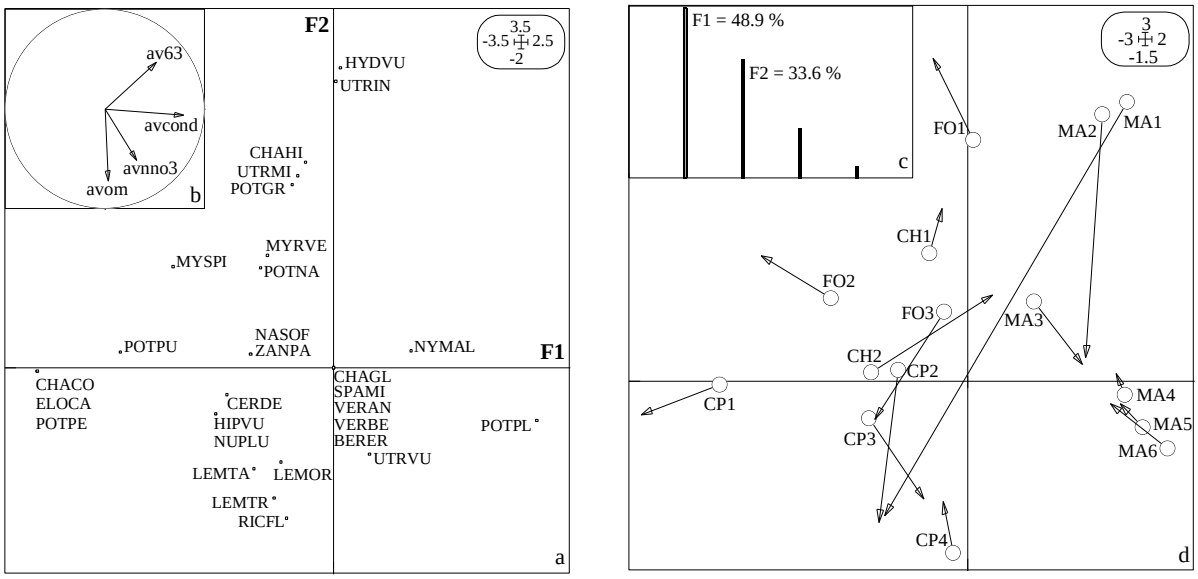


Figure 6.4 Graphical interpretation of the co-inertia analysis between the Correspondance Analysis (COA) on the hydrophyte species and the Principal Component Analysis (PCA) on the state variables. a. F1 x F2 factorial map of the hydrophyte species, b. correlation circle of the state variables, c: histogram of eigenvalues, d: F1 x F2 factorial map of the pools as described by their state variables (circles) and species composition (arrows).

6.4 Discussion

6.4.1 Species richness at the scale of the region, the sectors and the pools: comparison with other aquatic ecosystems

The 29 macrophyte species recorded in the 15 pools over the three-year study period represent as much as 56% of the "Grande-Cariçaie" species pool, as estimated from Lauber and Wagner (2001). At this scale (region), the macrophyte species richness of the "Grande-Cariçaie" (GC) is close to the macrophyte species richness recorded by Balocco-Castella (1988) (RH_o and AI_o), Bornette *et al*. (1998a) (RH_n) and ourselves (AI_n), in the Rhône (RH) and the Ain (AI) River floodplains, in a relatively similar number of cut-off channels and over a comparable area (Figure 6.5). Comparisons with studies conducted on "isolated pools", i.e. pools in a non-alluvial, agricultural or forested context, were more difficult because of different study conditions. Friday (1987) however, recorded only 12 macrophyte species in a region of similar size, encompassing 16 pools. Oertli *et al*. (2000) recorded 39 species in 18 pools scattered over the Swiss Plateau (SP), but the much wider geographical area makes the comparison more difficult (Figure 6.5). At the scale of the pools, mean species richness of the "Grande-Cariçaie" was closer to that of the Swiss plateau pools (SP) and the Rhône sites (RH_n and RH_o), characterised by mean species richness per pool under 10, than to the Ain sites (AI_n and AI_o), characterised by mean species richness per pool above 12 (Figure 6.5). When the sectors of the

"Grande-Cariçaie" were considered separately, mean species richness per pool in pool sectoral groups CP and CH was closer to values characterising the Ain sites.

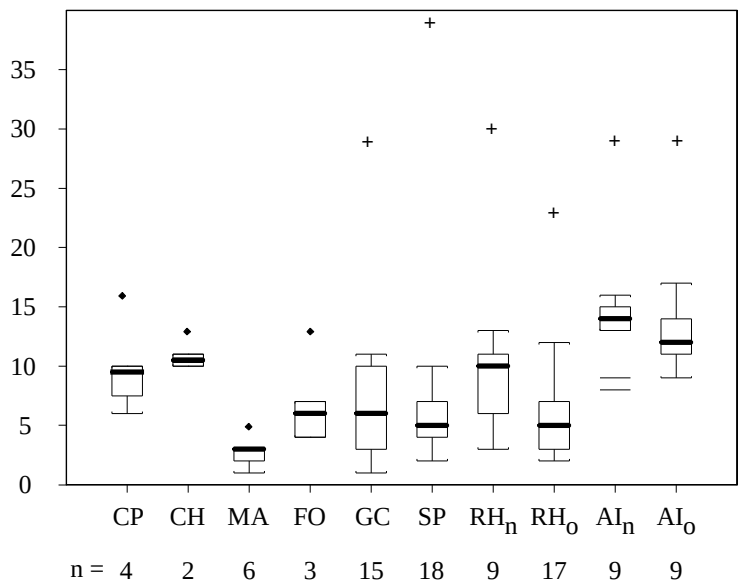


Figure 6.5 Mean hydrophyte species richness per pool in a) the four sectors of the "Grande-Cariçaie" considered independently (CP: Champ-Pittet, CH: Châbles-Perron, MA: la Maladaire, FO: Font), b) the "Grande-Cariçaie" region (GC), c) the Swiss Plateau (SP), d) the Rhône River region (RH_n and RH_o) and e) the Ain River region (AI_n and AI_o). RH_o and AI_o from Balocco-Castella (1988); RH_n from Bornette *et al*. (1998a); AI_n from chapter 8 of this thesis ♦ hydrophyte species richness at the scale of the sector; + hydrophyte species richness at the scale of the region.

The comparable species richness observed at regional scale (entire set of pools) in the "Grande-Cariçaie" and the floodplains of the Ain and Rhône Rivers, suggests similarities in the functioning of the two aquatic ecosystems. In riverine floodplains, high faunistic and floristic species richness is often explained by the high spatial and temporal heterogeneity characterising these ecosystems at the scale of the region (Ward *et al*. 1999; Amoros and Bornette, 2002). This high diversity of habitats results from fluvial dynamics acting at hierarchical spatial scales, "fluvial sectors", water bodies and "mesohabitats" (Amoros, 2001), in concert with different water supplies, degrees of connectivity to the river and successional rates. In a study conducted in the "Grande-Cariçaie", on the same set of 15 pools, we also demonstrates a high diversity of abiotic conditions, in terms of water physico-chemistry and sediment characteristics at the scales of region, sector and pool (chapter 5 in this thesis). This high diversity of habitat conditions, as in the riverine floodplain ecosystems, results from natural processes such as the action of waves, the various water supplies, different degrees of connectivity to the lake and successional rates, but also from human actions. Indeed, most Grande-Cariçaie pools studied were

dug at different dates and this process mimicates – to some extent – the abandoment of cut-off channels by the river.

In addition to average species richness, regions and sectors are also characterised by varying heterogeneity in pool species richness. The "Grande-Cariçaie" and RH region displayed the widest range in pool species richness values, as measured by the inter-quartile range (Figure 6.5). The Ain sites (AI_n and AI_o) can thus be envisaged as exhibiting species rich water-bodies (high mean species richness per pool) of homogeneous specific composition (between water bodies). Other sites (GC) would, in contrast, be characterised by species poor water-bodies (lower mean species richness per pool) with more contrasted floras, resulting in a higher regional species richness.

Attention has already been drawn to the different degrees of heterogeneity in β diversity exhibited by the Rhône and Ain River floodplains in respect of macroinvertebrate assemblages (Castella *et al*., 1991), interpreted as being due to the influence of geomorphological and historical factors on floodplain communities. In the Rhône floodplain, successive meandering and braiding phases evidently left highly diversified fluvial landforms, which became permanent following embankement of the Rhône River. Greater groundwater feeding of the channels on one side of the floodplain then added further to the differences between channel faunas. The geomorphological history of the Ain River, on the contrary, is more homogeneous and channels, despite river incision, may still experience the homogenising effects of floods (Bornette *et al*., 2001). In several respects, the situation in the "Grande-Cariçaie" resembles that of the Rhône River floodplain. Pools of different ages and origins (man-made pools in Font or "la Maladaire" and natural pools in Champ-Pittet) co-exist, to a variable extent receiving water from different origins (lake, groundwater, river) and have become quasi-permanent features due to the decreased frequency of flooding caused by regulation of lake water-levels.

One scale below, i.e. within the CP sector, pools CP1 and CP2 are characterised by higher pool species richness than pool CP4. The influence of the lake upon the former pools can be perceived as resulting in the creation of a variety of patches, as shown e.g. by the heterogeneity in sedimentation rates (chapter 5 in this thesis), and increases the number of available niches for colonisation. In pool CP4, on the contrary, the absence of wave action promotes autogenic processes resulting in very fluid, highly organic sediments, unfavourable for recruitment (Barrat-Segretain, 1996). Bornette *et al*. (2001) showed that cut-off channels of the Rhône River, devoid of mud and with a gravel floor, have the highest species richness. This high species richness is thus the probable indirect result of flood scouring, which permits regular rejuvenation of sites and prevents competitive exclusion. In pools CP1 and CP2, mean species richness and species coverage per plot were low, but the species complement differed betwen plots (high β diversity), whereas in pool CP4, mean species richness and coverage per plot were high, but species complements were similar (low β diversity). In calcareous grassland stands, Pärtel *et al*. (2001) observed that α and β diversities were negatively correlated. They

explained these results by the fact that when species richness (α) is high, the community is close to having almost all species from the community species pool in all plots, so variability in species composition is then low.

Interestingly, species richness of aquatic gastropoda measured in the same ponds and at the same dates (GC, SP, RH_n, RH_o, AI_n, AI_o) provided a quite different picture of these systems, when compared with the aquatic macrophytes (Antoine, 2002). The mean species richness per water-body was maximal in the pools of the "Grande-Cariçaie" and very close to the values of the Ai_o and Rh_o (Antoine, 2002). The pools of the Swiss Plateau had the lowest richness.

6.4.2 Species status and representation of the regional species pool

Among the 29 species recorded in the 15 pools studied, 52% are threatened (e.g *Hippuris vulgaris*, *Hydrocotyle vulgaris*, *P. gramineus*, *U. minor*) or very threatened (e.g. *P. plantagineus*, *Sparganium minimum* Wallr., *U. intermedia*) at the scale of the Western Swiss plateau (Landolt, 1991). Further, 30% of the species are threatened at the Swiss scale (e.g. *U. ochroleuca*, *Zannichellia palustris* L.) (Landolt, 1991). None of these species, however, appear to be at the limit of their range in the Neuchâtel Region. But Casper and Krausch (1980, 1981) and Lauber and Wagner (2001) mentioned that *U. intermedia*, *U. ochroleuca* and *Z. palustris* have a very scattered distribution within their range. They also note the uneven distribution of *Hippuris vulgaris* L. and *Hydrocotyle vulgaris*, ranging from very common in some places to less frequent, or absent, in others. The rarity of *Lemna minuta* Humb. & al. is explained by its very recent introduction to Switzerland (less than 50 years ago). Although the range of this species in Switzerland continues to expand, its presence in the "Grande-Cariçaie" was not yet recorded. None of these species were categorised by Landolt (1991) as threatened at the European scale, but Mériaux (1982) did indicate that several of them were in regression in, or even absent from, north-western France (among others, *H. vulgaris*, *P. plantagineus*, *U. intermedia*). Casper and Krausch (1980) mentioned the strong decline in Germany of *P. gramineus*, *P. plantagineus*, and *S. minimum*. Eutrophication, drying, filling and pollution were the primary reasons given for these species regressions.

6.4.3 Temporal changes

Comparison of our results with those of Oihénart *et al*. (1988) demonstrates a species replacement in the sector of Champ-Pittet and a decline in species richness in Châbles-Perron (19 species were recorded between 1984 and 1986 vs. 13 between 1997 and 1998).These differences may be inherent to the sampling methods or to the areas covered, in the case of Champ-Pittet. They could also be caused by problems of identification, given the presence of numerous hybrids of *Potamogeton* species and difficult groups like the *Utricularia* species group. The species loss in the CH sectoral pools may also

partly result from dredging works,conducted in this area in 1992 for the creation of pool CH1. In Champ-Pittet, mesotraphent species (*P. gramineus* and *Myriophyllum verticillatum* L.) have been replaced by eutraphent ones (except for *C. contraria*), which could indicate a tendency toward eutrophication. But the absence of water chemistry analyses for the 1984-1986 period provides neither support nor contradiction of such hypotheses. Changes could also be interpreted as expression of pool unpredictability. As suggested by Jeffries (1997), it may be pointless to search for consistent relationships between species change and any deterministic process such as water quality modification, because "unpredictability seems to occur at the medium scale, such as variation in the distribution of taxa between ponds in a region or over several years" (Jeffries, 1997). The studies of Oihénart *et al*. (1988) and ourselves demonstrate the occurrence of between-year variations in species richness and abundance and the coming and going of species, which correspond to the "vagaries of the redistribution of species" that have been called "chance" (Jeffries, 1997). Despite these vegetation changes, the total number of species in pool groups CP and CH remained high throughout the 1984 - 1998 period (26 species out of the 29 sampled in the 15 pools), and both sectors preserved their fundamental differences in species composition (16 and 13 species respectively, but only three species in common).

6.4.4 Species-environment relationships

The literature available on relationships between vegetation (richness and composition) and environment is abundant and contradictory, and shows that results may depend largely upon the geographic scale at which studies are conducted. Thus Friday (1987) evidenced no significant relationships between macrophyte species richness and composition, and water chemistry and morphometric factors. For Heegaard *et al*. (2001) species composition and conductivity were associated, while in Jeffries (1991) biogeographical location, pH and area influenced plant communities. The wide geographical range, large number of pools/lakes and wide pH range involved in the latter studies may favour the identification of vegetation-environment relationships. Even over extended gradients, Jeffries (1998) found only weak relationships between plant assemblages and northing, easting, altitude and extent of drying.

In the present study, pool species richness has been found to be significantly and positively correlated to pool surface area. This result agrees with the findings of other studies that evidence, in the absence of dominant driving forces like floods (see Tockner *et al*. 1999), positive correlation between species richness and surface area (Møller and Rørdam, 1985; Gee *et al*. 1997; Jeffries, 1998; Oertli *et al*. 2002), although Friday (1987) and Linton and Goulder (2000) provide contrary-examples. In addition to surface area, species richness in the 15 pools studied here appeared to be correlated with water conductivity and percentage of fine mineral particles in sediment. As is often the case, factors involved in these relationships integrate more complex processes. The relationship between conductivity and species richness reflects in fact the type of water supply. At one extreme, pools CP1 and CP2 are

connected to the lake and experience low water conductivity and a higher disturbance regime. At the other extreme, the MA pools are groundwater fed, experience no wave action and exhibit higher conductivity values. Along the conductivity gradient of the co-inertia analysis (axis 1), *C. contraria*, *E. canadensis* and *P. pectinatus* are associated with the lowest conductivity sites (pool CP1), while *P. plantagineus* is associated with the highest conductivity sites (pools MA4, MA5 and MA6). *E. canadensis* was regarded by Barrat-Segretain *et al*. (1998) and Bornette *et al*. (2001) as a flood-tolerant species (adapted to periodical disturbances) and *Chara* species as occurring on newly deposited, frequently reworked substrate (Corillion 1975). These conditions indeed prevail in pool CP1. *P. plantagineus* is known to indicate a supply of hard groundwater (Bornette and Amoros, 1991, Buchwald *et al*. 1995) and is described as oligo- to mesotraphent, preferring fine sediments (Bornette and Amoros, 1991; Buchwald *et al*. 1995; Bornette *et al*., 2001) and winter warm waters (Buchwald *et al*. 1995). The water chemistry conditions in pools MA4, MA5 and MA6 corroborate these observations. The nitrate concentrations in these pools, although the highest observed among the 15 pools studied, is still well below the lowest measured in the Ain River, where *P.plantagineus* was found to be among the most abundant of the species observed (Bornette *et al*., 2001). The water in pools MA4, MA5 and MA6 had, moreover, high calcium concentrations and the sediment grain size was fine. Indirect relationships between environmental factors and vegetation (as seen above with conductivity) have been reported frequently, as in Jeffries (1998) or Heegaard *et al*. (2001).

The relationship, between species richness and the percentage of fine sediments, expresses in turn the consequences of an accidentally-induced (important) sediment input, which has prevented any colonisation in pool MA1 and allowed the survival of only *N. alba* L. in MA2, explaining the low species richness where high percentages of fine sediments occur. At the other extreme, pool CP1 was found to have a higher proportion of coarser sediment particles, as a result of wave action. In this site, as in pool CH2 (connected to the lake through a channel), succession to organic sediment colonised by competitive species (like *N. alba* in the MA pools) is retarded by the influence of the lake.

6.4.5 Species richness: potential and limits

Limits to the use of species richness analysis in, for example, evaluating the state of an ecosystem and in monitoring change occurring within it, have been discussed by various authors. Usseglio-Polatera *et al*. (2000) refer to the impossibility of extending the use of aquatic invertebrate species richness to all river types, because of naturally occurring regional variation in communities. They also point out the loss of the ecological information inherent to the use of this approach and the risk it entails, of inducing erroneous judgement and thus bad decisions or inappropriate recommendations. This debilitating feature of species richness use can be addressed by incorporation of ecological information into the analysis procedure, in the form of species traits, i.e. morphological, physiological and ecological characteristics of the species. Knowledge of trait-environment relationships should permit explanation of the local distribution of species (Usseglio-Polatera *et al*. 2000). Furthermore,

incorporation of trait information provides insights into functionnal diversity and redundancy, the consideration of which is crucial in the conservation of biological diversity (Walker *et al*., 1999; Keddy, 2000).

One example can be found in Pärtel *et al*. (2001), who combined species richness with traits analysis to explain differences in species richness within and among (calcareous grassland) vegetation stands. They identified the existence of a positive correlation between α diversity (mean number of species per plot) and the number of core species (species present in more than 75% of the plots) found in a stand, and found a positive correlation between β diversity (within stands) and the number of satellite species (species present in up to 25% of the plots) present. The pools CP4 and CP1 of the present study might exemplify analagous correlations for water-bodies in a lake-fringing wetland. Indeed, the six species observed in pool CP4 were all core species (sensu Pärtel *et al*. 2001): in this pool α diversity (plot species richness) was high and β diversity (pool species richness) low (Figure 6.2). In pool CP1, most species were present in less than 25% of the plots (satellite species): in this pool α diversity (plot species richness) was low and β diversity (pool species richness) high.

6.4.6 Conclusion

Species richness is easily measured (in comparison with other components of site characterisation) and allows the integration of several taxonomic groups into the procedure. As in the case of macrophyte species richness considered here, or as demonstrated by Tockner *et al*. (1999) in the Danube River floodplain and Antoine (2002) for molluscs in lake-fringe pools, analysis of the spatial and temporal heterogeneity of several taxonomic groups can provide radically different views. From the perspective of conservation and management actions, reference to several taxonomic groups might therefore be advisable. Of course, the "contradictory" conclusions potentially contributed by each group may lead to unsatisfactory compromises or decisions favouring maintenance of certain situations at the expense of others. But it can lead (see Ward *et al*. 1999) to a more holistic consideration of biodiversity, integrating consideration of species and genetic diversity with functional and habitat diversity, in effort to restore the functional integrity of a system.

In the present vegetation study, analysis of the species richness of a sub-set of 15 of the pools present within the "Grande-Cariçaie" wetland has shown that they have high conservation value, at both regional and national levels, despite exhibiting relatively low species richness at the level of the individual pool. They support more than half of the higher-plant species known from the "Grande-Cariçaie" reserve, among them 15 nationally or regionally threatened species. From the conservation point of view, Austin (1999) has pointed out that poorer sites (in species number) can shelter different, and even more valuable species than their richer homologues. He thus recommended not neglecting apparently poorer zones. Crosbie and Chow-Fraser (1999) also concluded that there is need to

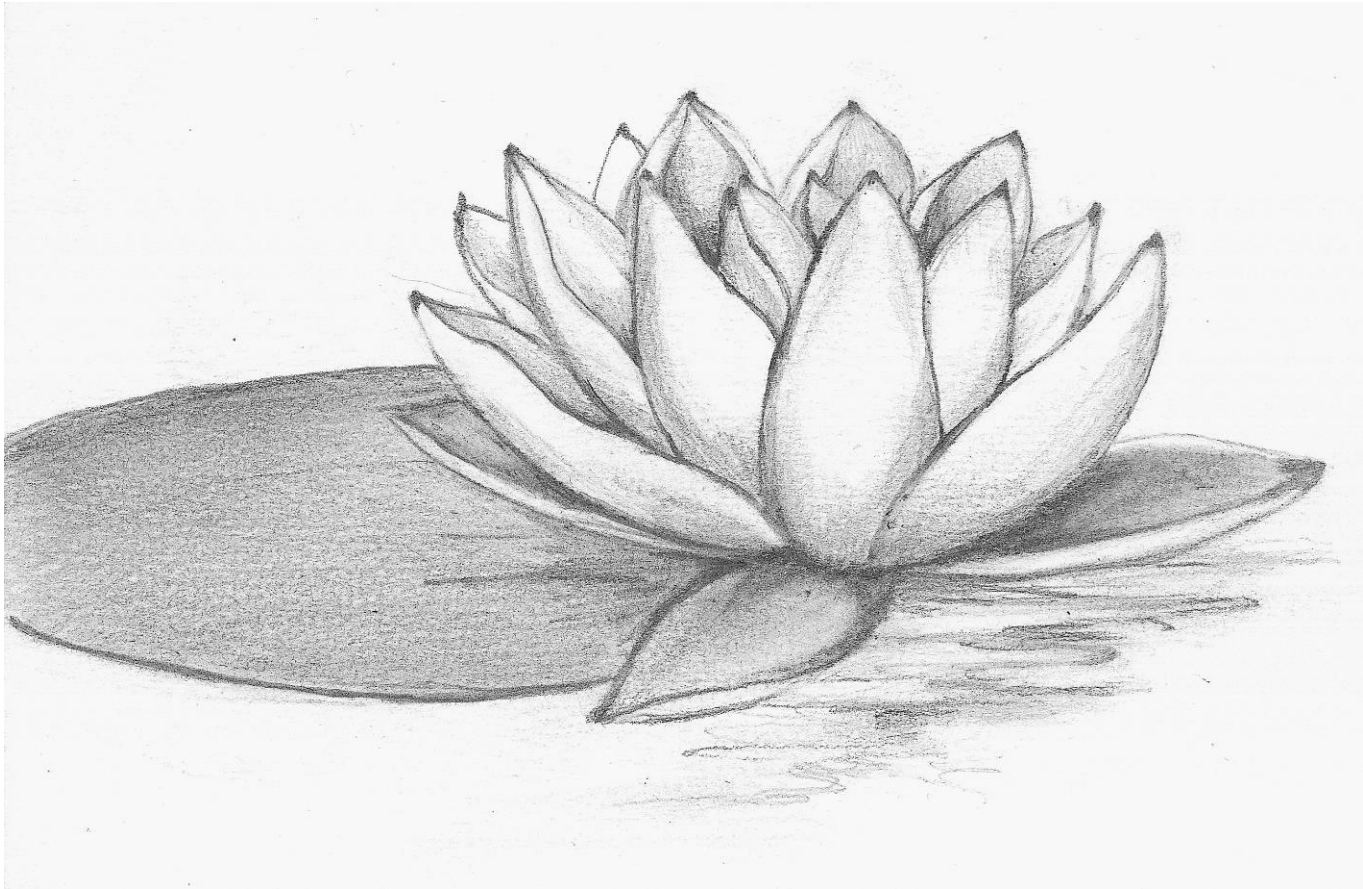
consider both the species richness and the species composition of wetland ecosystems when evaluating the possible impact of land use changes.

Although the species richness/pool surface area relationship was positive in the present study, we also note that two small pools CH1 and CH2 (separated) can support more species than the largest one (CP3). This corroborates the observations of Helliwell (1983), Gee *et al*. (1997) and Oertli *et al*. (2002), who found a greater biodiversity in several small pools than in a single large pool of similar total area. Fisher and Lindenmayer (2002) similarly highlight the high conservation value of small remnants of native eucalypt forest patches in two case studies on birds. These authors recommend examination of the value of small patches, to avoid their removal just because they are small. Fenton (1997) also highlighted the financial advantage of restoration programmes using smaller patches. This criterion would certainly apply to pool-creation work in the "Grande-Cariçaie" reserve, where the costs of dredging are extremely high.

Finally, the diversity of water physico-chemistry and sediment characteristics, manifest from the "mesohabitat" scale to the regional scale, in the pools studied here (chapter 5 in this thesis), has to be regarded as of primary importance in maintaining the high aquatic macrophyte diversity observed (Bornette *et al*., 1998b; Amoros, 2001). The diversity of water supplies feeding the "Grande-Cariçaie" reserve (lake-, river-, surface run off and groundwater) offers the possibility of creating small pools in diverse environmental conditions. The “microhabitat” scale (Antoine, 2002) deserves attention as well, during the process of pool creation. Within-pool heterogeneity, in depth and sediment characteristics, may offer conditions for several species of various growth forms, which can, in turn, help to maximise spatial complexity of pools, as shown in this study. Chesson and Huntly (1989) also proposed that “environmental variability, including spatial heterogeneity, often facilitates the coexistence of species representing different life histories and successional status”. Grace and Wetzel (1981), finally, suggested that habitat partitioning (shallow and deeper zones) facilitates the coexistence of both submerged (in deeper zones) and floating-leaved (in shallower zones) macrophytes. Creation of additional pools can be expected to enhance the species richness at the scale of the reserve, reinforce the populations of threatened aquatic macrophyte species present there, as well as bringing the surface-area of open waters within the wetland closer to that found prior to the losses that occurred during the last century. The dredging of pools could also contribute to the re-creation of a pool network and an increase in connectivity, even possibly with the lake. However, in considering such issues it is necessary to bear in mind that the pools in a lake-fringe wetland represent only one type of mosaic element within that wetland, which comprises also marshes, fen, swamps, etc, and the long-term “survival” of all of these elements depends upon continuing fluctuation in lake water levels. In the absence or limitation of such fluctuations – as it is the case in the Grande-Cariçaie, where they do not exceed 1m and are limited to a 50-meter wide band – maintenance of habitat diversity (including pools) is achieved only at the expense of human mitigation actions.

Chapitre 7

Hydrophyte traits-environment linkages in lake-fringe wetland pools (Lake Neuchâtel, Switzerland)



7.1 Introduction

Efforts have been made recently to synthesise the literature about plant life strategies with that relating to plant trait-environment linkages, and to provide clarification and increased comparability of the terms and methods employed in these closely related fields of study (Lavorel *et al*., 1997; Weiher and Keddy, 1999; Weiher *et al*., 1999; McIntyre *et al*., 1999a,b). Two observations can be made from these works: i) plant response to disturbance is the most commonly studied context within which plant strategies or traits are brought into play (e.g. McIntyre *et al*., 1999a,b; Kleyer, 1999; Lavorel *et al*., 1999), ii) terrestrial plant communities form the core of these studies, aquatic communities being seldom considered (but see Kautsky, 1988; Murphy *et al*, 1990; Bornette *et al*., 1994a; Willby *et al*., 2000). In aquatic ecosystems, the need to predict species composition and traits (i.e. morphological, phenological and physiological characteristics) of plant communities, reflecting specific responses to the character and condition of the environment, is of crucial importance, given the general acute threat to freshwater resources, and the concern for the restoration of aquatic and wetland habitats.

Southwood (1977, 1988) considered that "the habitat provides the template on which evolution forges characteristic life history strategies". Later, Keddy (1992) represented the environment as a set of sieves or filters, acting on a given regional species pool by removing those species lacking the combinations of traits (or strategies) necessary to establish, develop and reproduce under given environmental conditions. These filters act at decreasing hierarchical scales, from the region to the microhabitat. They comprise forces like climate, elevation, geological substrate, hydrological regime, fertility, and, at more local scales, biotic interactions.

In the context of terrestrial vegetation, Grime (1974, 1977, 1979) grouped these abiotic and biotic forces into two broad categories: *stresses* the factors that limit productivity (like shortage of nutrients, water and/or light) and *disturbances*, responsible for partial or total biomass destruction, such as scouring floods, herbivores, pathogens or human activities. In response to these environmental pressures, plants develop stress- or disturbance tolerant strategies. In the absence of both constraints, competitive species establish.

In aquatic ecosystems, wave action (Kautsky, 1988), water current (Haslam, 1978; Henry *et al*., 1994), weed control procedures (Sabbatini and Murphy, 1996) and navigation (Sabbatini and Murphy, 1996; Willby *et al*., 2001) may act as disturbances while shortage of light and/or nutrients and sub optimal temperatures may act as stresses (Grime, 1979; Kautsky, 1988). Water level fluctuations can be view either as a disturbance or as a stress, depending on its effects on vegetation (Kautsky, 1988; Sabbatini and Murphy, 1996).

Studies of aquatic plant communities concerned with the relation between species traits and environmental conditions have either encompassed a wide array of ecosystems (e.g. pools, rivers, lakes, canals) considered over a large geographical area (Willby *et al*., 2000) or focused upon disturbance-driven ecosystems (Kautsky, 1988; Murphy *et al*., 1990; Bornette *et al*., 1994a; Henry *et*

al., 1996). Few studies have focused on more homogeneous aquatic habitats (but see Sabbatini and Murphy, 1996 or Willby *et al*., 2001).

The first objective of the present study was to ascertain the strength of the relationships between aquatic plant traits and water and sediment characteristics, in fourteen alluvial pools scattered in the largest fringing wetland of Switzerland, the “Grande-Cariçaie”. In comparison with cut-off channels in riverine floodplains, which are frequently submitted to the scouring and rejuvenating effects of floods, the pools in the “Grande-Cariçaie” experience no major disturbances. Under these conditions the dynamics of the plant communities in these shallow pools can be determined primarily by two environmental factors: seasonal fluctuations and nutrient status. The "Grande-Cariçaie" wetland thus offers the possibility to set up a habitat template integrating i) a gradient of seasonal fluctuations (or “seasonality”) through consideration of temperature and water level fluctuations and ii) a "nutrient status" gradient defined by sediment organic matter content and total phosphorus and nitrates concentrations in the water. This template can then be used to test predictions about trait-environment relationships in more homogeneous environmental conditions than those usually considered.

Following from the work of Grime (1979) and of others, aquatic macrophytes inhabiting the “fertile corner” of the template and experiencing low seasonal variation can be expected to display "competitive" traits, usually encompassing tall stature, large, floating or emergent, short-lived leaves, yearly flowering but low reproductive output, low regeneration and colonisation capacity and extensive lateral spread (Grime, 1979; Barko *et al*., 1991; Duarte and Roff, 1991; Barrat-Segretain *et al*., 1999; Willby *et al*., 2000; Barrat-Segretain, 2001). At the opposite corner, where seasonal variations are stronger and fertility is lower, aquatic macrophytes are predicted to exhibit "stress-tolerant" traits such as shorter stature, smaller and longer-lived leaves, less frequent flowering but larger reproductive output and higher regeneration and colonisation capacities (Grime, 1979; Barrat *et al*., 1999; Willby *et al*., 2000).

As seen from the literature (Kautsky, 1988; Bornette *et al*., 1994a; Sabbatini and Murphy, 1996; Díaz and Cabido, 1997; Willby *et al*., 2000), digitisation of species traits, as well as the statistical analyses of such trait-by-species arrays, can be carried out in different ways. Thus, a second objective of the present study was to determine the influence of two different numerical expressions of species traits on the strength and the significance of species trait-environment relationships.

7.2 Materials and Methods

7.2.1 Study site

The study site, the "Grande-Cariçaie", is the largest fringing wetland in Switzerland (mean altitude: 429.3 m), on the margin of Lake Neuchâtel, and is recognised as being of international significance by the Ramsar Convention. The origin of this 40 km-long wetland dates from the first phase of modification of the hydrological system of the Swiss Jura catchment (1869-1888): 2000 ha of lake bottom deposits were exposed on the southern shore of the lake, as a consequence of a 2.7 m lowering of the water level in Lake Neuchâtel. Nowadays, and despite severe problems of erosion on the lake-ward side and terrestrialisation on the land-ward side, the wetland comprises a complex mosaic of vegetation types dependent upon water-level: inundated and non-inundated reed-beds mix with sand dunes, pools, small and tall sedge beds and alluvial forest. The origins of the waters feeding the wetland are varied. Since water-level fluctuations in the lake became regulated in the 1970's, the direct influence of the lake has become limited to a 50-meter wide band, which can be further reduced in width by the presence of sand dunes. Water-level fluctuations do not now exceed 1m. Levels are maximal in spring (May-June), decrease during summer and are minimal in winter. Where distance from the lake increases or sand dunes disconnect the wetland from the lake, the relative importance of groundwater influence increases. In addition to lake surface water and groundwater, water from two other origins may contribute to the water reaching pools within the wetland. In those sectors of the lake margin where the wetland is restricted to a narrow strip between the lake and cliffs, water input can occur through surface water runoff from the cliffs. Finally, streams reaching the lake from its hinterland (most often agricultural) constitute a fourth substantial water input in some sectors. The climate of the region is temperate. Meteorological data obtained for 1996, 1997 and 1998 indicate a mean temperature of 0.03 °C in January and 17.8 °C in July, accompanied by mean precipitations of 295 mm in January and 1078 mm in July.

Fourteen pools at four different locations (sectors) were selected for the purpose of this study: Champ-Pittet (CP1 to CP4), la Maladaire (pools MA2 to MA6), Châbles-Perron (pools CH1, CH2) and Font (pools FO1 to FO3). Except for CP and MA3, these pools are all man-made. Their surface area ranges between 260 m^2 and 9600 m^2. Some of these pools are connected to one another, while others are not: a connection exists from CP1 through to CP4, as between CH1 and CH2 and FO2 and FO3. Moreover, the pools exhibit different degrees of connection to the lake (at mean lake water level): CP1, CP2 and CH2 are directly connected to it, through a channel. The connection of CP3 and CP4 to the lake operates through their connection to CP2 and CP1. The other pools are separated from the lake by a more or less developed sand dune, which is flooded only during high lake water levels. Pool MA2 was considerably affected by the input of a small stream at the beginning of this study, but its influence

subsequently decreased and became irregular. The two most distant pools (CP1 and FO3) are 12 km apart.

7.2.2 Water and sediment physico-chemistry

The "Grande-Cariçaie" sites were sampled quarterly (5 dates) between January 1997 and January 1998, except for pools FO1, FO2 and FO3, that were not covered during January 1997. On each occasion, conductivity, pH, dissolved oxygen and temperature were measured in the field using WTW probes (WTW Cond LF 320, WTW pH 320 and WTW Oxi 320, respectively, WTW GmbH, Weilheim, Germany). Other parameters recorded on-site were water transparency (with a Snellen tube) and water level. Laboratory analyses were performed a few hours after water sampling. They included ammonia, nitrate and nitrite concentrations, determined using the salicylate, cadmium reduction and diazotization methods, respectively. Total phosphorus concentrations were determined by per-sulphate acid digestion. The sum of the three nitrogen forms was used for further calculations.

Sediment organic matter content was assessed on the uppermost five centimetres of sediment cores, from weight loss on ignition (Rostan *et al*., 1987). Five bottom sediment samples were taken in all pools during the winter of 1997, except in the largest (CP3), where eight cores were taken, and their average value used for further analyses.

7.2.3 Environmental frame

Two groups of environmental parameters were selected to represent 1) the seasonal variability in each site and 2) site nutrient status. The first group of variables comprised water temperature and depth. Temperature was chosen because of its strong seasonal pattern in temperate zones, which can, in turn, be influenced by the type of water supply (Bornette *et al*., 1998a). It is known to influence plant growth (Haag and Gorham, 1977, in Rooney and Kalff, 2000) as well as biomass production, time of flowering and seed production (Haag, 1983, in Rooney and Kalff, 2000). Water level fluctuations have received much attention in freshwater habitats, through their capacity to influence habitat structure (Rørslett, 1984; Murphy *et al*., 1990; Ali *et al*., 1995, Weiher and Keddy, 1995; Weiher *et al*. 1996; Blanch and Walker, 1998). For both parameters, the min-max range was identified as the preferred measure of variability for purposes of the present study (Table 7.1).

The two variables of nutrient content of water (total nitrogen and total phosphorus), and organic matter content of sediments, were used as surrogates for the assessment of site nutrient status. Sediment organic matter content not only integrates organic matter production and decomposition, but also disturbance forces that might export organic matter (Wilson and Keddy, 1985; Wilson and Keddy, 1986; Rostan *et al*., 1987). It has a critical influence on the seed germination of submersed plants (Barrat-Segretain, 1996), on growth of both seedling and adult plant (Anderson and Kalff, 1988; Spencer, 1990; Duarte and Roff, 1991; Stockey and Hunt, 1992; Spencer and Ksander, 1995) and thus also on distribution and abundance (Ali *et al*., 1995). Total nitrogen, total phosphorus and organic

matter were used as state variables and thus expressed as mean values (Table 7.1). The three variables were log-transformed to achieve normality prior to calculations.

Table 7.1 Variables constituting the "environmental frame". Depth (mmdepth) and temperature (mmtemp) - expressed as the difference between the maximum and the minimum value recorded between January 1997 and January 1998 - represent the "seasonal variability" of the pools. Total nitrogen and total phosphorus concentrations in the water, expressed as the average of the values recorded between January 1997 and January 1998 represent the nutrient status of the pools. Sediment organic matter content is expressed as the average of all replicates sampled during the winter 1997.

	mmdep	**mmter**	**av_tot**	**av_tot**	**av_or**
	[cm]	[°C]	[mg l⁻	[mg l⁻	[%]
CP1	38	22.4	1.15	0.05	1.7
CP2	43	21.1	1.21	0.08	12.9
CP3	33	21.6	0.66	0.07	17.8
CP4	24	18.2	0.83	0.04	34.8
CH1	31	20.4	0.24	0.02	11.1
CH2	31	18.8	0.25	0.02	18
MA2	23	17	0.55	0.08	9.4
MA3	15	15	0.18	0.03	15
MA4	7	16	1.67	0.02	12.6
MA5	14	16.6	1.73	0.02	9.4
MA6	21	14.8	1.55	0.02	14
FO1	7	23.2	0.1	0.02	6.4
FO2	12	20.2	0.13	0.03	9
FO3	12	26.7	0.4	0.05	9.9

7.2.4 Vegetation sampling

Plant species composition and cover were recorded during the summer of 1997 using a modified Braun-Blanquet coverage index: 1: < 5%; 2:] 5-25%]; 3:]25-50%]; 4:]50-75%]; 5: > 75%. Depending on pool surface area, plots of 50 x 50 cm were distributed every 5 to 10 m along transects perpendicular to the longest axis of the pool, and separated from each other by 10 - 20 m. This method ensured a satisfactory and standardised coverage of the pools. The present study is focussed on strictly aquatic macrophyte species (i.e. hydrophytes), as defined by Casper and Krausch (1980) and Preston (1995) and on charophytes. The nomenclature employed follows Lauber and Wagner (2001), except for charophytes for which Corillion (1975) has been used.

7.2.5 Selection of species traits

Nine plant traits corresponding to morphological, phenological and reproductive characteristics were chosen, to represent dispersion and colonisation (*vegetative perennation ; lateral spread*), growth and morphology (*growth form; height; leaf form and leaf area*) and sexual reproduction (*flowering, flowering duration* and *seed size*). They were selected in the light of previous studies and according to the availability of data on them in the literature.

Information was principally gathered from Corillion (1975), Heß *et al*. (1972, 1976, 1977), Grime *et al*. (1988), Aeschimann and Burdet (1989), Frank & Klotz (1990), Casper & Krausch (1980, 1981), Preston (1995), Krause (1997), Lauber & Wagner (2001), Willby *et al*. (2000), augmented by personal experience of the authors, and coded according to the fuzzy coding approach proposed by Bournaud *et al*. (1992) and Chevenet *et al*. (1994).

A distinction was made between coding of the trait "height", for which data were continuous values, and the other traits, which had distinct categories. In order to maximise its discriminative character, "height" was coded for its maximal potential values, instead of the range of all potential values. For all traits, a condition cited in the literature as being of frequent occurrence was coded "3", while conditions deemed rare were coded "1". This coding strategy produced a table in which the cells are coded "3", "1" or "0" (a condition not represented in the species concerned). The species traits and their categories used here are shown in Annex 4.

7.2.6 Data analysis

7.2.6.1 Constitution and analysis of the trait-by-pool matrix

A pair of complementary trait-by-pool matrices was produced. In one, henceforth referred to as the "percentage matrix", the average of the association codes (i.e. 0, 1, 3) of all species recorded in the pool for that trait category was weighted by the frequency of the species in the set of sampling plots for the pool. In the other, the "coverage matrix", the average of the association codes was weighted by the average coverage index (ranging between 1 and 5) of the species. Both matrices were analysed using a covariance Principal Component Analysis (covPCA).

7.2.6.2 Constitution of the environmental frames

Three environmental frames were produced on the basis of the "seasonal variability" and "nutrient status" parameters presented above. The first frame was based on all five parameters, while the other two were based on the "seasonal variability" parameters and the "nutrient status" parameters, respectively. All frames were subjected to a correlation matrix Principal Component Analysis (corPCA). There are thus three sets of explanatory variables.

7.2.6.3 Analysis of the traits-environment linkages

The relationships between the trait-by-pool matrices (dependent variables) and the environmental frames (explanatory variables) were explored with PCA on Instrumental Variables (PCAiv, Sabatier *et al*. 1989; Lebreton *et al*. 1991). PCAiv is a generalisation of the Canonical Correspondence Analysis (ter Braak, 1989). The PCAiv procedure comprised 1) projection of the trait categories onto the environmental frame (i.e. identification of the part of the trait variability that is correlated with the explanatory variables), 2) assessment of the significance of the trait-environment relationships with a Monte-Carlo permutation test, 3) derivation of the overall percentage of trait variance explained by the environmental variables and 4) calculation of the percentage of variance explained for each trait category, considered individually. The six combinations of analyses (two sets of dependent variables x three sets of explanatory variables) were compared. All computations were carried out using the ADE-4 software (Thioulouse *et al*., 1997).

7.3 Results

The environmental frame constituted by all five variables ("seasonal variability" and "nutrient status" parameters) explained the trait variability with both trait-by-pool matrices (Table 7.2). However, the relationship was best described with the "coverage" matrix", where 74.1% of the trait variability was significantly explained ($p<0.001$) (Table 7.2).

Table 7.2. Percentage of trait variance explained by the environmental variables. p = Monte-Carlo permutation test (1000 permutations).

	Explanatory variables	**Total environmental frame**	**Seasonal variability**	**Nutrient status**
	(environment)	(5 variables)	(2 variables)	(3 variables)
Dependent variables (species traits)	"percentage"	61.3% p = 0.025	37.1% p = 0.02	29.0% p = 0.27
	"coverage"	74.1% p = 0.001	56.6% p = 0.003	37.0% p = 0.11

In this PCAiv (Figure 7.1), the first factorial axis (F1) ordinated the pools (from left to right) along a continuous and increasing gradient of "seasonal variability" (temperature and depth seasonal variations), while the second factorial axis (F2) ordinated the pools (from bottom to top) along an increasing gradient of "nutrient status" (totN, om and totP).

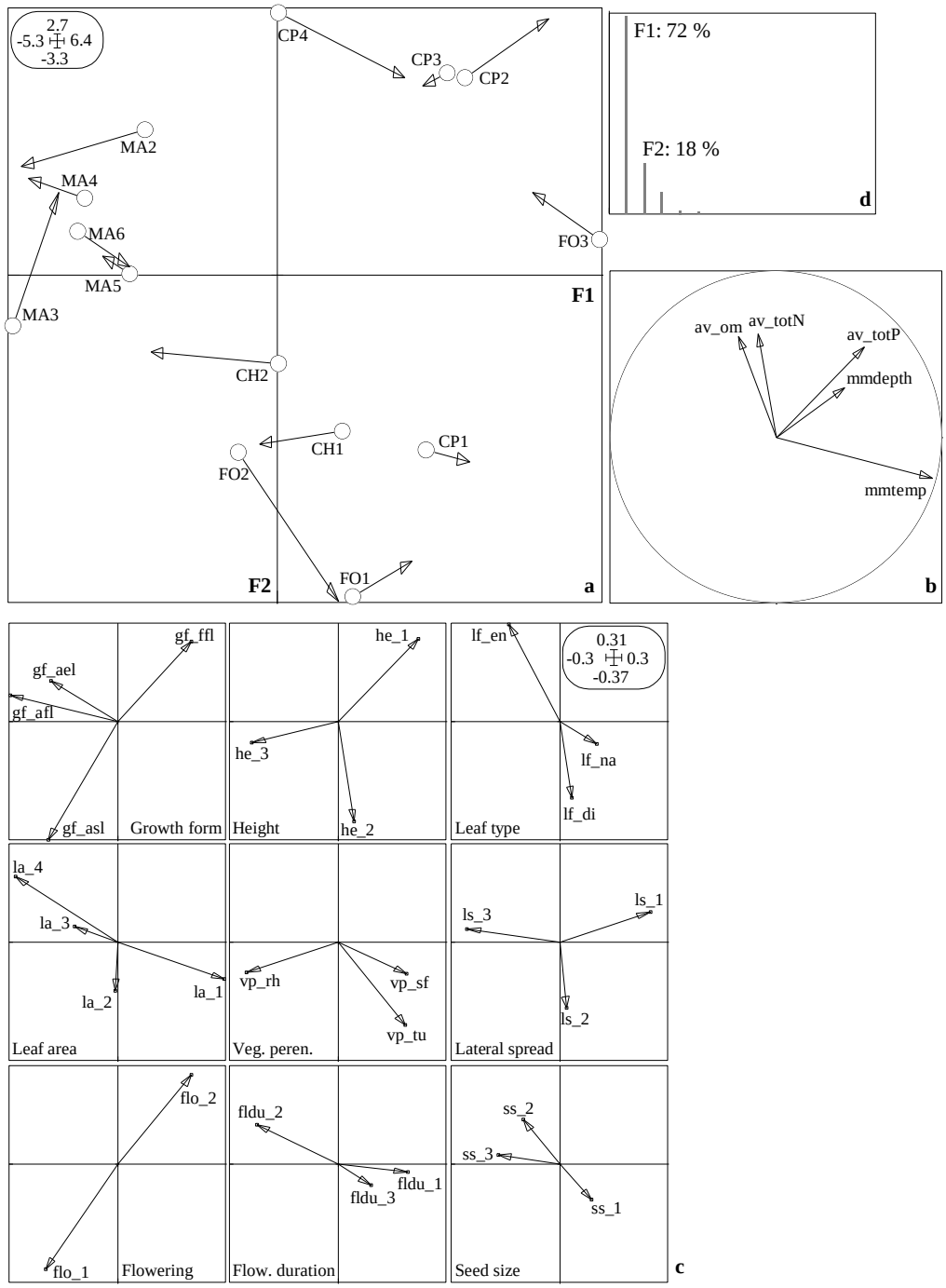


Figure 7.1 Graphical interpretation of the PCA on Instrumental Variables between the "coverage" pool-by-trait matrix and the seasonal variability and nutrient status parameters. **a**. F1 x F2 factorial map of the pools as described i) by the trait composition of their plant assemblages (circles) and ii) by the environmental model of the trait composition (tip of the arrows), b. correlation circle of the environmental frame variables, c. factorial maps of the trait categories, d. histogram of eigenvalues.

The good agreement between the pool's ordination by the trait composition of their plant assemblages (circles, Figure 7.1a), and their ordination by the environmental model of the trait composition produced by the PCAiv (arrow tips, Figure 7.1a) was visible in that grouping of the pools on the factorial plane was preserved if either the circles or the arrow tips were considered.

Table 7.3 Percentage of explanation of the trait categories by the environmental frame in the PCA on Instrumental Variables performed between the "coverage" pool-by-trait matrix and the seasonal variability and nutrient status parameters. * values above the mean percentage of explanation.

Trait	Tr	% explana	Trait	Tr	% explana
	categ	of trait c		categ	of trait c
Growth f	gf_	75.5(*	Veg. pere	vp_	72.9
	gf_	72.5		vp_	94.4(*
	gf_	86.2(*		vp_	71.4
	gf_	80.3(*	Lateral spr	ls_	72.9
Heigh	he_	85.5(*		ls_	84.2(*
	he_	74.7(*		ls_	69.3
	he_	73.6	Flowerir	flo_	87.1(*
Leaf ty	lf_	71.3		flo_	82.6(*
	lf_	55.8	Flow. dura	fldu	66
	lf_	61.2		fldu	72.2
Leaf ar	la_	74.5(*		fldu	81.2(*
	la_	74.2(*	Seed siz	ss_	39
	la_	74.7(*		ss_	54.5
	la_	80.6(*		ss_	61.4

The MA pools, characterised by lower seasonal temperature and depth variations and average to high total nitrogen and sediment organic matter contents, were positively associated with an increased representation of anchored plant species with entire, large, floating or emergent leaves, with important lateral spread through rhizomes, experiencing intermediate flowering duration and producing intermediate- to large sized seeds (Figure 7.1c). The pools CP4, FO2, CH2, CH1 and FO1 all experienced intermediate "seasonal variability", associated with either higher- (CP4) or lower fertility (FO2, CH2, CH1 and FO1) (Figure 7.1a, 7.1b). Small, free-floating species with entire leaves were well represented in CP4, while anchored plants of intermediate height and lateral spread, with submerged, narrow or dissected leaves of rather small area, dispersing mainly through shoot fragments or bublets, turions or dormant apices, and experiencing long flowering durations, characterised FO2, CH1, CH2 and FO1 (Figure 7.1c). Seasonal variations were highest in CP3, CP2, FO3 and CP1 (right side of Figure 7.1a and 7.1b). When associated with higher nutrient status as in CP3, CP2, FO3, the pools were characterised by small, free-floating species, rarely or never experiencing flowering. In CP1, high seasonal variability was correlated with low nutrient status and linked to presence of species

of intermediate to small size, with small and narrow leaves, intermediate lateral spread and very long or very short duration of flowering (Figure 7.1c).

On average, all traits, except “seed size”, were well explained by the environmental variables (Table 7.3). The capacity of the environmental parameters to explain the trait categories could be more variable, with some categories better explained (e.g. vp_tu) than others (e.g. vp_rh; vp_sf) within one trait (Table 7.3)..

Table 7.4 Percentage of explanation of the traits “Height”, “Leaf type” and “Flowering” and their categories by the nutrient status parameters. Results were obtained from the PCA on Instrumental Variables performed on the three traits considered individually. * values above the mean percentage of explanation.

Trait	% explanat	Tra	% explanatio
	of the tra	categ	of the trait categ
Height	49.3%	he_	56.1(*)
	p = 0.03	he_	65.6(*)
		he_	33.9
Leaf type	45.3%	lf_	44.5
	p = 0.04	lf_	44.3
		lf_	46.6(*)
Flowering	54.3 %	flo_	58
	p = 0.04	flo_	50.7

When the “seasonal variability” parameters were considered alone, the environmental frame again significantly explained the variability in trait composition (Table 7.2). Further, the relationship was again closer when the “coverage matrix” was involved (Table 7.2). All results were confirmed by the Monte-Carlo test (Table 7.2). On the contrary, when the environmental frame comprised the “nutrient status” parameters only, no significant relationships were evidenced between trait variability and these environmental parameters (Table 7.2). However, nutrient status parameters significantly explained (at the p = 0.05 level) the traits height, leaf form and flowering when analyses were performed on traits taken individually (see Table 7.4 and Figure 7.2). Moreover, when used alone, the nutrient status parameters formed two groups de-correlated from one another: the water nutrients (tN and tP) on one side and the sediment organic matter on the other. This segregation was less apparent when all parameters (seasonal variability and nutrient status) were used together (Figure 7.1).

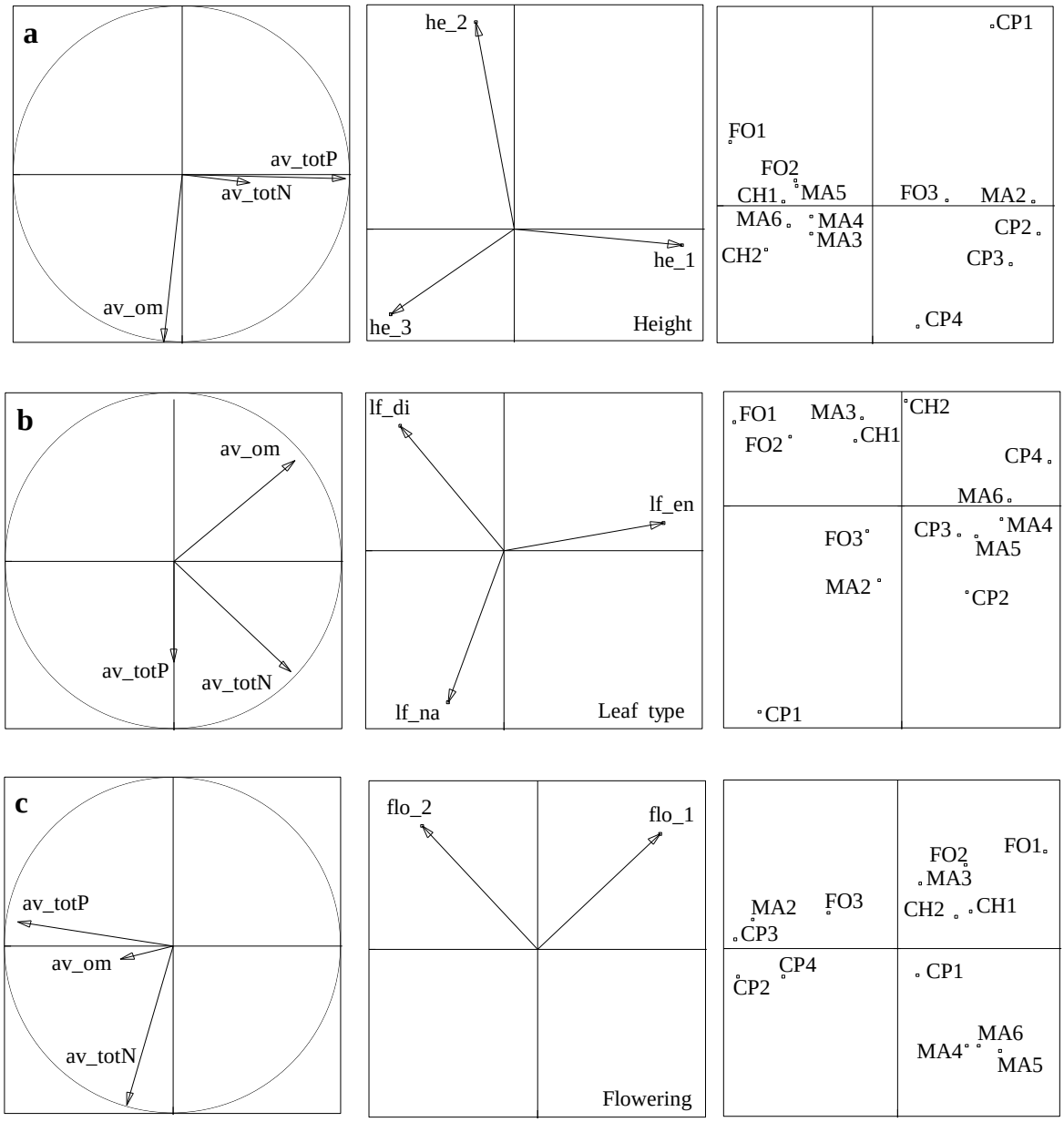


Figure 7.2 Three PCA on Instrumental Variables carried out separately on the traits “height” (a), “leaf type” (b) and “flowering” (c) with the three “nutrient state” variables as explanatory.

7.4 Discussion

In this study, variations in trait composition among aquatic plant assemblages were significantly explained by the combination of seasonal variability and nutrient status environmental parameters. This tends to suggest the validity and applicability of currently accepted models of trait-environment linkages, even in the absence of marked driving forces such as flood disturbances in some alluvial wetlands.

Species colonizing "fertile" and "seasonally stable" pools were expected to display competitive traits. The MA pools were identified as such, i.e. presented high sediment organic matter contents and nitrogen concentrations in the water and experienced weak seasonal variations in temperature and water levels. The dominant species in these pools, *Nymphaea alba L*. is anchored and displays large, entire, floating leaves, a high capacity to spread via rhizomes, a yearly flowering and the production of large seeds. These traits fit the definition of "competitive" traits, as predicted. The result obtained for these pools thus conforms with the results of Barrat-Segretain *et al*. (1999), Willby *et al*. (2000) and Barrat-Segretain (2001). These authors stated that the presence of large to very large-leaved species, with extensive lateral spread, important vegetative structure, low regeneration capacities (from shoots) as well as low colonisation abilities is characteristic of environments experiencing low stress and low disturbance. Extensive lateral spread can be considered as a competitive attribute because it allows more efficient resource capture (Grime, 1979; Kleyer, 1999; de Kroons and Hutchings, 1995) and as an efficient (re)colonisation mechanism. The very large rhizome of *N. alba* allows colonisation, but at very slow rates and regeneration from rhizomes seems difficult. Barko *et al*. (1991) and Keddy (2000) both suggest that the presence of rhizomes or high root:shoot ratios were traits observed in response to competition and burial, in sites with high sedimentation rates or in sites with unfavourable sediment properties. MA2 indeed was submitted to intense deposition of silty sediment.

Two species coexisted with *N. alba* in these pools, *Potamogeton plantagineus* Roem et Schult. and *Utricularia gr. vulgaris*. *P. plantagineus* presented a group of traits similar to that of *N. alba*, i.e. important height, entire, large floating leaves and extensive underground lateral spread. Its presence can be associated with groundwater inputs and corroborates the observations of Bornette *et al*. (1998a) and Buchwald *et al*. (1995) on this species in groundwater-fed sites. One consequence of groundwater supply is to decrease the amplitude of seasonal temperature variation (Bornette *et al*., 1998a) in water bodies receiving groundwater inputs. It could thus explain the maintenance of well-developed stands of *P. plantagineus* in winter (Rooney and Kalff, 2000), which certainly represents a competitive advantage and allows its coexistence with *N. alba*. The second species, *Utricularia gr. vulgaris*, displays some contrasted characteristics. It is also large, but free-floating and submerged, with small dissected leaves. It reproduces vegetatively through the production of shoot fragments or turions, and produces small seeds. Its presence in fertile sites is in accordance with the findings of Givnish (1987) who noted a higher incidence of species with narrow, dissected leaves in nutrient-rich lakes.

Coexistence between *Utricularia gr. vulgaris* and *N. alba* may be possible because of *Utricularia*'s phenology (individuals develop in late summer as *N. alba* beds regress) and its partly heterotrophic mode of nutrient acquisition. Grime (1979) also suggested that the coexistence of alternative strategies might be explained by phenological divergence, i.e. species which develop in different seasons may indeed face different conditions and therefore adopt contrasted strategies. Species richness per pool in this group was very low (between 1 and 3 species), which tends to confirm that "nutrient rich " and "stable" systems are dominated by few competitive species.

Seasonally more variable but nutrient rich pools, for example CP4 and CP3, were strongly associated with *Lemna (L. minor* L., *L. minuta* L. and *L. trisulca* L.*), Riccia (Riccia fluitans)* and *Utricularia (Utricularia* gr. *vulgaris),* in addition to *N. alba*. These species were found either not at all (*Lemna* species, *Riccia fluitans*) or only rarely (*Utricularia gr. vulgaris*) in the seasonally more stable pools. These relations do not corroborate the findings by Willby *et al*. (2000), who indicated strongly negative associations between some traits of these species (free-floating and very small body size) and temporally variable habitats. This discrepancy may be partly due to the different scales at which these two studies were carried out. Our results seem to be in better agreement with Bornette *et al*. (1994a), who expected and observed "small-sized" and "non-anchored" species, in habitats experiencing no disturbances but high temporal variability.

The high percentage of sediment organic matter content measured in pools CP3 and CP4, considered as seasonally variable pools, could explain the presence of *N. alb*a L. there and of *Nuphar lutea* (L.) Sm. in CP3. Both species exhibit an opposite set of traits to that displayed by the *Lemna* and *Utricularia* species: large size, vegetative dispersal through stolons or rhizomes, extended lateral spread, yearly flowering and large seed size. It is known from the literature that rooted, submerged macrophytes tend to be replaced by floating-leaved species as sediment organic matter accumulates (Barko *et al*., 1991). Such an occurrence of contrasted sets of traits in a given habitat is not unusual. Bornette *et al*. (1994a) observed very small, non-anchored *Lemna* species together with very large, anchored plant species in former channels experiencing no disturbance but high temporal variability. The coexistence of *N lutea* and *L. minor* in the same kind of environmental conditions was noted by Barrat-Segretain (1996) as well. The potentially negative consequences for plants of higher "seasonality" (temperature and/or water level fluctuations) may be compensated for by the high nutrient availability, represented in the present case by high percentages of sediment organic matter content and high total phosphorus concentrations in the water. This mixed situation could call for what Grime (1979) named the "stress-tolerant competitors". Stress-tolerant species are described as robust perennials with lateral vegetative spread, by rhizomes or expanding tussocks, differing from true competitors in the longer life-span of their leaves (evergreen with a marked decline in shoot biomass during the winter) and a pronounced peak of biomass production in the summer. *N. alba* and *N. lutea* were observed to have a very important peak of biomass production during the summer, after which

they produced new leaves that overwintered as a small size and were the first occupying the water column in spring. This phenology represents a significant competitive advantage. The small size of the *Lemna* species is also the sign of a competitive ability in productive aquatic habitats (Bornette *et al*., 1994a) in that coverage by *Lemna* species can be important and thus their competition for light very efficient. As mentioned by Willby *et al*. (2000), "alternative attribute-groups can be effective under the same level of spatio-temporal heterogeneity, because of trade-offs between individual traits". Species are adapted to water level fluctuations either by being free-floating or by having a long and flexible petiole (Willby *et al*., 2000). They extract nutrients in dissolved form from either the sediments (*N. alba*) or the water (*L. minor*), or in particulate planktonic form (*Utricularia* gr. *vulgaris*). They adapt to fluid organic sediments (as in CP3 and CP4) either by use of rhizomes allowing strong anchorage (like *N. alba*), or by choosing to float (like the *Lemna* or *Utricularia* species). The existence of three sets of traits among the dominant species of the pools corroborated Grime (1998) and Walker *et al*. (1999), who expected dominant species to be functionally dissimilar (to allow co-existence) but each with its equivalents among the minor accompanying species. But this interpretation would not seem entirely adequate, since Bornette *et al*. (1994a) demonstrated that *N. lutea* , *L. minor* and *Utricularia* gr. *vulgaris* show a low agreement between their traits and habitat utilisation. Willby *et al*. (2000) also observe that *N. alba* and *N. lutea* display high variations in habitat use. Indeed, *N. alba* was observed all along the "seasonal variations" gradient, being present in the "more" as well as in the "less" seasonal pools.

At the “intermediate seasonal variability” and low “nutrient status” positions on the template, it would be predicted for pools to be colonised by species exhibiting more "stress-tolerant" traits, i.e. smaller stature, smaller and longer-lived leaves and larger reproductive output (high number of propagules per cycle). Pools CH1, CH2, FO1 and FO2 conformed to both criteria, i.e. displayed lower sediment organic matter content, lower nutrient concentrations in the water and more important seasonal variations of temperature and water levels. Partly in agreement with the results of Barrat-Segretain *et al*. (1999) and Bornette *et al*. (1994a), these pools were colonised by anchored species, of intermediate height and lateral spread, with submerged, narrow or dissected leaves of smaller area, dispersing frequently through shoot fragments or specialised structures like turions, bublets, etc. These dispersal modes certainly provide a higher colonisation and regeneration capacity, suited to habitats where water-level fluctuations disperse these propagules. The dominance of anchored, submerged species in place of more nutrient conservative floating-leaved species was in accordance with Barko *et al*. (1991). Pools CH1 and FO1 were both characterised by dense stands of *Chara hispida* L., which exhibited “stress-tolerant” traits, like small stature, production of high number of small seeds and small evergreen leaves. In pool FO1, these stands resisted periods of desiccation. At this position in the template, environmental conditions preclude dominance of few competitive species, observed in

the stable and fertile pools. Hence, the absence of strong competitive species allowed the development of a higher species richness per pool (between 4 and 10 species).

Pool FO2 could be regarded as an exception in this group. A monospecific stand of *Myriophyllum spicatum* L. is there slowly being replaced by *N. alba.* The presence of *M. spicatum* in this pool was certainly mainly the result of the pool's creation, which offered a new space, empty of competitors. With time, sediment organic matter content increases, offering conditions better adapted to competitive species, like *N. alba*.

The pool CP1 experienced high seasonal variations associated with low nutrient status. It was weakly colonised by *Potamogeton pusillus* L., *P. pectinatus* L., *Elodea canadensis* Michx. and *Utricularia* gr. *vulgaris*, potentially tall species but very tiny in the present case. The most abundant group was the Characeae, which displayed all expected "stress-tolerant" traits. *P pusillus* and *P. pectinatus* were reported by Sabbatini and Murphy (1996) as stress-tolerant species.

Results obtained here also showed that the two environmental frames considered separately did not have the same capability to explain trait variability between pools. The two variables describing seasonal variability considered alone, still explained a significant part of the trait variations. That was not the case for the three “nutrient “ variables. This discrepancy would seem to indicate that, for the fourteen pools considered, hydrological drivers were of predominant importance in shaping aquatic plant communities. Indeed, both seasonal variations in water level and temperature seemed to be largely dependent upon the surface and groundwater connections of a given pool with the lake (water level fluctuations) and the local aquifer (water temperature buffer).

However, this result had also methodological implications regarding trait-environment analyses. It was shown that, even if non significant when the whole suite of traits was considered, some significant relationships could be established between the “nutrient” variables and some traits considered in isolation. These observed linkages proved coherent with expectations that could be derived from published sources. Variations in height and leaf form are commonly associated to the competitive ability of plants (Gaudet and Keddy, 1988, 1995; Shipley *et al*., 1989; Duarte and Roff, 1991; Boutin and Keddy, 1993), while flowering (sexual reproduction) seems to be predominantly associated with stressed or disturbed conditions (Wiegleb and Brux, 1991). In our case “entire leaves” did coincide with the richer side of the nutrient gradient (as expressed by organic matter and total nitrogen, Figure 7.2b) and the potential to flower regularly did coincide with the poorer side of this gradient (expressed mostly by total nitrogen and total phosphorus, Figure 7.2c). Such results suggest that analysis of individual traits in conjunction with the different components of environmental conditions taken separately could provide more precise results, or evidence relationships that could be hidden when several traits are amalgamated into a single analysis.

Another methodological aspect relates to the use of plant traits compiled mostly from the literature sources. Such information provides insights into the potential of each species. However, what a species actually realises in terms of traits in a given environment, might be a very restricted part of its

potential. This could lead to discrepancies (Poschlod *et al*., 2000). For example, in pool CP1 species like *P. pusillus*, *P. pectinatus*, *E. canadensis* and *Utricularia* gr. *vulgaris*, had a short stature and were smaller than their maximum potential coded in the analysis. Such was also the case with *P. gramineus* in pool FO1. There is certainly a rich potential for incorporating consideration of the deviation between a species' potential (as derived from literature) and its actual traits realised on site, into analyses of trait-environment linkages. This is probably even more relevant in the case of aquatic plants that are known to be highly plastic in their morphology and reproductive traits (Willby *et al*., 2000; Pilon and Santamaria, 2002; Santamarìa, 2002).

Finally, one objective of the study was to compare two ways of producing the trait-by-sites matrices for incorporation into the analysis with environmental parameters. In one case, only the frequency of each species in the set of sampling plots per pool was used to calculate the frequency of trait category per pool. In the second, trait categories per pool were weighted by the average coverage index of the species in the pool. The two methods led to very similar results in terms of pool ordination, and to slightly higher percentages of variance explanation by the environmental parameters in the "coverage" option. Therefore, results obtained here support the idea that the way plant traits are selected and combined is more important than the way their distribution is calculated for analysis of trait-environment linkages.

Chapitre 8

Does variability matter ? A comparison of state *vs*. dispersion variables in the explanation of aquatic vegetation metrics alluvial wetlands

8.1 Introduction

Under the impulsion provided by the work of Grime (1974, 1979) and Grime *et al*. (1988) in the plant sciences, consideration of species traits (i.e. their morphological, ecological and life-cycle characteristics) has been disseminated as a prominent way of investigating the diversity and function of living communities. Combinations of traits considered as proxies for the characterization of a species' strategy are being implemented in procedures aiming at the prediction of the composition and /or changes of species assemblages (Keddy, 1992; Weiher and Keddy, 1999). An important body of literature has been produced about species traits – environment linkages in plant and animal communities, both in terrestrial and aquatic ecosystems (Kautsky, 1988; Townsend and Hildrew, 1994; Bornette *et al*., 1994; Lavorel *et al*., 1997; Díaz and Cabido, 1997; Díaz *et al*., 1998; Kleyer, 1999; Weiher *et al*., 1999; McIntyre *et al*., 1999a,b; Willby *et al*., 2000; etc.). These works suggest that plant trait-environment relationships are scale-dependent (Díaz and Cabido, 1997; Díaz *et al*., 1998, McIntyre *et al*., 1999b) and that their modelling is difficult – especially in the aquatic environment – because of the high plasticity of a majority of the species involved and of trade-offs between traits (Willby *et al*., 2000).

A consequence of these studies was the development of statistical methods adapted to the analysis of digitised species traits in conjunction with distribution data and environmental variables (Bournaud *et al*. 1992; Castella and Speight 1996; Chevenet *et al*., 1994; Dolédec and Chessel, 1994; Dolédec *et al*., 1996), and the calculation of indices of trait diversity (Chessel and Champely, 2000).

Considering the welter of approaches adopted in the analysis of traditional species-by-sites data collections and the possibilities offered by the above mentioned statistical techniques, the objective of the paper was to use a single set of vegetation releves to compare approaches that are seldom used in conjunction. Four types of data were derived from the vegetation releves: i) the species composition per site (i.e. the untransformed species-by-sites data matrix containing average species cover per site), ii) a set of "diversity" indexes, iii) the species traits composition per site (i.e. a trait-by-site matrix derived from combination of the raw data and of a species trait database), iv) a measure of the diversity of plant traits per site. We compared these four types of data in their ability to be explained (in a statistical sense) by a set of environmental variables measured at the same sites.

A second objective of the paper relates to the expression of these explanatory environmental variables. Habitats conditions are most frequently described by mean values, rather than by an expression of their variability. However, the respective influence of mean level *vs*. variation of environmental parametres upon biotic communities has been debated (Keddy, 1991; Palmer *et al*., 1997; Palmer and Poff, 1997; Mérigoux *et al*., 2001; Henry *et al*., 2002) and incorporated into conceptual models, such as the river habitat templet (Townsend and Hildew, 1994). As stated by Palmer *et al*. (1997) most work focused on how the mean environmental parametres are likely to influence biotic variables. But ecological systems vary over space and time and "focus on variability (=heterogeneity) may yield new

and exciting insights". We therefore compared the respective potential of average environmental values and of their seasonal variability to explain variations in the four sets of biotic data listed above.
The data sets (aquatic vegetation and environmental data) selected for the purpose of these tests were obtained with comparable sampling strategies in twenty-four water bodies of a lake-fringe wetland (Lake Neuchâtel, Switzerland) and of a riverine floodplain wetland (the Ain River, France). These two sectors were selected for several reasons: i) they can be regarded as building up a gradient of hydrological function from more dynamic (i.e. subjected to regular flooding) water bodies (the Ain floodplain), to more stable ones (the lake fringe), ii) from a biogeographical point of view, they share the same pool of potential hydrophyte species, iii) similarities in their function were depicted: in both regions the relative influence of allogenic forces (mineral sediment input, wave or current action, originating from the river or the lake) and of autogenic forces (*in situ* production and accumulation of organic matter in each water body) is a major driver of the functions and successions in each individual water body (Bornette *et al*., 1998b; Amoros and Bornette, 2002; Antoine *et al*., 2004; chapters five and six in this thesis).

8.2 Material and Methods

8.2.1 Study sites

One study region (further abbreviated "NEU"), on the Southern shore of Lake Neuchâtel, is the largest fringing wetland in Switzerland (mean altitude: 429.3 m), known as the "Grande-Cariçaie". The origins of the waters feeding the wetland are many and varied. Since water-level fluctuations in the lake became regulated in the 1970's, the direct influence of the lake has become limited to a 50-meter wide band, which can be further reduced in width by the presence of sand dunes. Water-level fluctuations do not now exceed 1m. Levels are maximal in spring (May-June), decrease during summer and are minimal in winter. When distance from the lake increases or when sand dunes disconnect the wetland from the lake, the relative importance of groundwater influence increases. In addition to lake surface water and groundwater, water from two other origins may contribute to the water reaching pools within the wetland. In those areas of the lake margin where the wetland is restricted to a narrow strip between the lake and cliffs, water input can occur through surface water runoff from the cliffs. Finally, streams reaching the lake from its hinterland (most often agricultural) constitute a fourth substantial water input in some sectors.
Fourteen pools (or sites) at four different locations (sectors) were selected: Champ-Pittet (pools CP1 to CP4), la Maladaire (pools MA2 to MA6), Châbles-Perron (pools CH1, CH2) and Font (pools FO1 to FO3). Except for CP and MA3, these pools are all man-made. Some of these pools are connected to one another, while others are not: a connection exists from CP1 through to CP4, as between CH1 and

CH2 and FO2 and FO3. Moreover, the pools exhibit different degrees of connection to the lake (at mean lake water level): CP1, CP2 and CH2 are directly connected to it, through a channel. The connection of CP3 and CP4 to the lake operates through their connection to CP2 and CP1. The other pools are separated from the lake by a more or less developed sand dune, which is flooded only during high lake water levels. For more information see Buttler (1987) and chapter five in this thesis..

The highly dynamic lower Ain River floodplain (France), still unconstrained and submitted to a flash-flood regime has been selected as second study region (further abbreviated "AIN"). The lower course of the river (i.e. the last 15 km before its confluence with the Rhône River) presents a remarkable set of meanders naturally cut-off from the main channel during the second half of the 20th century. Four cut-off channels were selected and ten sites sampled along them: the "Brotteaux" (BX2, BX23 and BX3), the Planet (PL1, PL2 and PL3), Puitss-Novet (PN11, PN12 and PN2), and Port-Galland (PG). These sites differ in their degree of connectivity to the main channel through 1) their position along the longitudinal gradient of the river and 2) their transversal position in a given cut-off channel. The "Brotteaux" and the "Planet" are both disconnected from the Ain River by an alluvial plug at their downstream end (BX3 and PL3, respectively). However, as water level increases in the main channel, both sites are flooded, as are BX23, BX2 and PL2. PL1 is only occasionally connected to PL2. In "Puits-Novet", PN11 represents a small pool only rarely connected to its downstream neighbour PN12, which in turn is permanently connected to PN2. PN11, PN12 and PN2 are regularly flooded during high water level conditions. Finally, Port-Galland is the only site in direct connection to the Ain River. These sites were considered as analogous to the pools of the Grande-Cariçaie in that 1) they constitute discrete water bodies (i.e. those sites located along the same cut-off meanders are separated by shallower sections or alluvial plugs), 2) they differ from each other in their degree of connectivity to the main channel and 3) their water feeding is multiple. It is indeed constituted by a surface- and a ground water component, the respective influence of which varies with sites. PL1 and PL2 are mainly fed by the left-hand hillside aquifer, while the Brotteaux, Puits-Novet and Port-Galland are mostly influenced by river seepage (Bornette *et al*., 1998b). The two regions differ however in the amplitude of water level fluctuations, which lead to dry phases in some of the Ain sites that do not exist in the Grande-Cariçaie.

8.2.2 Sampling regime

8.2.2.1 Water physico-chemistry

The "Grande-Cariçaie" and the "Ain" water bodies were sampled quarterly (5 dates) between January 1997 and January 1998, and between March 2000 and March 2001, respectively. On each occasion, conductivity, pH, dissolved oxygen and temperature were measured in the field with WTW probes (WTW Cond LF 320, WTW pH 320 and WTW Oxi 320, respectively, WTW GmbH, Weilheim, Germany). Laboratory analyses were performed a few hours after water sampling. They included

ammonia, nitrate and nitrite concentrations, determined using the salicylate, cadmium reduction and diazotization methods, respectively. Total phosphorus concentrations were determined by persulfate acid digestion. The sum of the three nitrogen forms (total nitrogen) was further used for calculations.

8.2.2.2 Aquatic vegetation

Aquatic plant species composition and cover were recorded in summer 1997 in the Grande-Cariçaie, and in summer 1999 in the Ain floodplain. In the Grande-Cariçaie pools, plots of 50 x 50 cm were distributed every 5 to 10 m along transects perpendicular to the longest axis of the pools, and separated from each other by 10 - 20 m (depending upon pool surface area). In the Ain sites, plant composition and cover were directly assessed after inspection of 2m-wide transects perpendicular to the channel. In both sectors a modified Braun-Blanquet coverage index was used to express vegetation cover (1: < 5%; 2:] 5-25%]; 3:] 25-50%]; 4:]50-75%]; 5: > 75%). Individual plots from the Grande-Cariçaie sites were amalgamated per transect to enable comparability with the Ain data.

The nomenclature followed Lauber and Wagner (2001), except for charophytes (Corillion, 1975). Analyses were restricted to the hydrophytes defined as such by Casper and Krausch (1980) and to the charophytes.

8.2.3 Data structure

8.2.3.1 Environmental data

The seven water chemistry parametres (temperature, oxygen, pH, conductivity, depth, total nitrogen and total phosphorus) were expressed i) as mean values per pool (except temperature, see below) to build up the “state” set of explanatory variables and ii) as max-min differences, to represent their temporal variability. Max-min differences were preferred to variances or inter-quartile ranges because of the limited number of values per site (n = 5). In the “state” variable set, water temperature was expressed as the difference between the winter temperature of a given pool and the average winter temperature of all pools of the same sector (further called “temperature difference”). This was done to focus upon potential differences in thermal regimes between pools, especially as a consequence of groundwater supply and also because we considered winter temperatures to be critical for the ability of biota to withstand the cold period. Both average and max-min total nitrogen were log-transformed after examination of the distribution of all explanatory variables.

8.2.3.2 Plant species composition and diversity

The data matrix (“VEG”) containing the average coverage note of all species recorded in the 24 water bodies was used to derive two indexes:

- "RICH": the number of species per site

- "UNIQ": a uniqueness index integrating the degree of rarity of the species. It was calculated according to Bornette *et al*. (1998a) but developed to produce a numerical index. Within each of the two regions, each species was given a score based upon the proportion of water bodies in which it occurs (e.g. species occurring in less than 10% of the water bodies were given a "10" score, species occurring in 10 to 20% of the water bodies were given a "9" score, until the species occurring in 90% of the water bodies or more, which were given a "1"). A weighted average was then calculated for each pool given the number of species falling in each uniqueness category.

8.2.3.3 Plant traits and trait diversity

Nine plant traits corresponding to morphological, phenological and reproductive characteristics were chosen, to represent dispersion and colonisation (*vegetative perennation ; underground parts spread*), growth and morphology (*growth form; height; leaf form and leaf area*) as well as sexual reproduction (*flowering, flowering duration* and *seed size*). They were selected in the light of previous studies and according to the availability of data in the literature.

Information was mainly gathered from Corillion (1975), Heß *et al*. (1976), Grime *et al*. (1988), Aeschimann and Burdet (1989), Frank and Klotz (1990), Casper and Krausch (1980, 1981), Preston (1995), Krause (1997), Lauber and Wagner (2000), Willby *et al*. (2000), augmented by personal experience of the authors, and coded according to the fuzzy coding approach proposed by Bournaud *et al*. (1992) and Chevenet *et al*. (1994).

A distinction was made between coding of the trait "height", for which data were continuous values, and the other traits, which had distinct categories. In order to maximise its discriminative character, "height" was coded for its maximal potential values, instead of the range of all potential values. For all traits, a condition cited in the literature as being of frequent occurrence was coded "3", while conditions deemed rare were coded "1". This coding strategy produced a table in which the cells are coded "3", "1" or "0" (a condition not represented in the species concerned).

The "VEG" (species-by-sites) and "TRAIT" (species-by-trait categories) matrices were multiplied to produce a site-by-trait categories matrix ("SITE-TRAIT"), which expressed the trait composition per site. In this matrix, the average of the association codes (i.e. 0,1,3) of all species recorded in a site for a trait category was weighted by the average coverage index of the species.

The "SITE-TRAIT" matrix was subsequently used to calculate a trait diversity index per site (matrix "TRAIT-DIV"). For each trait and site, a Simpson index of diversity (SIM) was calculated to account for the evenness of the frequency distribution of trait categories per site (Magurran, 1988).

$$\mathrm{SIM} = 1 - \sum_i p\, i^2$$

With *p i* the relative frequency of the ith modality of a trait in a given pool.

The more evenly distributed the categories within one trait, the highest the diversity and thus the Simpson index value. An average index of trait diversity can be obtained by averaging the diversity index of all traits in a given pool.

8.2.4 Data analysis

8.2.4.1 Differences between sectors

A non-parametric Wilcoxon test was performed on the environmental variables and on the biotic variables (species richness, community uniqueness and average trait diversity) in order to identify between-sector differences (Ain *vs*. Lake Neuchâtel).

8.2.4.2 Inter-correlation between explanatory variables

Pearson's correlation coefficient was calculated for each pair of environmental variables to detect potential redundancies between explanatory variables prior to regression with the biotic data (see below). Wilcoxon tests, correlation calculations and the associated graphs were performed using the S-Plus software (Anonymous, 1999).

8.2.4.3 Multivariate biotic data

Prior to the analysis of their relationships with environmental data, the multivariate vegetation data (i.e. species and trait compositions per site, trait diversity per site) were described with the appropriate multivariate ordination technique. VEG was analysed with a Correspondence Analysis (COA) (Greenacre, 1984). SITE-TRAIT was analysed with a Multiple Correspondence Analysis (MCA) adapted for fuzzy-coded variables (Chevenet *et al*., 1994). TRAIT-DIV was analysed with a Principal Component Analysis on covariance matrix (covPCA) (Hotelling, 1933; Lebart *et al*. 2000). In each case a between-sector analysis (Dolédec and Chessel, 1987, 1989) followed each of the three ordinations to assess and test (Monte-Carlo permutation test, 10'000 permutations) the amount of between-sector (i.e. AIN *vs*. NEU) variability.

8.2.4.4 Explanation of vegetation data by the environmental variables

The description of the relationship between the vegetation data and the environmental explanatory variables, as well as the measurement of the associated percentage of explained variation, was achieved using PCA on instrumental variables (PCAIV, Sabatier *et al*., 1989; Lebreton *et al*., 1991; Chessel, 1997). Monte-Carlo permutation tests (10'000 permutations) were used to ascertain the significance of the percentage of explained variation. In all the PCAIVs the explanatory environmental variables (both the state and max-min data) were first ordinated with a correlation matrix PCA

(corPCA) (Hotelling, 1933; Lebart *et al*. 2000). The ADE-4 programme library (Thioulouse *et al*., 1997) was employed for all multivariate data analyses and production of the associated graphs.

8.3 Results

8.3.1 Differences between sectors

Out of the seven state environmental variables, two had non-significant differences between the AIN and NEU sectors: the winter temperature difference and total nitrogen concentration (Figure 8.1). On average the AIN water bodies were deeper, had lower mineralization and higher phosphorus content than the NEU pools. Out of the seven variability parametres, three had non-significant differences between the AIN and NEU sectors: the conductivity, oxygen saturation and total nitrogen (Figure 8.2). On average, the AIN water bodies had higher depth and total phosphorus fluctuations, and more reduced temperature and pH fluctuations than the NEU pools.

In the three "diversity" indexes (Figure 8.3), the AIN sector had both higher species and trait diversities, but no significant differences in uniqueness could be detected between sectors. Both trait diversities and uniqueness per pools were more heterogeneous within the NEU than within the AIN sector.

8.3.2 Correlations between explanatory variables

Examination of the correlations between environmental variables (Table 8.1) led us to define three sets of explanatory variables that will be used separately in further analyses:

V1: a set of four state physico-chemical variables (conductivity, temperature difference, oxygen saturation and pH). These state variables had low or non-significant correlations with their variability counterparts (max-min values).

V2: three state variables (depth, total phosphorus and log-total nitrogen) that had very high correlations with their variability counterparts (0.79, 0.91 and 0.93 respectively), implying that the use of the former as explanatory in a regression model would provide similar results than the latter.

V3: the max-min expression of the four variables from the V1 set (max-min of: conductivity, temperature, oxygen saturation and pH).

Consideration of three smaller sets of explanatory variables (3 to 4 per set) would subsequently improve their ratio to the number of sites (24) in the PCAIV regressions.

Table 8.1. Pearson correlation coefficients between environmental explanatory variables. The associated significance levels are: NS: p>0.05, *: p<0.05, **: p<0.01, ***: p<0.001.

	Cond.	Temp diff.	Oxy.	pH	Depth	TotP	TotN	Mm Cond.	Mm Temp	Mm Oxy.	Mm pH	Mm Depth	Mm TotP
Temp diff.	0.34 NS												
Oxy.	-0.60 **	-0.37 NS											
pH	-0.78 ***	-0.42 *	0.60 **										
Depth	-0.68 ***	0.02 NS	0.29 NS	0.56 **									
TotP	-0.53 **	-0.03 NS	0.37 NS	0.62 **	0.64 ***								
TotN	0.15 NS	0.13 NS	-0.01 NS	0.26 NS	0.22 NS	0.26 NS							
Mm Cond.	-0.009 NS	0.35 NS	-0.22 NS	-0.04 NS	0.11 NS	0.13 NS	-0.03 NS						
Mm Temp	0.30 NS	-0.40 NS	0.17 NS	-0.29 NS	-0.67 ***	-0.45 *	-0.40 NS	-0.26 NS					
Mm Oxy.	0.24 NS	0.09 NS	-0.25 NS	-0.27 NS	-0.17 NS	0.08 NS	-0.11 NS	0.24 NS	-0.05 NS				
Mm pH	0.73 ***	0.005 NS	-0.27 NS	-0.54 **	-0.78 ***	-0.68 ***	-0.06 NS	-0.14 NS	0.76 ***	-0.005 NS			
Mm Depth	-0.74 ***	-0.12 NS	0.41 *	0.67 ***	0.79 ***	0.65 ***	-0.01 NS	0.06 NS	-0.56 **	0.07 NS	-0.78 ***		
Mm TotP	-0.58 **	-0.02 NS	0.36 NS	0.68 ***	0.67 ***	0.91 ***	0.35 NS	0.09 NS	-0.54 **	0.09 NS	-0.69 ***	0.67 ***	
Mm TotN	0.17 NS	0.02 NS	-0.07 NS	0.28 NS	0.16 NS	0.23 NS	0.93 ***	-0.10 NS	-0.35 NS	-0.05 NS	-0.02 NS	-0.02 NS	0.33 NS

8.3.3 Variation in species composition and its explanation by environmental variables

Ordination of the VEG species-by-sites matrix showed a far stronger differentiation between the NEU pools than between the AIN water bodies. The latter were described as very similar and grouped at one extreme of the first ordination axis F1 (Figure 8.4). Although the two sectors shared only one third (13 species) of the total species pool (38 species), the compositional difference between the two sectors proved non significant in the COA (17.9% of the variability, permutation test p=0.13).

The three sets of explanatory variables (V1, V2, V3) yielded comparable and significant percentages of explanation of the species composition (i.e. between 26.7 and 37.3%, Table 8.2). Different suites of species were explained by the three explanatory sets (only 5 species out of 38 were well explained by the three sets: *Nymphea alba*, *Ceratophyllum demersum*, *Utricularia vulgaris*, *Nuphar lutea and Hottonia palustris*. All three PCAIVs tended to segregate the AIN and NEU sectors along their first axis (Figure 8.5).

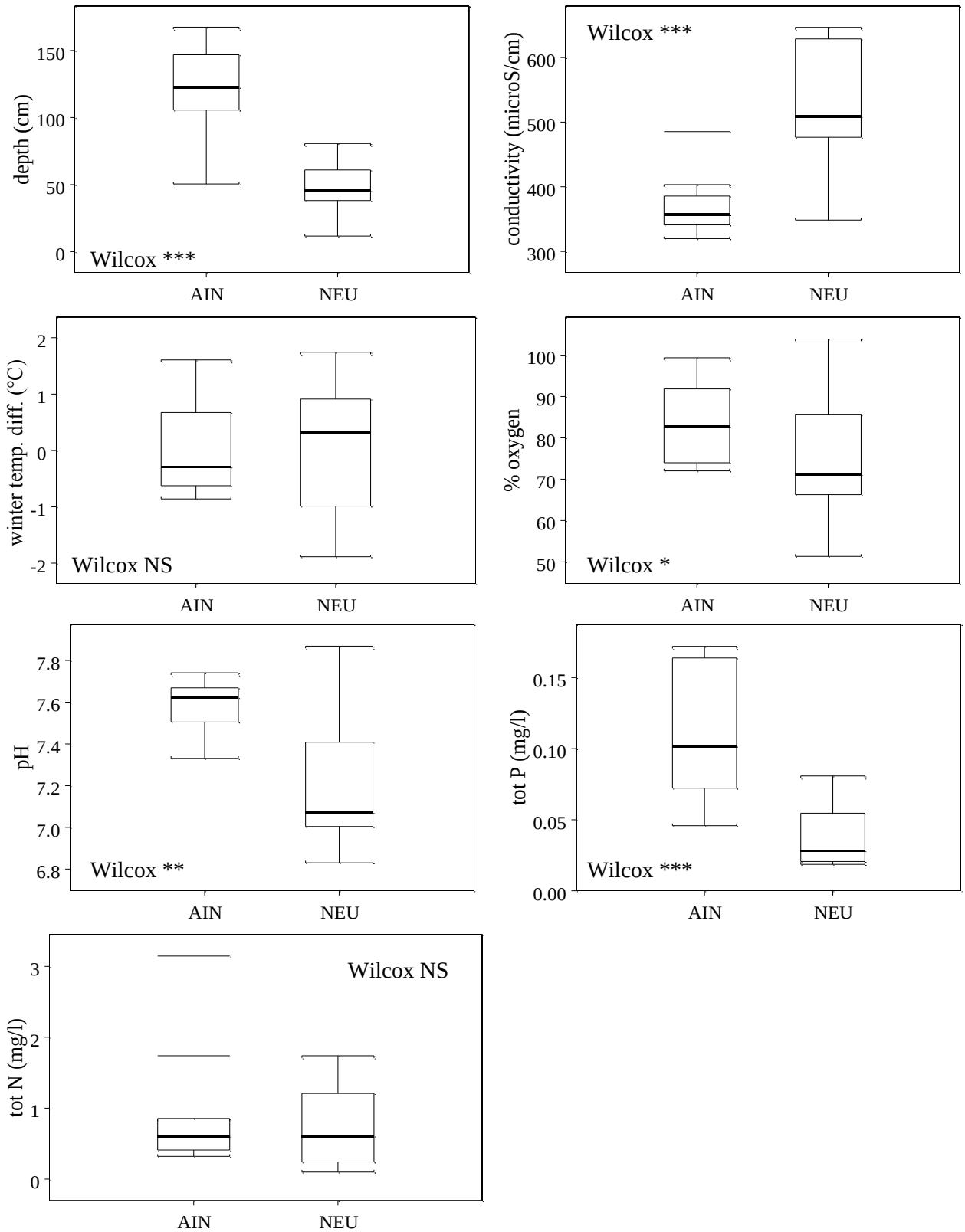


Figure 8.1. Distribution of the state environmental variables in the Ain and Grande-Cariçaie (NEU) sectors. Box-plots provide: the median (bold line), the Q75 – Q25 inter-quartile interval (box), values not beyond Q75+1.5(Q75-Q25) or Q25-1.5(Q75-Q25) (whiskers) and outliers (bars beyond the whiskers). Wilcox: p value of a Wilcoxon test between sectors (NS: p>0.05, *: p<0.05, **: p<0.01, ***: p<0.001).

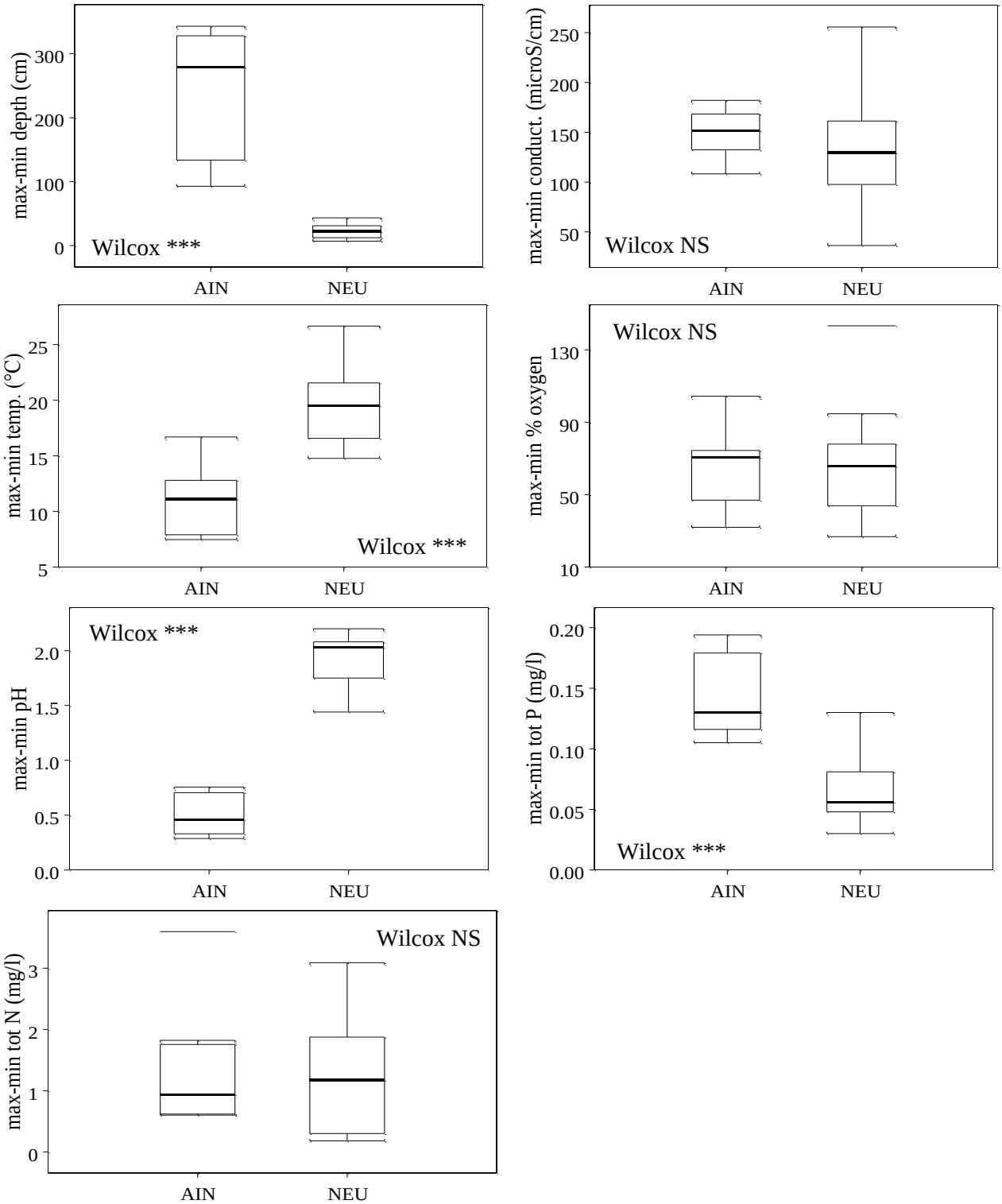


Figure 8.2. Distribution of the seasonal variability environmental variables in the Ain and Grande-Cariçaie (NEU) sectors. Box-plots provide: the median (bold line), the Q75 – Q25 inter-quartile interval (box), values not beyond Q75+1.5(Q75-Q25) or Q25-1.5(Q75-Q25) (whiskers) and outliers (bars beyond the whiskers). Wilcox: p value of a Wilcoxon test between sectors (NS: p>0.05, *: p<0.05, **: p<0.01, ***: p<0.001).

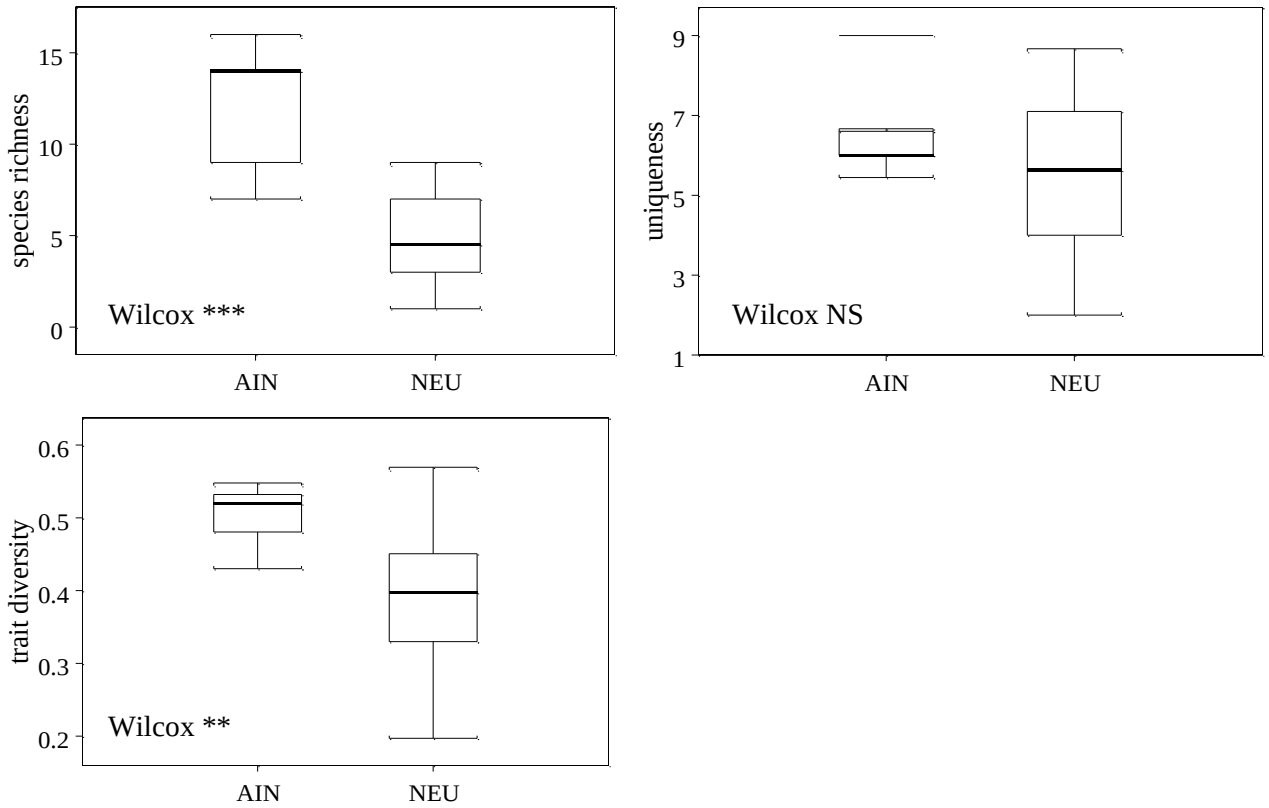


Figure 8.3. Distribution of the diversity variables in the Ain and Grande-Cariçaie (NEU) sectors. Box-plots provide: the median (bold line), the Q75 – Q25 inter-quartile interval (box), values not beyond Q75+1.5(Q75-Q25) or Q25-1.5(Q75-Q25) (whiskers) and outliers (bars beyond the whiskers). Wilcox: p value of a Wilcoxon test between sectors (NS: p>0.05, *: p<0.05, **: p<0.01, ***: p<0.001).

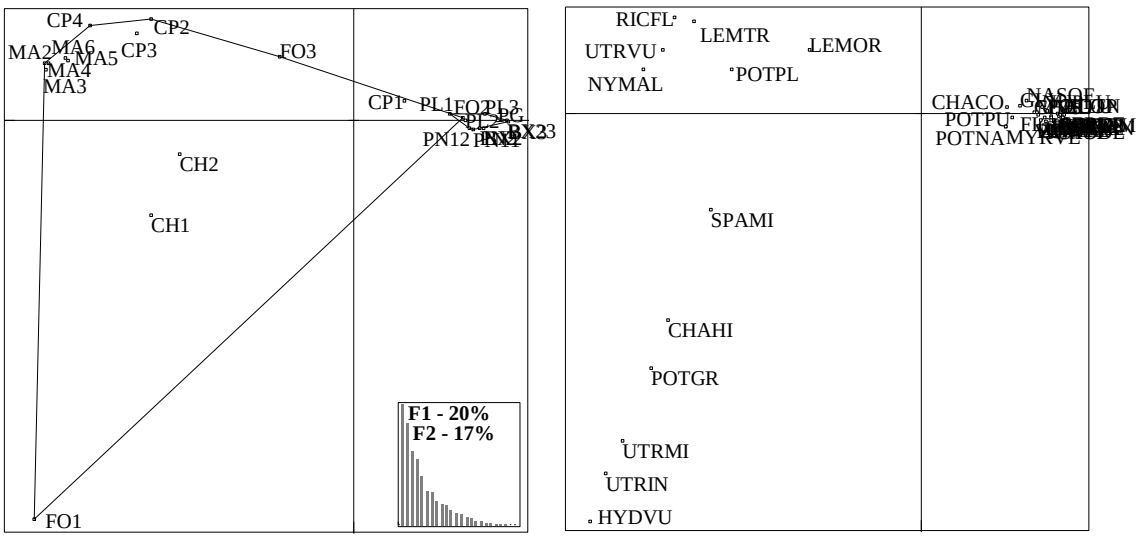


Figure 8.4. Correspondence Analysis of the vegetation composition (species-by-sites data). Left: F1 x F2 factorial plot of the sites grouped per sector with the corresponding % of explained inertia. Right: F1 x F2 factorial plot of the species.

Table 8.2 Results of the PCAIVs of the species composition data with three different sets of explanatory variables. Blanks in the % explanation of the species denote values below the average of all species.

	Set of explanatory variables		
	V1	V2	V3
% of explained variance	37.3	26.7	29.9
p value (10'000 permutations)	0	0	0.0004
best explanatory variables (F1 axis score above the average)	cond oxy pH	depth totP	mmtemp mmpH
best explained species (% of explanation above the average)			
RICFL	77		
NYMAL	73	48	83
LEMTR	67		
CERDE	65	39	33
UTRVU	57	36	58
POTPE	53	29	
RANTR	52		35
CHAHI	50		
LEMOR	44		
NUPLU	43	62	33
HOTPA	41	31	40
POTPF	41		
SPAMI	37		
CALSP		69	37
RORAM		60	52
GRODE		41	
POTPL		38	32
VERAN		34	40
POTGR		32	33
ELONU		30	
CHAVU			35
POTLU			32

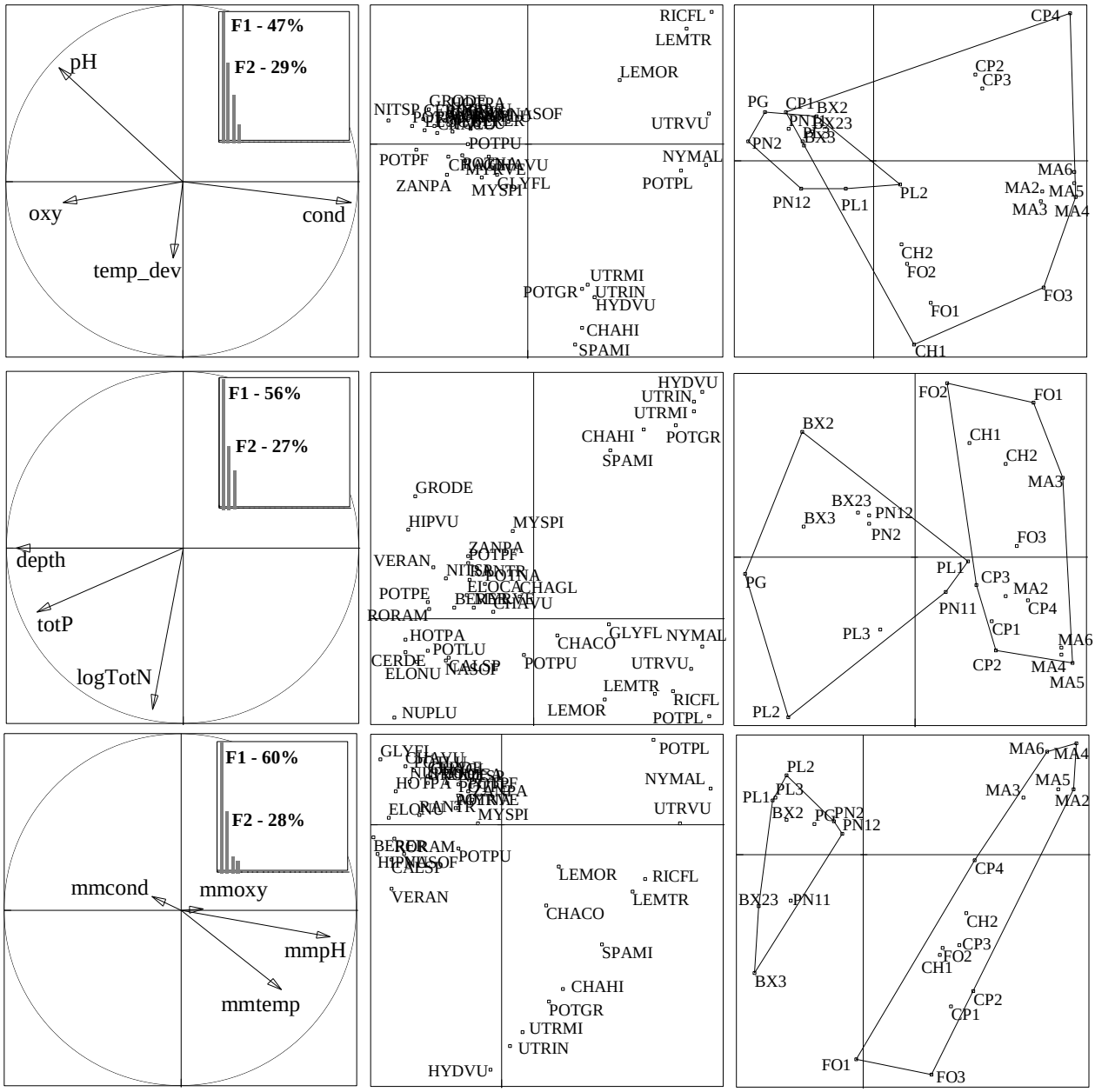


Figure 8.5. PCAIV of the vegetation composition (species-by-sites data) and of the environmental explanatory variables (V1: first row, V2: second row, V3: third row). Left: F1 x F2 correlation circles of the explanatory variables with the corresponding % of explained inertia. Center: F1 x F2 factorial plots of the species. Right: F1 x F2 factorial plots of the sites grouped per sector.

8.3.4 Variation in trait composition and its explanation by environmental variables

Ordination of the SITE-TRAIT matrix (trait categories-by-sites) also showed a stronger differentiation between the NEU pools than between the AIN water bodies (Figure 8.6). Along its first axis, the spectrum of trait combinations appeared far wider in NEU. Traits contributing to this gradient were mostly related to plant size and morphology (growth form, maximum size, leaf area, underground spread). Here, the part of the trait variability that could be explained by differences between sectors, although small (11.5%), was significant at the 5% level (permutation test, p=0.03).

Among the three sets of explanatory variables, V2, which associated phosphorus, nitrogen and depth, proved to be unable to explain the variation in trait composition among sites (Table 8.3) and the corresponding analysis was therefore not represented. The other two sets had higher explanatory capabilities than for species composition (54.2 and 43.9 %). The best explained traits were also the four mentioned above, plus two related to reproduction (flowering duration and seed size). Two traits (flowering and leaf type) were poorly explained both by V1 and V3. There was a great similarity between the trait categories explained by the state variable set (V1) and the variability one (V3): only 5 categories (out of the 18 well explained ones) were explained only by one of the two sets (Table 8.3).

Contrarily to the species composition analyses, both trait composition PCAIVs did not segregate the AIN and NEU sectors along their first axis but provided a continuous gradient mixing sites from the two sectors (Figure 8.7).

8.3.5 Variation in trait diversity and its explanation by environmental variables

Prior to their ordination, we examined the inter-correlations between the nine series of Simpson diversity indexes per trait (Table 8.4). Numerous traits had highly (positively) correlated diversities (i.e. above r=0.70). Therefore, five were selected (growth form, maximal size, leaf area, flowering and seed size) to simplify the trait diversity matrix and keep variables with limited redundancies.

Ordination of the "TRAIT-DIV" matrix (Figure 8.8) evidenced a conspicuous concentration of the AIN sites at high diversity of the traits "maximal size" and "flowering". The NEU pools covered the whole spectrum of diversity conditions from low-diversity pools (e.g. MA2 to 4 along F1), to pools with diversity similar to that of the Ain water bodies (e.g. CP4). The between-sector component of the total variability was limited (16.5%) but significant at the 1% level (permutation test, p=0.0025).

As in the case of trait composition, the V2 set of explanatory variables proved unable to explain significantly the variations in trait diversity and the corresponding analysis was not represented (Figure 8.9, Table 8.5). Diversity in "maximal size" and "flowering" proved well explained by both the V1 and V3 environmental sets. Diversity of these traits increased with decreasing mineralization and variability in seasonal variability. Leaf area diversity also increased with decreasing temperature variability (Figure 8.9).

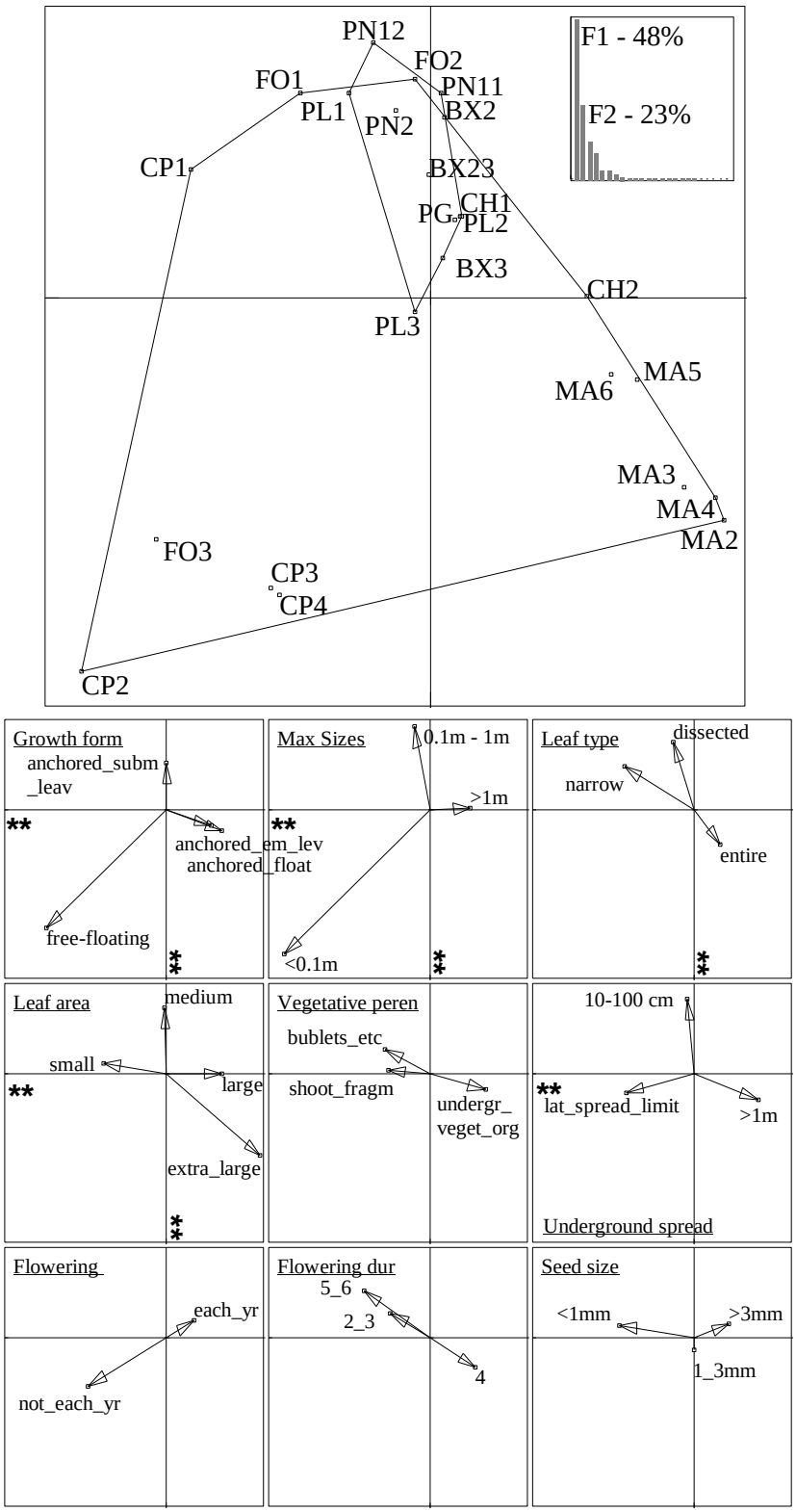


Figure 8.6. Fuzzy Multiple Correspondence Analysis of the trait composition (traits-by-sites data). Top: F1 x F2 factorial plot of the sites grouped per sector with the corresponding % of explained inertia. Bottom: F1 x F2 factorial plot of the categories of each trait. ** denotes traits with the highest contributions to the ordination of sites.

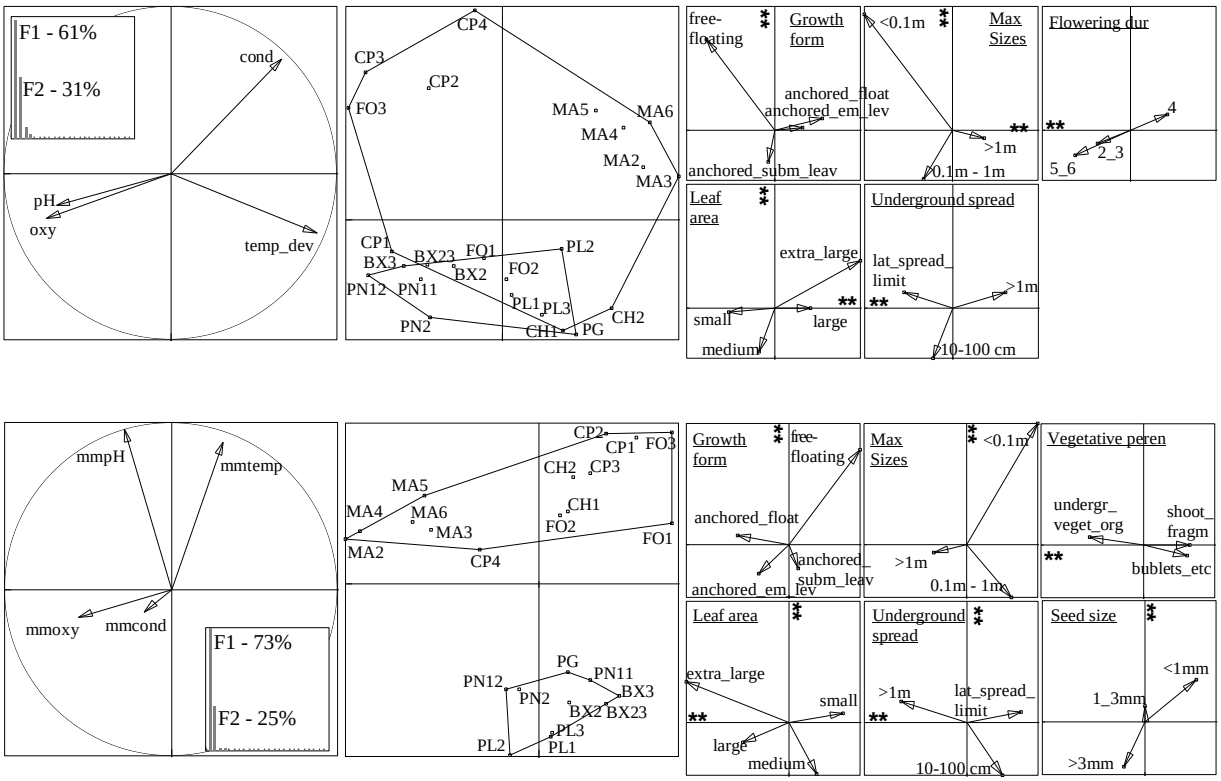


Figure 8.7. PCAIV of the trait composition (traits-by-sites data) and of the environmental explanatory variables (V1: first row, V3: second row). Left: F1 x F2 correlation circles of the explanatory variables with the corresponding % of explained inertia. Center: F1 x F2 factorial plots of the sites grouped per sector. Right: F1 x F2 factorial plots of the trait categories. Only traits contributing to one of the two factorial axes were drawn.

Table 8.3 Results of the PCAIVs of the trait composition data with three different sets of explanatory variables. Blanks in the % explanation of the trait categories denote values below the average of all categories.

	Set of explanatory variables		
	V1	V2	V3
% of explained variance p value (10'000 permutations)	54.2 0	18.1 0.16	43.9 0
best explanatory variables (F1 axis score above the average)	temp_diff oxy (cond) (pH)		mmoxy
best explained trait categories (% of explanation above the average)			
Growth form / anchored_float	64		58
Growth form / anchored_subm_leav	63		
Growth form / free-floating	59		
Max Size / <0.1m	65		
Max Size / >1m	61		49
Max Size / 0.1m - 1m			46
Leaf area / extra_large	79		78
Leaf area / small	59		61
Leaf area / medium	55		61
Leaf area / large			51
Vegetative peren / undergr_veget_org	66		80
Vegetative peren / shoot_fragm	59		61
Vegetative peren / bublets_etc	56		63
Underground spread / >1m	67		73
Underground spread / 10-100 cm	61		56
Underground spread / lat_spread_limit	55		47
Flowering dur / 4	63		44
Seed size / >3mm	58		51

Table 8.4 Pearson correlation coefficients between the Simpson indexes of diversity per trait. The associated significance levels are: NS: p>0.05, *: p<0.05, **: p<0.01, ***: p<0.001.

	Growth form	Max Size	Leaf type	Leaf area	Vegetative perennation	Underground spread	Flowering	Flowering duration
Max Size	-0.04 NS							
Leaf type	-0.14 NS	0.73 ***						
Leaf area	0.48 *	0.19 NS	0.22 NS					
Vegetative perennation	-0.36 NS	0.71 ***	0.75 ***	0.23 NS				
Underground spread	-0.15 NS	0.73 ***	0.75 ***	0.53 **	0.84 ***			
Flowering	-0.25 NS	0.48 *	0.36 NS	0.03 NS	0.66 ***	0.47 *		
Flowering duration	-0.13 NS	0.84 ***	0.88 ***	0.16 NS	0.82 ***	0.69 ***	0.49 *	
Seed size	0.45 *	0.43 *	0.41 *	0.31 NS	0.02 NS	0.21 NS	-0.20 NS	0.41 *

Table 8.5 Results of the PCAIVs of the trait diversity data with three different sets of explanatory variables. Blanks in the % explanation of the trait diversity denote values below the average of all traits.

	Set of explanatory variables		
	V1	V2	V3
% of explained variance p value (10'000 permutations)	41.6 0.0002	19.9 0.09	42.3 0.0003
best explanatory variables (F1 axis score above the average)	cond pH (temp_diff) (oxy)		mmcond mmpH
best explained trait diversities (% of explanation above the average) Max Size diversity Leaf area diversity Flowering diversity	 48 74		 56 44 52

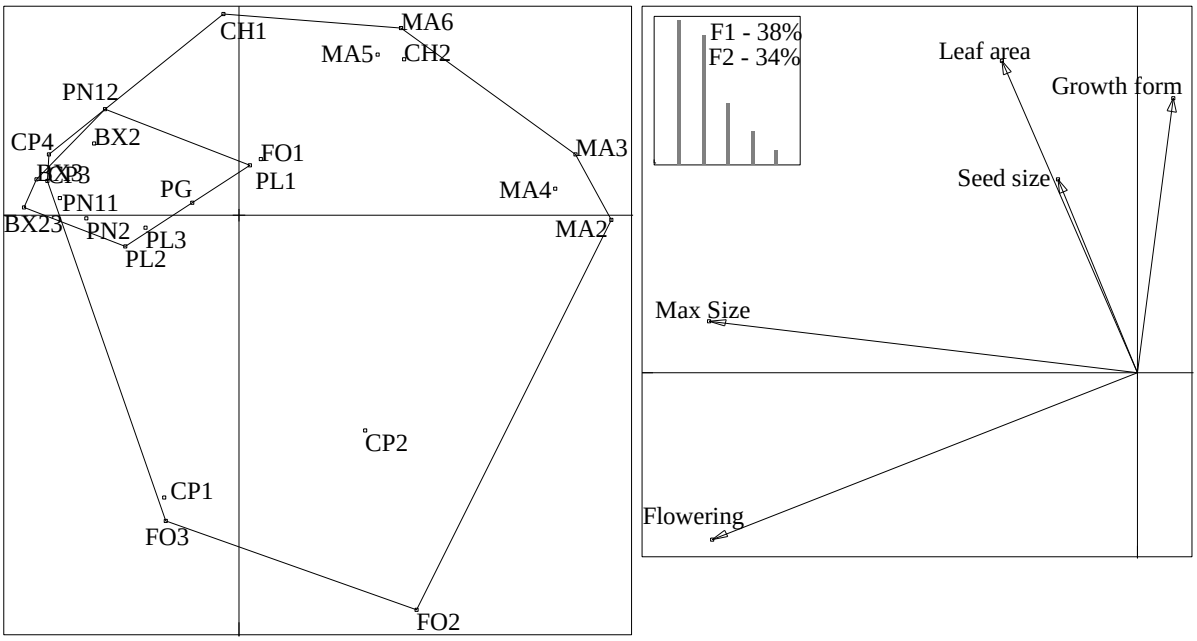


Figure 8.8. Principal Component Analysis of the trait diversity data. Left: F1 x F2 factorial plot of the sites grouped per sector. Right: F1 x F2 factorial plot of the five trait diversity indexes with the corresponding % of explained inertia.

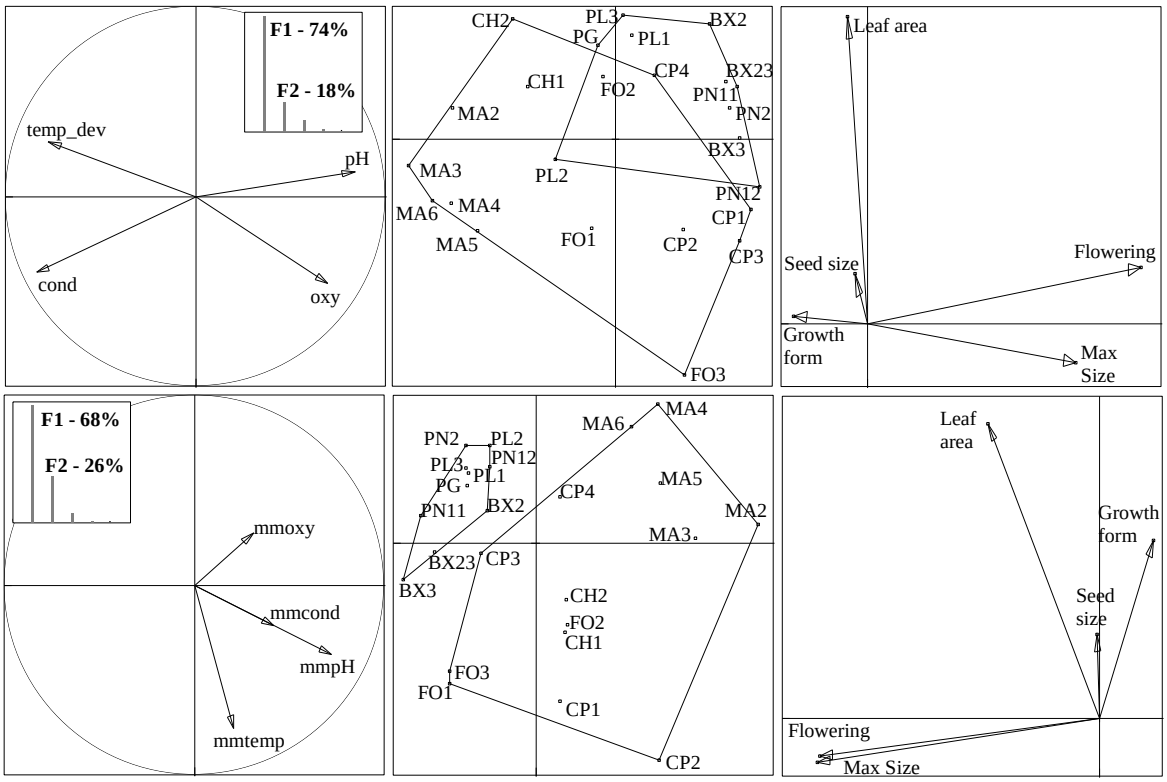


Figure 8.9. PCAIV of the trait diversita data and of the environmental explanatory variables (V1: first row, V3: second row). Left: F1 x F2 correlation circles of the explanatory variables with the corresponding % of explained inertia. Center: F1 x F2 factorial plots of the sites grouped per sector. Right: F1 x F2 factorial plots of the trait diversity indexes.

8.3.6 Explanation of univariate diversity indexes by environmental variables

Carried out with the same method as above, PCAIVs of the univariate diversity indexes were here comparable to multiple linear regressions and led to one-dimensional results. They are represented in Figures 8.10 and 8.11. The one-axis solution is here vertical and equivalent to the horizontal F1 axes of the preceding figures.

Species richness per site was very well explained by the three sets of explanatory variables (64.9 to 74.8% of explanation) and slightly better by the "variability" parametres (Table 8.6). Species richness correlated positively with depth and total phosphorus and negatively with conductivity and the variability of temperature and pH. With 44.8 to 59.7% explanation, both site uniqueness and the average trait diversity per site were also well explained, however less than species richness. The variability parametres (V3) provided the best explanation for all three diversity indexes.

Table 8.6 Results of the PCAIVs of three univariate diversity indexes (species richness, site uniqueness and average trait diversity) with three different sets of explanatory variables. The percentages of explanation are given (with the associated p value from the 10'000 permutations test in brackets), followed by the best explanatory variables (i.e. with factorial scores above the average) when the explanation is significant.

	Set of explanatory variables		
	V1	V2	V3
species richness	64.9 (0.0002) cond pH	71 (0) depth totP	74.8 (0) mmTemp mmpH
site uniqueness	44.8 (0.02) cond oxy	8.8 (0.60)	59.7 (0.0012) mmOxy mmpH
average diversity of 5 traits	28.9 (0.14)	20.2 (0.20)	49.2 (0.009) mmCond mmTemp mmpH

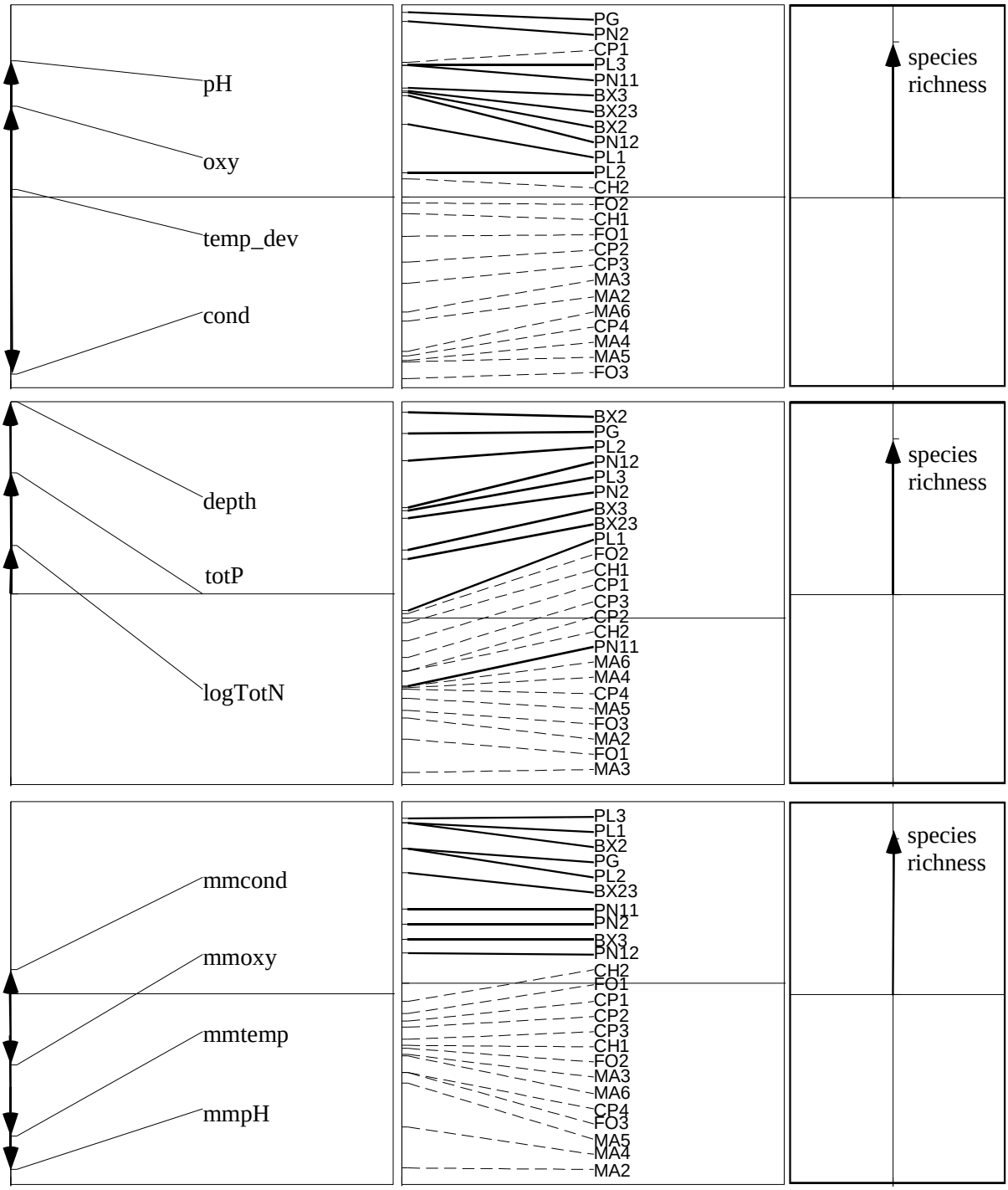


Figure 8.10. PCAIV of the species richness and of the environmental explanatory variables (V1: first row, V2: second row, V3: third row). Left: correlation of the explanatory variables with the unique ordination axis (vertical). Center: ordination of the sites along that axis. Right: direction of increase in species richness.

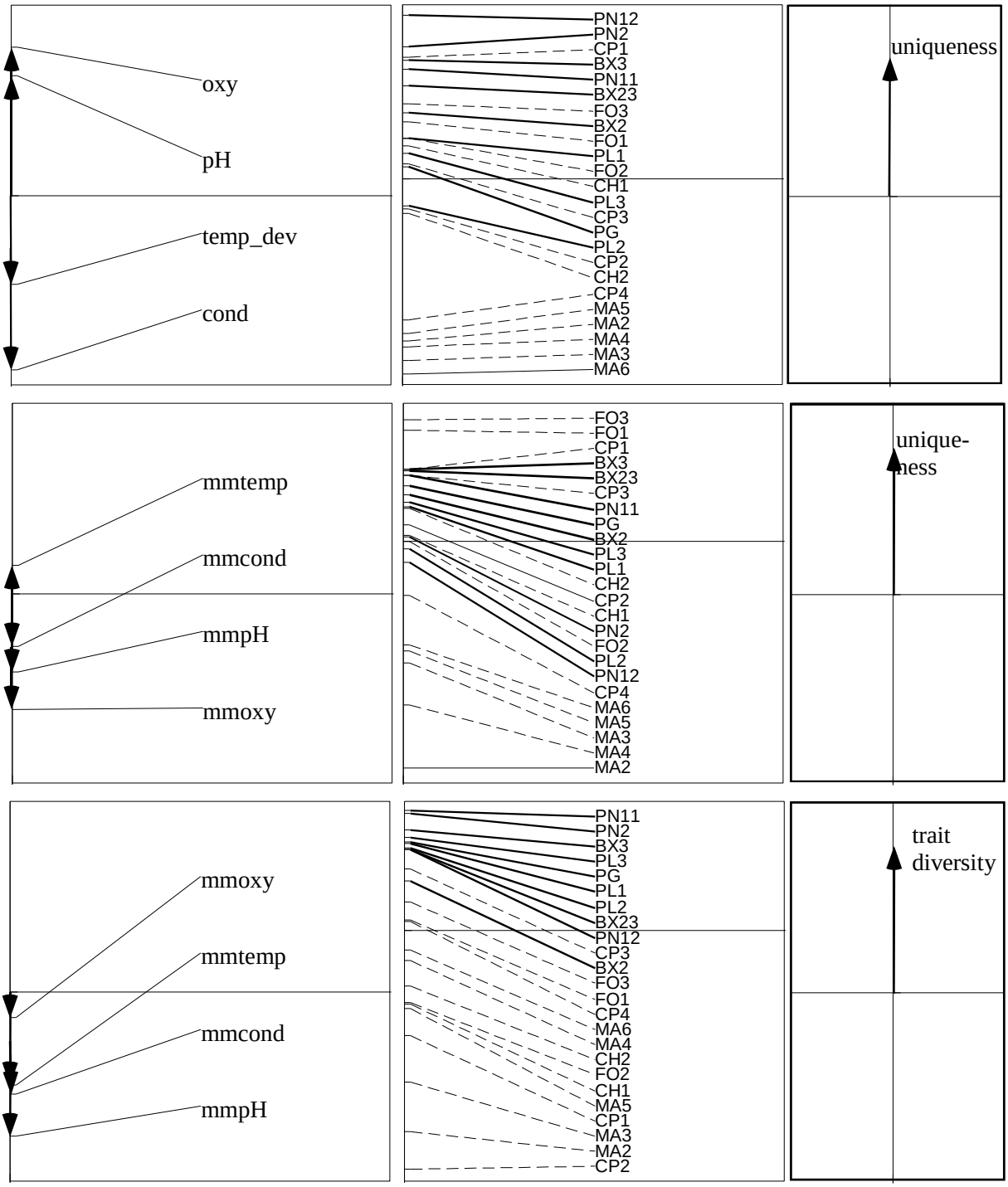


Figure 8.11. PCAIV of the site uniqueness and trait diversity per site, and of the environmental explanatory variables (V1: first row, V3: second and third row). Left: correlation of the explanatory variables with the unique ordination axis (vertical). Center: ordination of the sites along that axis. Right: direction of increase in species site uniqueness or trait diversity.

8.4 Discussion

8.4.1 Contrasts between sectors

One premise of this study was the melting of data from two types of alluvial water bodies: the Ain riverine sites and the Lake Neuchâtel-Grande-Cariçaie water bodies. The range of values obtained, both for the environmental and vegetation data, did prove that the two sectors built up a gradient of conditions that could be used to compare changes in species composition and traits. Especially, depth, conductivity, total phosphorus, species richness and trait diversity built up a wider range of conditions than one of the two sectors alone. The fact that the two sectors shared one third of their total species pool could also be regarded as a good basis for contrasting descriptions based upon species and upon trait compositions.

For all analyses, the Ain sites proved to be species richer and to have more diverse trait compositions than the Grande-Cariçaie ones. At the sector scale, however, they appeared far more homogeneous, both in terms of species assemblages and trait composition. These findings contrast with those of Antoine (2002) on freshwater gastropods in the same sites, who also found more diverse species assemblages between sites in the Grande-Cariçaie, but also an overall higher species richness. The general finding – common to aquatic plants and molluscs – that the between-site diversity in the lacustrine context is higher than in the fluvial one, could be related to the geomorphological and successional history of the Ain site where the former meanders all have a common natural origin and the approximate same age. Since their abandonnement by the river, they followed common patterns in succession and terrestrialization. This lead to relatively similar faunal and floral assemblages at the scale of the sector, a pattern already described by Castella *et al*. (1991) for aquatic macroinvertebrates. In the lacustrine Grande-Cariçaie, the set of pools comprises both natural and man-made water-bodies of varying ages that appeared more “individualistic” in the communities that settled and developed. They also lack the homogenizing impact of floods that occur in the riverine sector.

8.4.2 Levels of explanation of the vegetation metrics

Among the eighteen combinations (i.e. vegetation metric / explanatory variables) tested, five proved to be non-significant (Figure 8.12). All others yielded more than one quarter of explained information and reached three quarters (species richness / V3). Among the significant combinations, species richness was consistently the best-explained metric, while species composition (as described by Correspondence Analysis) was the least explained. Noticeably, trait composition was better explained than species composition by the V1 and V3 explanatory sets. This stands as a support for the promotion of species traits as a way to compare the function of communities across sites or geographic areas when differences in taxonomic pools may be regarded as a barrier (Dolédec *et al*., 1999; Statzner *et al*. 2001; Lamouroux *et al*., 2002; Díaz *et al*., 1998; etc.). When trait composition

was considered, differences between the two sectors did not stand out as the first level of differentiation, but sites from both sectors were mixed and displayed along gradients of trait category representation. The level of trait diversity, which has been rarely considered by authors, obtained levels of explanation that were comparable ton those of trait composition.

8.4.3 State vs variability explanatory variables

The three sets of explanatory variables provided insights into different aspects of the sites environmental conditions. V1 described the state of primary water physico-chemical variables and V3 the seasonal variability of the same. V2 could be seen as describing the nutrient status of the water plus the average depth of the water bodies. The initial variables differed in the way their average correlated with their variability (here Max – min intervals), only in V2 were average and variability well correlated. It is striking that the V3 (variability) set provided the overall best results in terms of statistical explanation (average 45%, Figure 8.12). Species richness, site uniqueness, average trait diversity and trait diversity were better explained by variability parametres than by their state counterparts. The "nutrient status" explanatory set (V2) proved the weakest of all, providing better statistical explanation for none of the vegetation metrics.

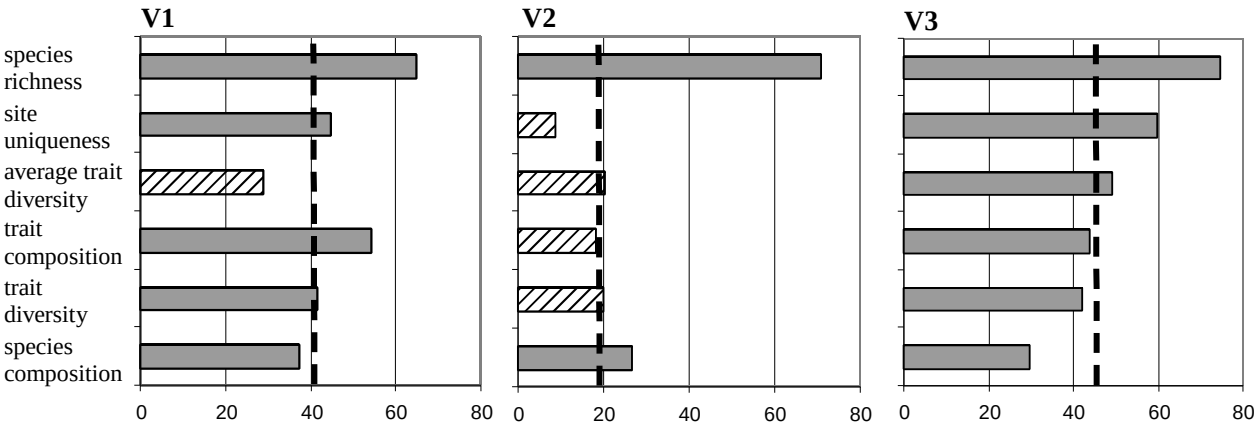


Figure 8.12. Percentages of explanation (derived from PCAIV) of different vegetation metrics by three sets of explanatory variables. V1: winter temperature difference, means for conductivity, pH, oxygen. V2: means for depth, total P and total N. V3: Max-min for the variables of V1. Hatched bars indicate non-significant values. Dashed vertical lines are the average level of explanation for the given explanatory set.

The main relationship described for plant traits and some of the diversity metrics along the environmental gradients are summarized in figure 8.13. At the scale of the gradients covered here, traits like the potential size and the flowering duration were most explained by the "state" gradients in water mineralization and winter temperature. Seed size and the type of vetetative perennation appeared mostly associated with seasonal variability gradients.

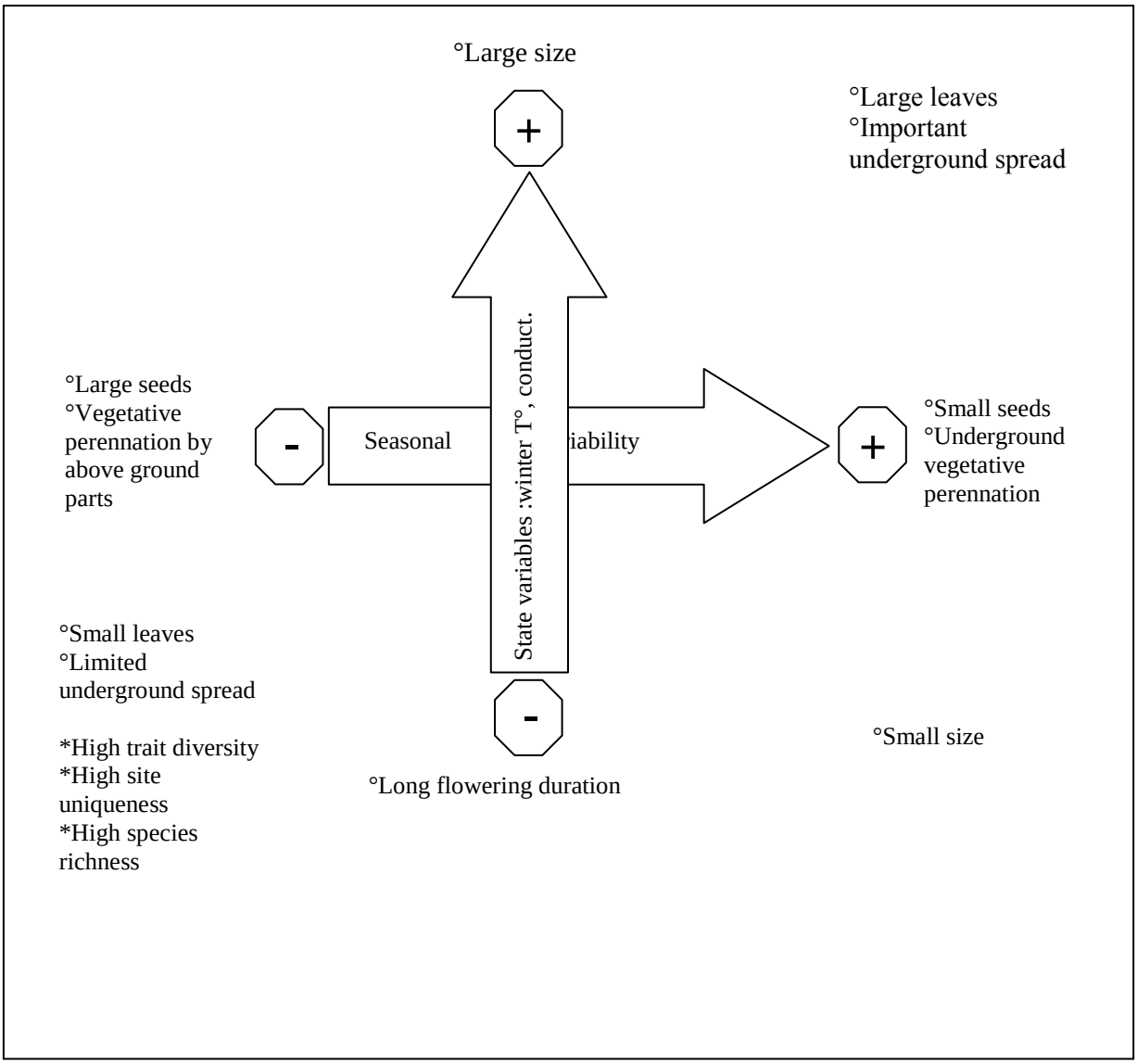


Figure 8.13. Summary of the main relationships described between plant traits and the environmental gradients.

The variables considered are certainly not the direct drivers of the vegetation composition and traits. They more certainly act as surrogates or tracers for ecosystems processes that are primary drivers. For example, water conductivity or temperature integrate water origin and therefore the degree of connection of the water body with groundwater or other surface waters, and hence sediment or propagule fluxes, but also potential disturbances by floods or wave action.

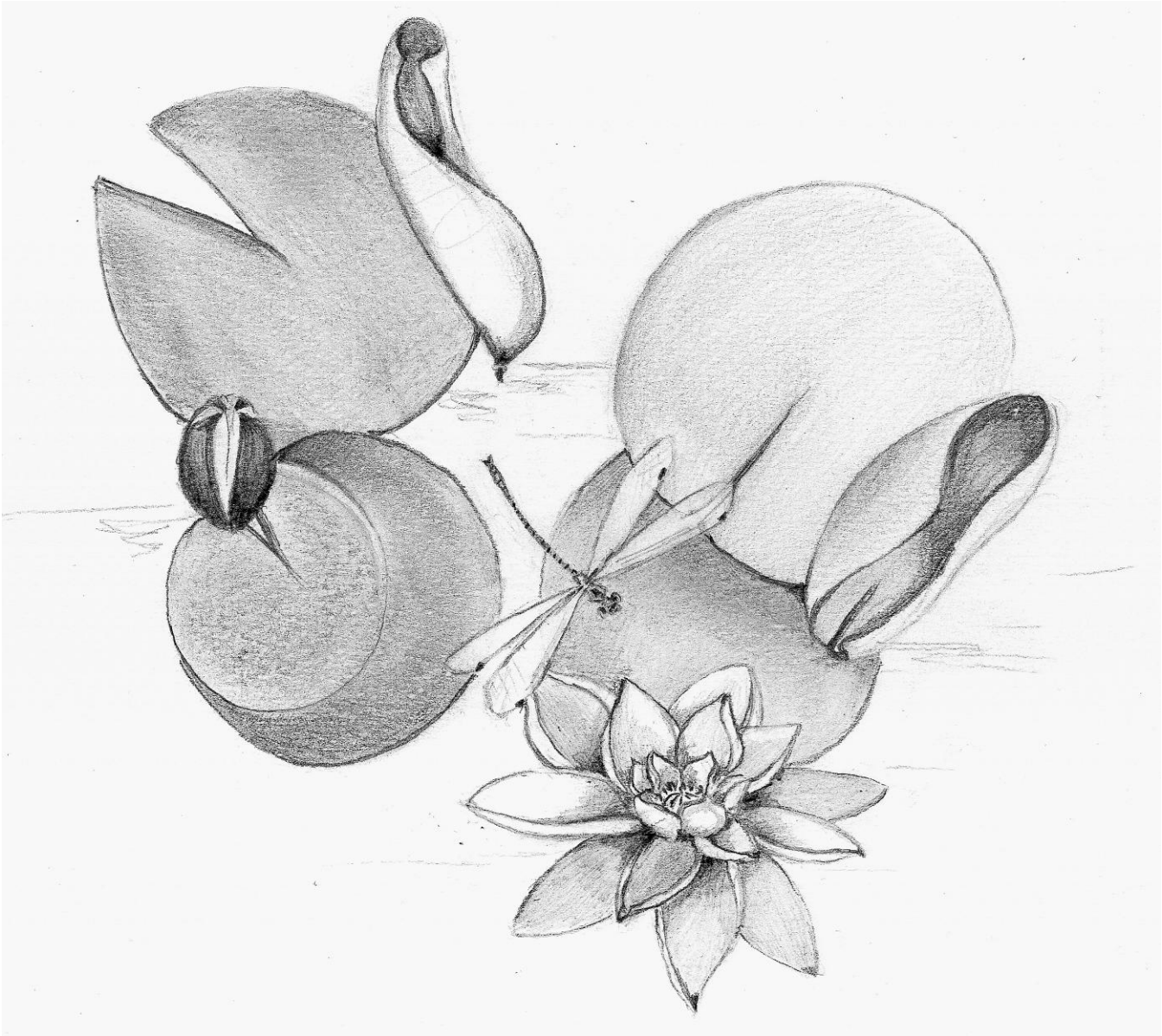
8.4.4 Methodological aspects

A uniform statistical method was used here to enable comparisons between combinations of explanatory and dependent variables. It also focused on a multivariate perspective, as sets of species, traits or trait diversity indexes were chosen as dependent variables. Principal Component Analysis on Instrumental variables (PCAIV) provided a framework – akin to multiple regression analyses – that

proved efficient. However, as evidenced by recent works (Dray *et al*., 2003, Nygaard and Ejrnaes, 2004), the question of the joined analysis of species distributions, species traits and site characteristics is a burgeoning field and open to many techniques and concepts. Implicit in our choice was the use of a two-table method by production of a site-by-trait matrix obtained by multiplication of the site-by-species and the trait-by-species matrices. There is obviously a current need for inter-comparison or calibration of methods that use different analytical techniques (Dolédec *et al*., 1996; Legendre *et al*., 1997; Nygaard and Ejrnaes, 2004) to compare implications they might have on the interpretation or validation of ecological results.

Chapitre 9

Discussion Générale



9.1 Mise en regard de deux types de zones alluviales, péri-lacustres et fluviales

9.1.1 Physico-chimie de l'eau et des sédiments et richesse floristique

Pour satisfaire des vocations économiques (production d'énergie, agriculture) et sociales (contrôle des crues), la deuxième correction des eaux du Jura, achevée dans le début des années 1970, a limité les fluctuations annuelles du niveau du lac de Neuchâtel à moins d'un mètre et provoqué un abaissement de la nappe phréatique (Buttler, 1987). Ces deux phénomènes ont conduit à une diminution de l'influence des processus allogènes, tels que les inondations, sur le fonctionnement de la Grande-Cariçaie et des étangs qu'elle comprend. Ils ont concouru à faire disparaître les processus naturels de rajeunissement ou de création de nouveaux milieux aquatiques. L'accélération de l'atterrissement qui en découle constitue une menace importante pour la diversité des habitats et donc pour la diversité biologique floristique et faunistique de cette zone alluviale péri-lacustre.

Les résultats des analyses physico-chimiques et sédimentologiques, obtenues au cours de deux années de suivi sur quinze étangs de la Grande-Cariçaie, ont mis en évidence l'existence d'une hétérogénéité spatiale importante des habitats aquatiques au sein de la région étudiée, comme en témoignent les différences significatives observées à la fois entre les quatre secteurs étudiés (Champ-Pittet, la Maladaire, Châbles et Font) et entre les étangs d'un même secteur pour tous les paramètres mesurés. Les paramètres sédimentaires ont par ailleurs montré une hétérogénéité spatiale au sein même des étangs.

L'hétérogénéité temporelle, quant à elle, s'exprime essentiellement par les variations saisonnières des paramètres mesurés. Pour plusieurs d'entre eux (p.ex. température, teneur en nitrates, teneur en ammoniaque, taux de sédimentation)., cette hétérogénéité temporelle est elle-même très hétérogène au sein de la région étudiée. En effet, les étangs alimentés par la nappe, comme MA4 et MA6, connaissent des fluctuations saisonnières de température moins marquées que les étangs dont l'alimentation en eau souterraine est plus limitée. Ces étangs bénéficient ainsi de conditions plus stables sur l'ensemble de l'année. D'autre part, la présence d'herbiers de végétation contribue fortement à limiter les variations journalières de température en été, comme en témoignent CP2, MA1 et FO3, peu colonisés par la végétation, qui connaissent de très fortes variations quotidiennes au contraire de CP4, MA2 et FO2, abondamment colonisés par les macrophytes aquatiques, qui connaissent des fluctuations de température beaucoup plus limitées (voir chapitre 5). La teneur en nitrates et en ammoniaque des eaux connaissent des fluctuations saisonnières particulièrement marquées dans les étangs influencés par le ruisseau. Pour les paramètres sédimentaires, et spécialement le taux de sédimentation, les variations saisonnières diminuent entre CP2, étang connecté au lac et CP4, plus éloigné de celui-ci (chapitre 5).

Les fluctuations inter-annuelles sont en revanche moins manifestes, notamment celles du niveau de l'eau des étangs. Si la régulation du lac explique en grande partie ces résultats, la période relativement courte au cours de laquelle les mesures ont été effectuées oblige à considérer ces données avec une certaine prudence.

L'importante hétérogénéité spatio-temporelle mesurée à différentes échelles de la région étudiée s'explique non seulement par la présence proche d'autres milieux aquatiques (tels que le lac, la nappe phréatique et des affluents extérieurs), mais aussi par la diversité des connexions existant entre les étangs et ces autres milieux. Le type et le degré de connexion hydrologique semblent en effet conditionner les processus physico-chimiques et sédimentologiques qui se déroulent dans les étangs, de même que l'amplitude de leurs fluctuations temporelles. Le rajeunissement par curage et la création de plans d'eau par l'homme sont utilisés pour remplacer l'action des forces allogènes naturelles manquantes et contribuent au maintien d'une grande diversité de stades successionnels caractérisés par autant de conditions environnementales différentes.

Les relevés phyto-sociologiques effectués dans les quinze étangs montrent que cette importante diversité des conditions de milieu génère une grande richesse spécifique d'hydrophytes à l'échelle de la région étudiée. Le nombre d'espèces recensées dans les étangs représente en effet 56% des espèces de la Grande-Cariçaie dans son ensemble et parmi elles se trouvent de nombreuses espèces menacées ou très menacées au niveau régional (52%) et national (30%) (Landolt, 1991). Une analyse des données botaniques révèle encore que cette richesse floristique est en moyenne faible à l'échelle des étangs eux-mêmes mais que le cortège spécifique (et celui des traits associés) varie entre étangs et entre secteurs en fonction du type et du degré de connexion hydrologique. Il résulte de cette situation que la diversité (en termes de richesse et de composition spécifiques) n'est maximale dès lors que l'ensemble du gradient de conditions environnementales (i.e. les quinze étangs) est considéré et qu'il est très difficile, dans ces conditions, d'identifier une «connectivité optimale». L'étude d'Antoine *et al*. (2004) révèle que les gastéropodes aquatiques échantillonnés dans les secteurs de Champ-Pittet et de la Maladaire représentent 70% des espèces de la Grande-Cariçaie et 36% des espèces de Suisse. Leur étude montre par ailleurs que la plus grande variabilité en termes de richesse spécifique, de composition spécifique et d'abondance s'observe à l'échelle des habitats (hélophytes, hydrophytes et substrat nu), avant de s'observer entre secteurs ou entre étangs.

Les résultats physico-chimiques, sédimentologiques et floristiques obtenus dans la Grande-Cariçaie corroborent en de nombreux points les résultats des recherches effectuées sur des secteurs de plaines alluviales fluviales encore soumis à une dynamique des crues, notamment dans le bas cours de l'Ain, le Haut-Rhône français ou le Danube. Les échelles spatiales au sein desquelles des différences significatives des paramètres environnementaux ont été identifiées dans la Grande-Cariçaie (secteurs,

étangs, intra-étangs) correspondent bien aux trois niveaux hiérarchiques identifiés par Amoros (2001) dans le contexte des zones alluviales fluviales: les secteurs fluviaux, les plans d'eau et les mésohabitats. Cet auteur définit le secteur fluvial comme une section de rivière (incluant la zone alluviale) caractérisée par un changement de pente et de largeur de la vallée par rapport aux sections adjacentes et qui comprend des plans d'eau de même origine géomorphologique. Ces plans d'eau représentent le niveau hiérarchique inférieur et diffèrent les uns des autres en fonction 1) de leur position dans la plaine alluviale (et donc de leur degré de connexion entre eux et avec le cours principal), 2) du type d'alimentation en eau (rivière, alimentation souterraine) et 3) de leur âge et stade successionnel, c'est-à-dire de l'époque à laquelle ils ont été abandonnés par le fleuve. Au sein même des plans d'eau, des patchs de conditions environnementales différentes représentent autant de «mésohabitats».

L'importante diversité des conditions environnementales observée dans les zones alluviales fluviales est le support reconnu d'une diversité biotique végétale (et animale) importante (Balocco-Castella, 1988; Bornette *et al*., 1994a; Bornette *et al*., 1996; Amoros et Bornette, 2002; Ward *et al*., 1999; Castella *et al*., 1991; Copp, 1989). Les richesses spécifiques dans les quinze étangs de la Grande-Cariçaie sont comparables à celles observées par Balocco-Castella (1988), Bornette *et al*. (1994b, 1996, 1998a et 1998b) pour des secteurs de la plaine alluviale du Haut-Rhône français et du bas cours de l'Ain. Les similitudes établies entre les deux types de systèmes au niveau de leur hétérogénéité spatio-temporelle sont ainsi révélées au travers de la richesse floristique. L'intérêt de ce constat réside dans le fait que cette richesse, quoique comparable à l'échelle de la région, se distribue différemment selon le fonctionnement et l'histoire de la zone alluviale considérée. Dans les secteurs étudiés de la plaine alluviale du Haut-Rhône français, la distribution des espèces s'apparente à celle observée dans la Grande-Cariçaie (faible richesse spécifique par étang et grande singularité des étangs les uns par rapport aux autres). L'histoire géomorphologique complexe de cette plaine alluviale (phases successives de méandrage et de tressage) a conduit à la création d'une grande diversité de plans d'eau, dont l'évolution est essentiellement dictée par des processus autogènes et les singularités se renforcent depuis l'endiguement du Rhône. Cette situation s'apparente à celle observée dans la Grande-Cariçaie où les plans d'eau d'origine variée (naturelle ou anthropique) sont eux aussi essentiellement régis par des processus autogènes. L'histoire géomorphologique moins complexe de la rivière Ain, de même que la force homogénéisatrice des crues qui parcourent encore régulièrement sa plaine alluviale, tout au moins certains de ses secteurs (Bornette *et al*., 2001), conduisent à une distribution de la richesse spécifique en moyenne élevée au sein des plans d'eau, qui diffèrent moins entre eux du point de vue taxonomique. L'identification d'un degré «optimal» de connectivité par rapport à la richesse de la végétation aquatique est également décrite comme difficile dans les plaines alluviales fluviales (Bornette *et al*., 1998a) puisque 1) la définition même de la connectivité est complexe, (Amoros et Bornette, 1999, 2002), et 2) que ses effets (sur la température, turbidité, teneur en matières nutritives et substrat, etc.) dépendent non seulement de sa nature (eau superficielle *vs*. eau souterraine; nappe

alluviale *vs*. nappe de pente), de son intensité (connexion permanente *vs*. temporaire), mais aussi des caractéristiques géomorphologiques du lit de la rivière (sinuosité élevée entraînant une faible capacité de décapage *vs*. sinuosité faible entraînant une forte capacité de décapage) (Bornette *et al*., 1998a). Les résultats de plusieurs études montrent par ailleurs que tous les groupes taxonomiques n'atteignent pas le maximum de leur richesse dans les mêmes types de milieux au sein de la zone alluviale (Tockner *et al*., 1998; Tockner *et al*., 1999; Amoros et Bornette, 2002). Ces observations confirment la difficulté, voire l'impossibilité, à identifier, à l'échelle de l'étang, un degré de connectivité optimal pour un groupe taxonomique donné, et à plus forte raison pour l'ensemble des groupes présents.

9.1.2 Traits et relations traits-environnement

La richesse spécifique est sans aucun doute le paramètre le plus fréquemment considéré dans les études scientifiques s'intéressant à la biodiversité des écosystèmes. Il a connu un regain d'intérêt important, témoignant d'une préoccupation croissante relative à l'érosion de la biodiversité et d'une conscience accrue des menaces qui pèsent sur elle (Ehrlich et Ehrlich, 1981; Groombridge, 1992; Lachavanne, 1997; Ward, 1998; Lévêque et Mounolou, 2001). La description de la biodiversité nécessite d'être accompagnée d'informations concernant la composition spécifique et l'abondance des espèces (Chapin *et al*., 2000; Mikola *et al*., 2002). L'étude des traits des espèces est également indispensable puisque les fonctions écologiques remplies au sein des écosystèmes, ainsi que la capacité de résistance et de résilience de ces derniers, sont déterminés par les traits des espèces, plus que par leur nombre (Lĕps *et al*., 1982; Macgillivray et al., 1995; Walker *et al*., 1999; Chapin *et al*., 2000; Díaz et Cabido, 2001). Keddy (2000) justifie d'ailleurs ses recherches sur les groupes fonctionnels par la nécessité de permettre aux gestionnaires de les associer à des fonctions remplies par les espèces au sein des écosystèmes, afin de permettre de conserver ou de restaurer au sein des communautés la redondance spécifique nécessaire aux capacités de résistance et de résilience des milieux.

Dans cette étude, les traits des espèces d'hydrophytes ont été codés au sein d'une base de données et utilisés pour identifier des relations entre ces traits et les conditions environnementales afin de tester, dans le contexte d'une plaine alluviale péri-lacustre les modèles et les prédictions établies à partir d'autres types d'écosystèmes aquatiques. Malgré l'absence de forces allogènes naturelles majeures, les analyses statistiques effectuées sur les étangs de la Grande-Cariçaie ont révélé la présence d'un gradient de conditions environnementales (double axe de productivité/variabilité temporelle) permettant d'expliquer de manière substantielle et significative la variation des traits et des catégories de traits entre les plans d'eau. Le pourcentage d'explication est très élevé par rapport à celui d'autres études (p.ex. Oertli *et al*., 2000; Mérigoux *et al*., 2001; Antoine, 2002). Il est à considérer avec réserve, dans la mesure où le rapport entre le nombre de plans d'eau étudiés (14) et celui des variables

explicatives prises en considération (5) est en limite d'acceptabilité. En effet, lorsque les groupes de variables sont considérés séparément, le pourcentage d'explication diminue, mais les relations restent toutefois significatives. L'intégration dans les analyses des dix sites étudiés dans la plaine alluviale de l'Ain apportent cependant une confirmation des résultats obtenus sur les quinze étangs de la Grande-Cariçaie considérés seuls, puisque les analyses ordonnent les sites de manière similaire. Les étangs les plus stables, isolés du lac et caractérisés par un substrat riche en matière organique et des eaux chargées en substances nutritives (MA4, MA5 et MA6), sont associés à des traits typiquement «compétitifs» (sensu Grime, 1979): taille importante de la plante, feuilles larges, entières et flottantes, capacité importante d'extension par un rhizome, floraison annuelle et production d'un petit nombre de graines de grande taille. Les étangs caractérisés par une variabilité saisonnière plus importante mais toujours riches en matières nutritives (CP3 et CP4) hébergent des espèces flottantes, non enracinées telles que les *Lemna* et les Utriculaires, très peu représentées dans les étangs plus stables. Les étangs exposés à une variabilité saisonnière intermédiaire et des conditions trophiques plus pauvres (CH1, CH2, FO1 et FO2) sont colonisés par des espèces plus «stress-tolérantes», enracinées, de taille intermédiaire, aux feuilles plus fines ou disséquées, de faible surface et parfois persistantes, produisant une grande quantité de graines et se dispersant fréquemment par des fragments de tiges ou de structures spécialisées.

Les résultats des analyses montrent également que plusieurs cortèges de traits correspondant à des stratégies différentes sont susceptibles d'être observés dans un même ensemble de conditions environnementales. Dans les étangs CP3 et CP4 par exemple, on observe la présence à la fois d'espèces enracinées à feuilles entières, flottantes et de grande taille, et d'espèces non enracinées à feuilles entières ou disséquées, flottantes et de petites taille.

Ces résultats corroborent ainsi dans une large mesure les relations traits-environnement prédites et observées par Grime (1974, 1977, 1979) en milieu terrestre, par Bornette *et al*. (1994a), Barrat-Segretain *et al*. (1999) et Barrat-Segretain (2001) en milieu fluvial et par Willby *et al*. (2000) dans le cadre d'une étude intégrant une grande diversité de milieux aquatiques. Il semblerait donc que certaines de ces relations soient généralisables au-delà du type de milieu étudié (terrestre *vs*. aquatique; courant *vs*. stagnant, etc). La co-existence de traits différents au sein d'un même milieu a également été constatée par plusieurs auteurs. Bornette *et al*. (1994a) notamment, décrivent la présence dans des milieux productifs, à la fois d'espèces enracinées à grandes feuilles entières (*Nymphea alba* L.) et d'espèces non-enracinées à feuilles minuscules (*Lemna* sp), toutes deux pouvant concourir recouvrir la surface d'un plan d'eau. Dans le cadre d'une étude sur les communautés lacustres de macrophytes, Mc Creary (1991) observe également la co-existence de trois stratégies et donc de trois réponses à un même environnement. En outre, Southwood (1988) n'écrit-il pas que «the templet constraints the range of life-history strategies but it does not impose uniformity" ? Pour certains auteurs, la diversité

des traits dans un écosystème constitue même la garantie d'une meilleure résilience face à une perturbation (Yachi et Loreau, 1999; Di Castri et Younès, 1990; mais voir Loreau et Behera, 1999).

L'identification de relations traits-environnement dans le cadre de cette étude et leur concordance avec des relations déjà observées est positive, mais comme le soulignent d'autres auteurs, ces relations demeurent relativement générales et souvent équivoques. Willby *et al*. (2000) associent la difficulté de mettre en évidence des relations traits-environnement pertinentes à la plasticité phénotypique importante développée par de nombreuses espèces aquatiques. Une espèce est en effet capable de modifier sa morphologie et sa physiologie en réponse à des conditions de milieu différentes (Schlichting, 1986). Plusieurs auteurs témoignent de ce phénomène comme Greulich *et al*. (2001) lors d'expériences de transplantation effectuées avec *Luronium natans* L.; Pilon et Santamaría (2002) lors d'expériences de transplantations avec *Potamogeton pectinatus* L.; Müller (1995) au cours d'une étude sur la distribution de trois espèces de *Potamogetons* dans le Léman (Suisse); Barrat-Segretain (2001) dans l'étude sur l'allocation de la biomasse chez *Berula erecta* (Hudson) Coville, *Groenlandia densa* (L.) Fourreau et *Myriophyllum spicatum* L. le long d'un gradient de perturbation par les crues.
Conjointement à l'approche globale adoptée dans le présent travail, plusieurs recherches ont été menées sur la plasticité des macrophytes aquatiques au sein de la Grande-Cariçaie, dans les étangs des secteurs de Champ-Pittet, la Maladaire et Font. Le travail de Dulac (1998), sur les populations de *Nymphea alba* L. des secteurs de Champ-Pittet et de la Maladaire révèle l'existence de différences significatives entre étangs pour une majorité de traits (mesurés in situ) de l'appareil végétatif et reproductif de cette espèce. Ainsi, la seule présence de *Nymphea alba* L. n'apporte aucune information sur les spécificités physico-chimiques et sédimentologiques des étangs qu'elle colonise tous. En revanche, la plasticité morphologique et phénologique considérable dont elle fait preuve témoigne de ces différences environnementales et de la capacité de cette espèce à répondre de manière très fine à des conditions de milieu variables. A une échelle spatiale plus limitée encore, Fontaine (2001) réussit à montrer que les herbiers de *Myriophyllum spicatum* L. d'un même plan d'eau (FO2-FO3) présentent des différences significatives au niveau de certains traits morphométriques le long d'un gradient de colonisation. L'auteur montre également qu'aucune différence significative n'existe en revanche pour les traits impliquant la biomasse de la plante.

La plasticité des espèces aquatiques soulève non seulement le problème de l'identification de relations traits-environnement pertinentes, de l'application de la terminologie des stratégies C-S-R de Grime (Sabbatini et Murphy, 1996; Willby *et al*., 2000; Barrat-Segretain, 2001), mais aussi celui de l'utilisation des bases de données de traits telles qu'elles sont de plus en plus fréquemment proposées et utilisées dans la littérature. En effet, le codage des traits s'effectue généralement à partir d'informations bibliographiques qui intègrent toute les potentialités des espèces pour une région ou un pays donné. L'intégration d'espèces à plasticité élevée conduit à une diminution du pouvoir

discriminant et à des discordances avec les situations réelles observées dans un site donné. Le problème se pose plus particulièrement encore lorsque l'on cherche à mettre en évidence des relations traits-milieux le long d'un gradient environnemental peu marqué.

Face à la difficulté d'expliquer de manière substantielle les cortèges de traits par les conditions environnementales, Mérigoux *et al*. (2001), dans une étude conduite sur des populations de poissons, suggèrent de distinguer au cours des analyses statistiques les phases juvéniles et adultes. Dans le cas de la végétation, plusieurs auteurs constatent également une absence de corrélation entre les cortèges de traits relatifs à la phase juvénile et ceux relatifs à la phase adulte (Shipley *et al*., 1989; McIntyre *et al*., 1995; Díaz et Cabido, 1997; Grime *et al*., 1997). Ce constat justifierait la considération des deux phases de façon indépendante (voir Lavorel *et al*., 1999). Harper (1977) note par ailleurs que les conditions environnementales nécessaires aux plantes «adultes» ne correspondent pas forcément à celles nécessaires à l'établissement des graines, dont les exigences ne se situent pas à la même échelle. De la même manière, certains auteurs préconisent d'effectuer les analyses en considérant séparément différent groupes fonctionnels d'espèces (McIntyre *et al*., 1999b; Yachi et Loreau, 1999; Warren et al., 2002), ou en distinguant les monocotylédones des dicotylédones puisque selon Grime *et al*. (1997) et Willby *et al*. (2000) beaucoup des traits essentiels montrent un fort biais lié à la phylogénie

9.2 Implication des résultats pour la gestion des zones humides

Afin d'augmenter l'hétérogénéité spatio-temporelle à l'échelle du paysage et ainsi la diversité des espèces et des traits, Amoros et Roux (1988), Bornette *et al*. (1998b), Amoros et Bornette (2002), Ward (1998), Tockner *et al*. (1998), Tockner *et al*. (1999), Buijse *et al*. (2002) ou encore Keddy (2000) préconisent la conservation et/ou la réhabilitation de la diversité des types et des degrés de connexions entre le cours principal du fleuve et les éléments de sa plaine alluviale, par la réhabilitation de la dynamique fluviale (sensu Henry et Amoros, 1995). Cette vision implique que soit dépassée la notion de la protection des espèces, trop limitée, au profit de celle des habitats, et que la réhabilitation soit effectuée dans la perspective de leur *durabilité*. Dans un système qui est normalement caractérisé par un régime de perturbations, Amoros (2001) suggère d'agir à la fois à l'échelle du secteur fluvial, au sein duquel la réhabilitation des crues pourra augmenter la diversité des plans d'eau et à l'échelle des plans d'eau eux-mêmes, au sein desquels la réhabilitation de la dynamique fluviale pourra augmenter la diversité des mésohabitats. Ces derniers contribuent en effet largement à l'explication de la composition des communautés biotiques (Frissell *et al*., 1986) et à augmenter la biodiversité (Castella *et al*., 1991). Hillbricht-Ilkowska (1999) constate également que la présence de «lacs fluviaux» le long du cours principal augmente la diversité des conditions environnementales non seulement à l'échelle du système dans son ensemble, mais aussi à des échelles spatiales plus fines, par la création de zones écotonales (delta, exutoire, etc.).

Le même raisonnement peut être tenu avec les zones alluviales péri-lacustres, elles aussi caractérisées par des relations multiples et complexes entre les différents éléments qui les composent. La réhabilitation de la dynamique des fluctuations du niveau du lac semble s'imposer comme seule solution durable dans le maintien ou la restauration de l'hétérogénéité des conditions environnementales aux échelles de la région, des secteurs et des étangs eux-mêmes. Comme dans le cas de beaucoup d'autres lacs, elle n'est toutefois pas envisageable. La conservation de la diversité des conditions environnementales doit en conséquence être (com-)pensée différemment. La notion de «durabilité» prend tout son sens dans le cadre de la gestion de la Grande-Cariçaie, puisque la diversité qui y est observée (habitats, végétation et faune aquatiques) dépend paradoxalement, dans une large mesure, d'actions humaines de restauration ou de création de nouveaux plans d'eau, d'intensives campagnes de faucardage et de débroussaillage des roselières. Un rapport récent sur l'effet de la politique de fauche pratiquée depuis vingt ans dans la Grande-Cariçaie montre néanmoins que cette mesure de gestion ne suffit pas à stopper l'avancement de la forêt sur le marais non-boisé (Le Nédic, 2002). Par ailleurs, les relevés de végétation aquatique effectués dans le présent travail, ainsi que les prélèvements de gastéropodes aquatiques effectués par Antoine *et al*. (2004), révèlent que la richesse spécifique de ces deux groupes est nettement moins élevée dans les étangs recreusés (MA) que dans les étangs naturels (CP). Il serait cependant précipité de conclure que richesse spécifique et naturalité sont directement liés. En effet, d'autres paramètres que celui de la naturalité, telle que la surface du plan d'eau et son âge, peuvent également avoir une influence sur la richesse spécifique (voir p.ex. Oertli *et al*., 2002). Les étangs naturels de Champ-Pittet sont en effet à la fois plus grands et plus anciens que ceux de la Maladaire, recreusés pour les plus jeunes d'entre eux, 5 à 6 ans avant l'étude. La complexité de la situation est illustrée par l'étang CH1, recreusé 6 ans avant l'étude, qui fait partie des étangs abritant la plus grande richesse d'hydrophytes alors que l'étang MA3, considéré comme naturel (plus de 100 ans d'âge) fait partie, comme les autres étangs du secteur MA, des étangs les plus pauvres en espèces de macrophytes aquatiques. La relative pauvreté des étangs de la Maladaire est toutefois compensée par le fait que leurs cortèges spécifiques diffèrent de ceux de Champ-Pittet (pour les macrophytes et les gastéropodes aquatiques). A l'échelle du secteur ou de la région la richesse spécifique s'en trouve donc augmentée et diversifiée.

Buttler (1987) souligne également l'ambiguïté qui accompagne parfois la volonté de retour à des conditions qui prévalaient avant la régulation du système par l'homme. En conclusion de son travail sur les marais non-boisés de la rive sud du Lac de Neuchâtel, il note en effet «qu'un retour aux conditions prévalant avant la deuxième Correction des Eaux du Jura ne serait pas souhaitable, car cela pourrait engendrer une évolution régressive et une disparition temporaire de certains milieux, ce qui irait à l'encontre des objectifs fixés». Les projets de renaturation dans certains secteurs du Rhin ont conduit à une situation similaire. Les vestiges de la plaine alluviale étant devenus le refuge non seulement des espèces fluviales, mais aussi d'espèces des milieux humides chassées par l'intensification de l'agriculture, la réhabilitation de la dynamique fluviale peut menacer de disparition

toutes les espèces non-alluviales qui ont trouvé là leur dernier refuge. Ces deux exemples illustrent les difficultés qui caractérisent les projets de renaturation, non seulement d'un simple point de vue technique, mais aussi et peut-être surtout éthique.

Malgré les difficultés de mise en œuvre et le succès parfois limité des mesures pratiquées, le travail des faucheuses et pelleteuses semble encore très souvent la seule alternative. Comme le disent Buijse *et al*. (2002) pour les zones alluviales fluviales, «restoration ecology is still in its infancy» et les premières expériences de renaturation sont encore trop récentes pour nous permettre d'en évaluer le succès à long terme (Henry et Amoros, 1995, 1996; Henry *et al*., 2002) et nous donner un recul suffisant. Ceci semble encore plus juste pour les zones alluviales péri-lacustres.

A l'heure actuelle, les législations de nombreux pays ne prennent en considération les zones humides qu'au delà d'une superficie minimale (Etats-Unis, p.ex.), alors que dans d'autres, la surface ne constitue pas un critère de sélection. Il apparaît toutefois clairement que les zones de petites tailles (0.2 à 0.4 ha pour Semlitsch et Bodie, 1998) ne sont souvent ni protégées, ni même inventoriées, alors que leur importance est soulignée par plusieurs auteurs (Semlitsch et Bodie, 1998; Gibbs, 2000). Au sein d'une région, leur nombre et la distance qui les sépare affectent en effet la dispersion des propagules et celle des animaux (Bedford, 1999), par ailleurs souvent largement sur-estimées (Harper, 1977; Strykstra *et al*., 2002). D'autre part, la taille des milieux influence aussi la probabilité de colonisation et d'extinction des espèces (Gee *et al*., 1997), cette dernière étant d'autant plus élevée que les milieux sont petits. Ainsi, outre les espèces rares que les zones humides de taille réduite peuvent abriter, elles assurent surtout, quand leur densité dans le paysage est suffisante, une connectivité satisfaisante et le maintien de la dynamique des populations.

Pour la catégorie de zones humides que représentent les étangs, Oertli *et al*. (2002) constatent également leur importance et il est vraisemblable que toutes les considérations vues ci-dessus s'appliquent aussi bien aux zones humides de manières générale qu'aux petits plans d'eau en particulier. Dans le contexte de la restauration, la création de plans d'eau de petite taille constitue en outre un avantage financier. Les étapes d'extraction et d'évacuation du matériel sont en effet les plus onéreuses. Dans la Grande-Cariçaie par exemple, le décapage ou la création de nouvelles surfaces d'eau libres semblent constituer la solution la plus efficace face à l'atterrissement (Le Nédic, 2002) mais à l'heure actuelle, ces mesures ne concernent que des surfaces très réduites (proportionnellement à la surface totale du bas-marais non boisé) en raison des coûts élevés qu'elles occasionnent.

En Angleterre, Davies *et al*. (2004) constatent que la création de nouveaux étangs est une activité très «populaire» comme mesure d'amélioration de la qualité de l'environnement et de conservation des petits plans d'eau. Ils déplorent en revanche le fait que les étangs creusés atteignent rarement le maximum de leur potentiel écologique parce que les emplacements choisis ne répondent pas à trois critères de base: absence de sources de pollution, proximité d'autres zones humides et bonne structure physique. En ce sens, mais cela peut paraître évident, la Grande-Cariçaie est un site favorable à la création de nouveaux plans d'eau, puiqu'elle répond, de manière générale, aux deux premiers de ces

critères. La richesse moyenne par étang des secteurs de Champ-pittet et de Châbles-Perron est en effet comparable à celles des sites étudiés dans la plaine alluviale de l'Ain par Balocco-Castella (1988), reconnus comme étant très diversifiés. Elle est également supérieure aux richesses mesurées dans la plaine alluviale du Rhône (Balocco-Castella, 1988) ou dans des étangs non alluviaux (Oertli *et al*., 2000; voir chapitre 6). Dans le référentiel de qualité des étangs élaboré par *Davies et al*. (2004), allant de 1 (low pond quality) à 4 (very high pond quality), ces deux secteurs correspondent à la catégorie 3 (high pond quality; entre cinq et dix espèces de macrophytes aquatiques). Les richesses moyennes par étang de la Maladaire sont en revanche largement en dessous des valeurs observées par Balocco-Castella (1988), Bornette *et al*. (1998a), Oertli *et al*. (2000), etc. (voir chapitre 6) et correspondent aux notes 1 (low-) ou 2 (moderate pond quality) (Davies *et al*., 2004). L'exemple de MA1 illustre par ailleurs l'influence néfaste de la pollution sur la faune et la flore aquatiques, puisqu'aucune espèces de macrophyte ni de gastéropodes n'y ont été observées au cours de l'étude. Si la Grande-Cariçaie semble constituer un site favorable dans son ensemble, il apparaît donc que certains secteurs sont plus riches en espèces que d'autres (CP et CH vs MA). L'emplacement de la création d'un futur étang dépend donc de l'objectif poursuivi. Si celui-ci est d'atteindre une richesse spécifique par étang importante, les secteurs de CP et CH seront plus adaptés que ceux de Font et de la Maladaire. Si la perspective est plus globale et cherche à favoriser une diversité maximale de conditions environnementales à l'échelle de la toute la Grande-Cariçaie, la considération de tous les secteurs, même a priori plus pauvres est souhaitable.

9.3 Perspectives

Dans le double contexte d'un nombre limité d'étangs (15) et d'un gradient de conditions environnementales restreint, la mise en évidence de relations entre les traits des macrophytes aquatiques et le milieu constitue un résultat intéressant, qui invite à la poursuite des recherches. L'intégration de nouveaux plans d'eau paraît indispensable pour permettre d'étendre la gamme des conditions environnementales considérées, en même temps que multiplier les réplicats. En termes statistiques la fiabilité et la pertinence des relations mises en évidence s'en trouveraient accrues par un rapport plus équilibré entre le nombre de sites étudiés et celui des variables environnementales retenues.

Si des types et des degrés divers de connexions hydrologiques entre lac, étangs et nappe phréatique ont été mis en évidence, la mesure de l'influence directe du lac sur les étangs, et de ses conséquences sur les communautés biotiques, est restée en revanche largement inexplorée. Comme le souligne Henry *et al*. (1994) pour les zones alluviales fluviales, la fréquence de décapage ou de sédimentation dans un plan d'eau ne dépend pas seulement de la distance qui le sépare du cours principal de la rivière, mais aussi de la géomorphologie locale et de la présence d'aménagements des rives ou/et de forêts

alluviales. Il en va de même dans les zones alluviales péri-lacustres, où l'influence effective du lac sur les étangs dépend non seulement de la distance qui les sépare du lac, mais aussi de la présence d'une dune littorale, de roselières plus ou moins développées (au sens de leur densité ou/et de leur étendue) ou encore de fossés ou d'ornières. A ce jour, le placement d'enregistreurs en continu du niveau de l'eau ou des valeurs minimales et maximales permettrait d'avoir une idée plus précise de la variation des niveaux de l'eau dans les étangs, mais cette technologie coûteuse ne permettrait toujours pas de mesurer les impacts des perturbations en termes de décapage et de sédimentation dans les milieux. Pour remédier à l'impossibilité d'être présent dans les sites au cours des crues et d'en observer directement les effets, il demeure la nécessité d'améliorer les pièges à sédiments actuels.

La durée de l'étude et la fréquence à laquelle les mesures ont été effectuées ont permis de percevoir des variations temporelles essentiellement aux échelles saisonnières et quotidiennes (pour la température), de même qu'elles ont permis de constater que ces variations temporelles diffèrent entre les étangs. Ces observations renvoient à la question plus générale des multiples échelles de perception des variations temporelles et de leur compatibilité avec la durée moyenne des projets de recherche. Le financement des études en écologie excède rarement une période de trois ou quatre années. Cette durée ne permet pas de distinguer les effets, sur les communautés biotiques, des différents processus en cours simultanément dans les écosystèmes, à savoir les processus de succession à l'échelle des décennies ou des siècles, les fluctuations inter-annuelles, saisonnières et quotidiennes, sur lesquelles des évènements stochastiques peuvent de plus venir se superposer. La durée de ces projets est d'autant plus contraignante que les cycles de vie des organismes étudiés sont longs. Un suivi à long terme serait souhaitable pour permettre d'observer et de comprendre l'évolution des relations entre les organismes et les conditions de milieux.

La littérature témoigne, dans les domaines de l'écologie terrestre et aquatique, d'un essor considérable dans la constitution de bases de données de traits, dans leurs améliorations et dans leurs utilisations. Il résulte de cette activité un foisonnement de méthodes d'analyses statistiques destinées à mettre en relation les traits et les paramètres environnementaux sous des formes non moins diversifiées. Il en résulte également une difficulté croissante à comparer les données entre les différentes études, alors même que l'approche fonctionnelle des communautés végétales par les traits devait les simplifier.
Devant cette diversité de situations certains auteurs, parmi lesquels Weiher *et al*. (1999), McIntyre *et al*. (1999b) et Nygaard et Ejrnaes (2004) ont cherché à comparer, synthétiser ou fédérer ces recherches. Une étape supplémentaire dans l'homogénéisation des études traits-environnement consisterait à former un groupe de travail, à l'image de ce qui a été fait pour le genre *Vertigo* (gastéropode terrestres de zones humides). En effet, les spécialistes de ce groupe taxonomique ont pris l'initiative de se réunir, dans la perpective d'identifier avec précision les catégories d'informations biologiques et écologiques des espèces du genre, et d'y associer le corpus de références

bibliographiques à la base de ces connaissances (Cameron *et al*., 2003). La deuxième étape consiste ensuite à coder de façon numérique les informations biologiques et écologiques contenues dans ces «species accounts». Il est vraisemblable qu'à ce jour les bases de données sur le groupe des diptères Syrphidae (Speight *et al*., 2000) et des mollusques (Falkner *et al*.,2001) soient les seules à bénéficier d'une connaissance aussi structurée, alors que cette démarche devrait sous-tendre toute constitution d'une base de donnée codée, puisqu'elle en constitue le fondement. Speight *et al*. (2000) et Falkner *et al*. (2001), insistent par ailleurs sur l'importance de telles de données codées, puiqu'elles synthétisent une quantité très importante de connaissances souvent connues des spécialistes seuls, et la rendent accessible à d'autres groupes de personnes. Une telle démarche bénéficierait également aux recherches effectuées dans le cadre de la végétation aquatique, puisqu'elle y apporterait une base de connaissances solide et un cadre de codification homogène.

Les recherches sur les relations traits-milieu pourraient également bénéficier d'une prise en compte indépendante i) des cortèges de traits relatifs à la phase juvénile et ceux relatifs à la phase adulte (Shipley *et al*., 1989; McIntyre *et al*., 1995; Díaz et Cabido, 1997; Grime *et al*., 1997), ii) des différentes formes de croissance ou les différents groupes fonctionnels (McIntyre *et al*., 1999b; Yachi et Loreau, 1999; Warren et al., 2002) et iii) des mono- et des dicotylédones.

Le second point évoqué ci-dessus consisterait à encourager le type d'études effectué par Dulac (1998) et Fontaine (2001) dans la Grande-Cariçaie, ainsi que par Barrat-Segretain (2001), Barrat-Segretain et Bornette (2000), Greulich et Bornette (1999) et Greulich *et al*. (2000, 2001) dans les plaines alluviales du Rhône et de l'Ain. Ces recherches fournissent en effet des résultats plus précis sur les relations entre des traits mesurés in situ ou en conditions expérimentales et les conditions de milieu. Il serait même envisageable, pour rejoindre les besoins d'une certaine homogénéisation i) de choisir un genre ou une famille, ii) d'identifer un ensemble de traits pertinents et facilement mesurables sur les plantes, iii) de standardiser les mesures de terrain pour les traits et des conditions de milieu et iv) de mener une campagne simultanée dans une variété de milieux aquatiques répartis sur une surface géographique importante (pays ou plusieurs pays). Les données acquises lors d'une telle entreprise permettraient non seulement d'apporter des informations sur l'écologie et la biologie des espèces, mais aussi d'alimenter un nouveau type de base de données, focalisée sur la plasticité des traits en relation avec le milieu plutôt que sur la représentation des traits en fonction des conditions environnementales. La couverture géographique importante permettrait également d'identifier les échelles spatiales auxquelles les différents traits sont les plus pertinents. Lavorel *et al*. (1999) notent en effet que le trait «life-form», lié à la réponse des plantes aux pertubations à l'échelle de la région, n'est plus significatif à l'échelle des communautés.

Enfin, l'aquisition homogène d'une telle quantité de données constitue le matériel idéal pour l'exploration et la comparaison de différentes mises en forme de l'information (absence de

pondération des traits, pondération des traits par le fréquence des espèces, pondération des traits par le recouvrement des espèces; tableau traits x espèces, tableau traits x sites) ainsi que de différentes analyses statistiques (méthodes multivariées, méthodes univariées).

La mesure de la plasticité des espèces in situ au travers d'un gradient de conditions environnementales constituerait non seulement une manière de mieux préciser les rôles respectifs des mécanismes locaux et régionaux susceptibles d'influencer la structure des communautés (Wiley *et al*., 1997), mais aussi d'apporter des éléments de réponse à une question de fond non encore résolue et soulevée par Wiegleb et Brux (1991). Ces auteurs estiment en effet que les traits observés représentent les réponses des plantes aux contraintes environnementales passées et permettent la prédiction des espèces face à des conditions futures, mais ne correspondent pas aux conditions dans lesquelles ils sont observés. Ce décalage potentiel n'est pas sans poser la question de la pertinence de la recherche de relations entre les traits et les conditions environnementales. L'étude de la plasticité des espèces pourrait permettre de s'approcher d'une concordance réelle entre les traits des espèces et les conditions environnementales, si l'on considère que la réponse plastique des plantes constitue une réponse rapide (en référence à leur durée de vie) aux conditions environnementales présentes. Peut-être aussi faudrait-il envisager l'analyse statistique de données ayant été récoltées à des périodes différentes. Ainsi, l'analyse conjointe de données physico-chimiques mesurées en 1990 avec celle de données phyto-sociologique et stratégiques échantillonnées en 1995 mettraient-elles en évidence des relations différentes et/ou plus pertinentes.

L'étape suivant logiquement la constitution d'une base de données des informations écologiqes et biologiques des espèces, sous une forme codée ou non, correspond à l'élaboration d'une méthode prédictive. Keddy (1992) représente certainement un précurseur dans ce domaine, avec le concept des «Assembly-» et des «Response Rules». Depuis, plusieurs modèles prédictifs ont été élaborés, dont ceux de Oertli *et al*. (2000) et de Speight *et al*. (2002). Ces deux modèles cherchent à la fois à évaluer les milieux et à prédire leur état face à des changements environnementaux (d'origine naturelle ou anthropique), sur la base d'une comparaison d'un état observé avec un état de référence.
L'outil développé par Oertli *et al*. (2000) est destiné à l'évaluation des petits plans d'eau et se base sur la prédiction des richesses spécifiques de la végétation aquatique et de différents groupes taxonomiques d'invertébrés. Cet outil se caractérise par la construction de modèles mathématiques sur la base des données issues des plans d'eau étudiés, d'une part et par l'absence de l'identité des espèces, d'autre part. De ce fait, ce modèle est restreint à l'univers des milieux dans lequel et pour lequel il a été bâti et s'appuie sur la comparaison de nombres d'espèces.
Speight *et al*. (2000) se basent sur le groupe des diptères *Syrphidae*, qui présentent l'intérêt d'occuper une grande majorité des niches écologiques de la planète.Aucun modèle mathématique ne sous-tend les prédictions, qui reposent sur une base de données de connaissances intégrant les macro- et les

micro-habitats (habitats occupés par les adultes et les larves, respectivement), l'écologie des espèces, leurs aires de distribution ainsi que leur statut de protection. Le modèle aboutit à la prédiction de listes d'espèces et non de richesses spécifiques, permettant i) l'évaluation de la proportion des espèces dans chaque compartiment (prédit-non observé, prédit-observé et observé-non prédit) et ii) la compréhension des raisons de la présence ou de l'absence des espèces, de même que l'émission des recommandations adaptées de gestion.

Dans le présent travail, l'objectif n'était pas d'évaluer la qualité des milieux, ni de formuler des prédictions, mais de tester la validité de relations traits-conditions environnementales mises en évidence dans d'autres types d'écosystèmes. Cette étape est importante puisqu'elle intervient dans les deux méthodologies présentées ci-dessus. Par ailleurs, cette démarche s'apparente à la méthode mise en œuvre par Oertli *et al*. (2000), dans le sens où les analyses statistiques utilisées correspondent à des régressions multiples se basant sur les données issues des quinze étangs étudiés.

La protection et la conservation des zones humides bénéficierait de l'élaboration d'un outil de prédiction basé sur les macrophytes aquatiques à l'image de celui développé par Speight *et al*. (2000). Cet outil nécessiterait la constitution (ou l'extension) des bases de données des macro- et micro-habitats (au sens de Speight *et al*. (2000)), de listes d'espèces pour des entités géographiques différentes, de statuts de protection et des données écologiques de toutes les espèces d'hydrophytes de Suisse. La base de données relative aux macro-habitats serait constituée des grands types de milieux aquatiques, tels que les fleuves, rivières, ruisseaux, lacs, étangs, mares, gravières, fossés, etc., alors que celle des micro-habitats comprendrait les différentes combinaisons de paramètres physico-chimiques (conditions de courant, teneurs en éléments nutritifs, etc.) et sédimentologiques (types de substrats, granulométrie, teneur en matière organique, etc.) susceptible d'être rencontrées dans les macro-habitats et d'influencer la germination des graines et des propagules. L'intérêt d'une telle démarche résiderait non seulement dans l'élaboration même de l'outil, mais aussi dans le transfert d'une méthode élaborée pour un groupe d'invertébrés, mobiles, à un groupe caractérisé par sa sédentarité d'une part, et le spectre écologique beaucoup plus important d'un grand nombre de ses espèces d'autre part. Ce transfert nécessiterait en toute vraisemblance des ajustements liés aux caractéristiques intrinsèques de la végétation aquatique (sédentarité et plasticité), à la fois dans les objectifs et la précision des prédictions. En Suisse, les listes d'espèces et les statuts de protection existent pour différentes entités géographiques, telles que les cantons, les régions biogéographiques ou l'ensemble du territoire helvétique. Il en résulterait la possibilité de comparer la précision et la pertinence des prédictions effectuées à différentes échelles spatiales, puisque «la nature et la force des relations entre la diversité et le fonctionnement des écosystèmes varie fortement à travers les échelles spatiales» (Díaz et Cabido, 2001).

9.4 Conclusion

Le présent travail a permis d'acquérir un corpus important de données sur un type d'écosystème encore peu représenté dans la littérature: les étangs en zone alluviale péri-lacustre. Les étangs ont été décrits sous des angles multiples: moyenne et variabilité des paramètres physico-chimiques de l'eau et des sédiments, d'une part et communautés d'hydrophytes (richesse et composition spécifique, uniqueness, composition et diversité des traits), d'autre part. Ces deux lots d'informations ont à leur tour permis i) la comparaisons des paramètres biotiques et abiotiques à différentes échelles spatiales et temporelles, ainsi qu'avec d'autres types de petits plans d'eau, ii) la mise en relation des variables biotiques et abiotiques dans le cadre d'analyses multivariées, iii) la comparaison des résultats des analyses multivariées entre gradients environnementaux différents (Grande-Cariçaie seule puis Grande-Cariçaie et plaine alluviale de l'Ain), iv) la comparaison des capacités explicatives des variables abiotiques, v) la comparaison des capacités des variables biotiques à être expliquées, vi) la comparaison des relations traits-environnement avec les observations effectuées dans d'autres types de milieux aquatiques. Associées aux recherches du Groupe d'Etude et de Gestion de la Grande-Cariçaie et à l'étude d'Antoine (2002), ces données constituent certainement un base utile pour des recherches futures, comme l'ont montré les perspectives.

Les études conduites dans les plaines alluviales fluviales et péri-lacustres, et sur les zones humides de manière générale sont essentielles pour permettre une meilleure compréhension de la structure, du fonctionnement et de la dynamique de ces écosystèmes. Elles sont donc indispensables au développement de la science de la restauration écologique qui n'en est encore qu'à ses prémices.
Depuis quelques années toutefois, il apparaît clairement aussi au sein de la communauté scientifique de la nécessité absolue d'informer le public, les politiciens et les gestionnaires de «l'énormité, de l'irréversibilité et de la rapidité des changements actuels de la biodiversité», de «l'importance des impacts écologiques et socio-économiques» qui en découlent et du fait que «ces changements ne peuvent être «annulés» une fois qu'ils se sont produits» (Chapin *et al*., 2000). A l'avenir, un engagement plus massif de la part des scientifiques et de toutes autres personnes informées est souhaitable pour informer la population et l'associer aux projets de protection ou de conservation des milieux dès leur initiation, afin que chacun se sente concerné et y participe activement.

Chapitre 10

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Annexes

	Pool set	Pools		LAC	CP1	CP2	CP3	CP4	CP	CH1	CH2	CH	MA1	MA2	MA3	MA4	MA5	MA6	MA	FO1	FO2	FO3	FO
Water levels [cm]	**	**	med	-	17.5	9	16	13.5	14.5	-4.5	-	-4.5	6	6	5	5	3	1	5	0	-	-2	0
			Q_{25}	-	3	-1	0	3	0.3	-6.8	-	-6.8	0.5	0	0.3	4	0	0	0	0	-	-5	-3.5
			Q_{75}	-	23.8	17	18	16	20.4	-0.3	-	-0.3	9	10	7	9	6	6	8	0	-	-2	0
			IQ	-	20.8	18	18	13	20.1	6.5	-	6.5	8.5	10	6.7	5	6	6	8	0	-	3	3.5
			min	-	-13	-11	-11	-19	-19	-26	-	-26	-14	-13	-6	-5	-7	-8	-14	-8	-	-12	-12
			max	-	47	28	38	38	47	17	-	17	26	28	27	28	25	24	28	1	-	0	1
Transparency [cm]	ns	**	med	9.3	7.7	9.6	1.3	10	6.6	6.7	8.6	8.6	-31	-31	9.2	14.2	14.2	14.2	6.7	4.4	4.8	-16.7	4
			Q_{25}	-2.6	-9.7	-5.1	-16.1	-16.5	-9.9	4.2	4.8	4.8	-36.3	-33	-0.3	9.6	9.6	10.3	-27.5	1.2	3.9	-22.1	-9.7
			Q_{75}	15	17.2	15.3	15.3	13.8	15	12.7	14.2	13.7	-28	-20.2	11.7	15.8	18.1	18.1	14.6	18.9	11.9	2.9	6.2
			IQ	17.6	26.9	20.4	31.4	30.3	24.9	8.5	9.4	8.9	8.3	12.8	12	6.2	8.5	7.8	42.1	17.7	8	25	15.9
			min	-38	-36.8	-9.7	-28	-27.4	-36.8	-21.4	-16	-21.4	-41.9	-41.4	-41.4	-21.9	-2.9	-10.9	-41.9	-22.3	-8.3	-31.3	-31.3
			max	19.6	28.1	28.1	22.1	28.1	28.1	14.8	18.7	18.7	3.7	3.7	26	26	26	26	26	26	26	5	26
Dissolved oxygen [mg l^{-1}]	ns	**	med	12.3	12.3	11.6	9	4.6	10.6	8.6	7.9	8.1	12.4	11.9	9.5	10.2	8.9	8.6	9.9	9.9	8.7	10.9	10.1
			Q_{25}	11.3	10.5	10.3	7.4	2.1	7.5	6.7	6.3	6.3	10.7	6.3	8.5	9.2	5.1	5.2	7.7	9	7.4	10.1	8.8
			Q_{75}	12.8	13.3	12.5	11.6	9.7	12.5	10.3	8.4	9.7	14.7	12.6	11.5	11.6	9.9	9.9	11.7	10.8	10.7	11.5	11
			IQ	1.5	2.8	2.2	4.2	7.6	5	3.6	2.1	3.4	4	6.3	3	2.4	4.8	4.7	4	1.8	3.3	1.4	2.2
			min	9.9	9.8	4.5	5.5	0.3	0.3	4.4	4	4	4.3	0.3	1.8	0.9	2.1	2.3	0.3	6.2	2.9	8.5	2.9
			max	14.7	15.4	14.5	13.7	12.6	15.4	12.5	10.3	12.5	22.8	20	14	15.3	11.4	11.2	22.8	11.6	12.4	13.4	13.4
pH	**	**	med	8.5	8.3	8.2	7.9	7.6	8.1	7.7	7.7	7.7	8.4	8.2	8	7.9	7.8	7.8	7.9	7.7	7.8	8	7.8
			Q_{25}	8.4	8.2	7.9	7.6	7.3	7.6	6.8	7.2	7	7.7	7.3	7.5	7.6	7.4	7.4	7.4	6.5	6.4	6.2	6.4
			Q_{75}	8.5	8.4	8.4	8.1	8	8.3	7.8	7.7	7.7	8.6	8.5	8.1	8.2	8	8	8.2	7.8	7.9	8.1	7.9
			IQ	0.1	0.2	0.5	0.5	0.7	0.7	1	0.5	0.7	0.9	1.2	0.6	0.6	0.6	0.6	0.8	1.3	1.5	1.9	1.5
			min	6.3	6.3	6.3	6.4	6.4	6.3	6	5.9	5.9	5.9	6	5.9	5.8	5.8	5.9	5.8	6.1	6.2	6.1	6.1
			max	8.6	8.7	8.5	8.5	8.1	8.7	7.9	8	8	8.6	8.7	8.7	8.2	8.1	8.1	8.7	8	8	8.2	8.2
Conductivity [uS cm^{-1}]	**	**	med	293	318	366	463	514	422	465	472	472	532	522	530	589	605	621	578	443	440	511	468
			Q_{25}	273	293	331	429	465	334	419	423	417	489	499	509	538	580	582	511	422	400	492	429
			Q_{75}	338	376	451	477	543	483	503	488	498	587	550	603	619	633	655	624	496	455	524	520
			IQ	65	83	120	48	78	149	84	65	81	98	51	94	81	53	73	113	74	55	32	91
			min	213	262	305	300	263	213	363	407	363	382	383	377	385	393	427	377	387	389	480	387
			max	356	428	622	535	614	622	574	548	574	683	733	717	695	696	696	733	563	549	556	563
Calcic hardness [mg $CaCO_3$ l^{-1}]	**	**	med	132	144	194	183	211	187	180	190	181	277	276	262	247	252	246	257	169	204	212	199
			Q_{25}	112	111	185	172	210	166	171	181	176	232	224	261	242	242	241	241	149	179	201	177
			Q_{75}	143	158	216	189	229	210	180	197	195	287	283	282	262	255	258	278	196	214	223	217
			IQ	31	47	31	17	19	44	9	16	19	55	59	21	20	13	17	37	47	35	22	40
			min	94	95	131	168	190	95	170	174	170	176	196	249	238	234	236	176	144	130	196	130
			max	159	182	273	199	260	273	210	200	210	292	295	320	279	278	260	320	227	215	226	227

Annex 1 Summary of the physico-chemical variables measured in Lake Neuchâtel (LAC) and in the pools of the fringing wetland.

	Pool set	Pools		CP1	CP2	CP3	CP4	CP	CH1	CH2	CH	MA1	MA2	MA3	MA4	MA5	MA6	MA	FO1	FO2	FO3	FO
Core organic matter .	**	**	med	1.6	13.4	19.3	35	18.6	11.2	13	11.3	8.8	9.8	17.2	9.4	9.1	14.2	12.3	6.4	10.5	9.7	7.6
[%]			Q_{25}	1	11.7	17.3	32.5	12.6	10.5	9.7	9.8	8.2	9.3	15.2	5.5	7.5	13.1	8.4	6.3	8.8	8.2	6.3
			Q_{75}	1.7	14.3	20.5	36.9	27.8	12.5	26.2	14.5	15.6	11.8	22.7	12.7	12.3	21.6	15.4	7.3	10.7	13.2	9.9
			IQ	0.7	2.6	3.2	4.4	15.2	2	16.5	4.7	7.4	2.5	7.5	7.2	4.8	8.5	7	1	1.9	5	3.6
			min	0.7	10.1	10.5	24.3	0.7	8.23	4.4	4.4	6.9	4.9	14.3	3.3	7	6.4	3.3	5.4	2.7	5	2.7
			max	2.6	16.9	24.8	43.4	43.4	13.9	32.5	32.5	18.6	15.4	23.7	15.7	15.1	26.8	26.8	8.2	12.5	13.4	13.4
			e	1.9	6.8	14.3	19.1	42.7	5.67	28.1	28.1	11.7	10.5	9.4	12.4	8.1	20.4	23.5	2.8	9.8	8.4	10.7
Particles <63um	**	**	med	15.7	49.6	35.4	36.2	37.8	56.2	40.1	48.8	90.6	91.7	57.4	58	54.7	61.5	67.4	72.4	37.6	37.9	54.4
[%]			Q_{25}	13.5	48.5	31.7	31.4	29.4	53.7	26.7	40.4	87.5	80.1	54.4	50.5	47.1	49.1	55.2	65.7	29	35.2	37.8
			Q_{75}	24.5	53.4	43.3	48.5	48.5	57.6	45.3	56.4	94.6	94.1	60.5	63.9	57.6	64.4	90.4	74.9	40.4	52.4	72
			IQ	11	4.9	11.6	17.1	19.1	3.9	18.6	16	7.1	14	6.1	13.4	10.5	15.3	35.2	9.2	11.4	17.2	34.2
			min	10.4	37.8	25.9	22.6	10.4	41	13.4	13.4	77.4	55.1	47.1	33.1	32.7	27.6	27.6	51.3	25	30.2	25
			max	40	64.7	62.9	74.9	74.9	63.4	59.9	63.4	97.3	96.3	68.3	72.9	69.5	76.5	97.3	82.9	45.6	56.4	82.9
Grain size Median	**	**	med	145	63.6	97.3	93.6	93.6	50.4	89.1	65.5	14.3	12.9	48	45.2	54	42.9	30.1	27.6	88	87.4	54.5
[%]			Q_{25}	133	56.8	76.8	65.8	65.6	46.6	76.7	49.4	12.5	12.2	44.9	30.8	47.9	39.6	14.2	24.3	87.2	58.3	27.7
			Q_{75}	270	65.7	106	112	119	55.1	132	88.6	15.8	17.2	54.3	61.4	69.5	64.9	50.3	36.7	124	91.1	87.5
			IQ	137	8.9	28.8	46.2	53.6	8.5	55.7	39.2	3.3	5	9.4	30.6	21.6	25.3	36.1	12.4	36.6	32.8	59.8
			min	98.5	37.6	41.6	20.7	20.7	36.4	40.9	36.4	10.5	11.2	33.1	18.9	27.7	19.4	10.5	18.3	72.9	50.7	18.3
			max	581	88.5	135	158	581	88.1	181	181	25	45.2	68.5	125	112	144	144	60.2	133	107	133
Sedimentation rate	**	**	med	2.5	3.2	1.7	0.8	1.5	0.1	0.1	0.1	6.5	4.7	2.7	0.5	0.5	0.6	1	0.02	0.4	0.8	0.5
[kg dry weight m^{-2} $month^{-1}$]			Q_{25}	2.4	1.3	1.3	0.7	1	0.1	0.1	0.1	3.6	2.1	1.3	0.2	0.1	0.2	0.4	0.02	0.4	0.6	0.2
			Q_{75}	2.6	3.5	2.2	1	2.5	0.3	0.4	0.3	14	15.2	3.3	1.2	0.5	1	4.1	0.03	0.8	1.8	1
			IQ	0.3	2.2	0.9	0.3	1.5	0.2	0.4	0.3	10.3	13.1	2	1	0.4	0.8	3.7	0.01	0.5	1.2	0.8
			min	2.2	0.1	0.5	0.6	0.1	0.03	0.01	0.01	0.3	0.3	0.6	0.1	0.1	0.1	0.1	0.01	0.2	0.03	0.01
			max	2.8	4.4	2.8	1.2	4.4	1.8	0.7	1.8	16.9	18.1	9.6	2.9	0.8	4.5	18.1	0.1	1.5	4.2	4.2
Trap organic matter.	**	**	med	-	15.7	25.2	39.4	24.5	21.4	41.7	31.6	9.2	9.8	11.7	13.7	18.5	20.7	13.3	20.9	15.8	15.5	16.1
[%]			Q_{25}	-	14.4	22.5	36.9	16.8	17.5	35.3	21.7	8.7	8.5	10.9	12.8	17.3	17.4	10	16.6	15.2	13.7	14.7
			Q_{75}	-	16.4	27.6	41.1	34.1	25.3	45.4	41.7	9.8	11.1	12.9	16.1	21.8	25.5	18.5	28	19.3	19.1	19.5
			IQ	-	2	5.1	4.2	17.3	7.8	10	20	1.1	2.7	2	3.3	4.5	8.1	8.5	11.4	4.1	5.3	4.8
			min	-	10.4	20.9	35	10.4	11.9	29.8	11.9	5.4	6.5	9.1	11.3	14.9	13.7	5.4	14.2	13.6	10.4	10.4
			max	-	18.2	31.4	45.7	45.7	38.7	55	55	17.1	22.5	22.4	34.3	26.9	31.5	34.3	29.7	32.4	22.8	32.4

Annex 2 Summary of the sedimentological variables from the Grande-Cariçaie pools. ** indicates significant differences between pools or pool sets (Kruskall-Wallis tests).

Pool x year	BERER	CERDE	CHACO	CHAGL	CHAHI	ELOCA	HIPVUL	HYDVU	LEMOR	LEMTA	LEMTR	MYSPI	MYRVE	NASOF	NUPLU	NYMAL	POTGR	POTPU	POTNA	POTPE	POTPL	RICFL	SPAMI	UTRVU	UTRIN	UTRMI	UTROC	VERBE	ZANPA	pR	Jack1	Jack2
CP196	-	-	1.04	-	-	0.07	-	-	0.25	0.25	0.04	0.04	-	-	-	-	-	0.71	-	0.11	-	0.11	-	0.04	-	-	-	-	-	10	12.9	13.9
CP296	-	0.03	-	-	-	-	-	-	0.88	0.88	0.35	-	-	-	-	0.24	-	0.21	-	-	-	0.59	-	0.18	-	-	-	-	0.06	9	10	9.1
CP297	-	-	-	-	-	-	-	-	0.96	0.96	0.92	-	-	0.08	-	0.2	-	0.12	-	-	-	0.92	-	0.04	-	-	-	-	-	8	8	7.1
CP396	-	0.02	-	-	-	-	0.02	-	0.06	3.35	0.92	-	-	-	0.58	1.35	-	-	-	-	-	0.85	-	3.23	-	-	-	-	-	9	11	12.9
CP397	-	-	-	-	-	-	-	-	1.54	1.54	1.2	-	-	-	0.38	1.45	-	-	-	-	-	0.8	-	0.76	-	-	-	-	-	7	7	7
CP398	-	0.08	-	-	-	-	0.01	-	0.16	2.34	2.12	-	-	-	0.39	1.74	-	-	-	-	-	0.35	-	0.45	-	-	-	-	-	9	10	11
CP496	-	-	-	-	-	-	-	-	2.19	2.51	2.89	-	-	-	-	4.46	-	-	-	-	-	3.89	-	2.49	-	-	-	-	-	6	6	6
CP497	-	-	-	-	-	-	-	-	1.54	1.54	1.94	-	-	-	-	3.8	-	-	-	-	-	3.34	-	0.83	-	-	-	-	-	6	6	6
CP498	-	-	-	-	-	-	-	-	2.88	2.88	2.82	-	-	-	-	3.79	-	-	-	-	-	2.67	-	1.24	-	-	-	-	-	6	6	6
CH197	-	-	-	-	1.92	-	-	-	-	-	-	-	0.84	-	-	2.44	0.48	0.08	0.8	-	-	-	0.08	0.24	0.2	-	-	-	-	9	10	10
CH198	-	-	-	-	3.23	-	-	-	-	-	-	-	1.23	-	-	1.5	0.23	0.2	1.47	-	-	-	-	-	-	0.17	-	-	-	7	7	7
CH297	-	-	-	-	-	-	-	-	-	-	-	-	0.6	-	-	2.96	0.76	0.36	1.04	-	0.12	-	-	0.04	0.04	0.12	0.04	-	-	10	12.9	14.8
CH298	-	-	-	0.03	-	-	-	-	-	-	-	-	0.36	-	-	3.24	0.64	0.03	0.64	-	0.03	-	-	-	-	-	-	-	-	7	9.9	12.7
MA196	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0
MA197	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0
MA198	-	-	-	-	-	-	-	-	0.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1
MA296	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.04	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1
MA297	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.19	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1
MA298	-	-	-	-	-	-	-	-	0.12	-	-	-	-	-	-	3.54	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	2
MA396	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.47	-	-	-	-	-	-	-	0.11	-	-	-	-	-	2	2	1.2
MA397	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.71	-	-	-	-	-	-	-	0.24	0.06	-	-	-	-	3	3.9	4.8
MA496	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.39	-	-	-	-	1.11	-	-	0.04	-	-	-	-	-	3	4	4.9
MA497	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.19	-	-	-	-	0.19	-	-	-	-	-	-	-	-	2	2	2
MA596	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.9	-	-	-	-	1.2	-	-	1.05	-	-	-	-	-	3	3	3
MA597	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.65	-	-	-	-	1.12	-	-	0.47	-	-	-	-	-	3	3	3
MA696	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.7	-	-	-	-	1.05	-	-	1.1	-	-	-	-	-	3	3	3
MA697	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.2	-	-	-	-	0.8	-	-	0.75	-	-	-	-	-	3	3	3
FO197	0.04	-	-	-	1.04	-	-	0.24	-	-	-	-	-	-	-	-	1.6	-	-	-	-	-	-	-	2.12	0.44	-	-	-	6	7	7.9
FO198	-	-	-	-	1.48	-	-	0.3	-	-	-	-	-	-	-	-	0.59	-	-	-	-	-	-	-	-	-	-	-	-	3	3	3
FO297	-	-	-	-	-	-	-	-	-	-	-	3.3	-	-	-	0.11	-	0.03	-	-	-	-	-	0.05	-	-	-	-	-	4	5.9	6.9
FO298	-	-	-	-	-	-	-	-	-	-	-	3.88	-	-	-	0.69	-	-	-	-	-	-	-	0.09	-	-	-	-	-	3	3	2.1
FO397	-	-	-	-	-	-	-	-	0.19	-	-	0.09	-	-	-	-	-	-	-	-	-	0.02	-	0.02	-	-	-	-	-	4	6	7.9
FO398	0.01	-	-	-	-	-	-	-	0.07	-	-	0.1	-	-	-	0.06	-	-	-	-	-	-	-	0.09	-	-	-	0.03	-	6	5.9	7.8

Annex 3 Average coverage of the plant species in the Grande Cariçaie pools (1996-98). pR : pool species richness ; Jack1, Jack2 : Jacknife estimates of the species richness.

		BERER	CALSP	CERDE	CHACO	CHAGL	CHAVU	CHAHI	ELOCA	ELONU	GLYFL	GRODE	HIPVU	HOTPA	HYDVU	LEMOR	LEMTR	MYSPI	MYRVE	NASOF	NITSP	NUPLU	NYMAL	POTGR	POTPU	POTLU	POTNA	POTPE	POTPF	POTPL	RANTR	RICFL	RORAM	SPAMI	UTRIN	UTRVU	UTRMI	VERAN	ZANPA
Growth form	free-floating			3					1	1						3	3															3			3	3	3		
	anchored_float		3								3				3							3	3	3			3			3				3					
	anchored_subm_leav	3	3	1	3	3	3	3	3	3	3	3	3	3				3	3	3	3	3	3	3	3	3	3	3	3	3	3		3	3	3		3	3	3
	anchored_em_lev	3									3		3	3	3					3		2	2										3	1				3	
Height	<0.1m				3			1								3	3															3							
	0.1m - 1m	3	3		3	3	3	3				3	3	3	3					3	3				3					3	3			3	3		3	3	3
	>1m	1		3		1		1	3	3	3		1		1			3	3			3	3	3		3	3	3	3				3			3		1	
Leaf type	narrow				3	3	3	3			3		3								3				3			3				3		3					3
	dissected			3										3				3	3												3				3	3	3		
	entire	3	3						3	3	3	3			3	3	3			3		3	3	3		3	3		3	3			3	3				3	
leaf area	small		3	3	3	3	3	3	3	3		2	3	3		3	3	3	3		3			1	3			3			3	3			3	3	3		3
	medium	2									3	3		3	3			1	1	3				3		3	3	2	3	3	2		3	3		2		3	2
	large	3																		3			1			3	3		1	3			1	2				1	
	extra_large	2																				3	3																
Vegetative perennation	undergr_veget_org	3									3	3	3	3	3			3	3	3		3	3	3	2	3	3	3	3	3			3	3				1	3
	bublets_etc			3		1	2	3	3	3		2		3		3		2	3					1	3		2	2	1						3	3	3		
	shoot_fragm	3	3	3					3	3		3	3	3	2	3	3	3	3					2		1	1	2	1	1	3		1		3	3	3	3	1
Lateral spread	lat_spread_limit		3	3	3	3	3	3	3	3						3	3				3				1						3	3			3	3	3	3	
	10-100 cm	3									3	3		3	3			1	3	3				3	3	3		3	3	3			3	3					3
	>1m										1		3		1			3	1			3	3				3												
Flowering	each_yr		3		3	3	3	3				3		3				3	3	3	3	3	3	3	3	3	3	3		3	3		3	3	3	3	3	3	3
	not_each_yr	3		3					3	3	3		3		3	3	3	1	1										3			3							
Flowering duration	2_3	3		3					3					3	3	3	3	3	3					3		3	3		3		3			3		3			
	4		3						1	3	3	3	3			1	1					3	3		3			3		3			3		3	1	3		
	5_6		1		3	3	3	3	1		1					1	1			3	3																	3	3
Seed size	<1mm				3	3	3	3													3											3			3	3	3		
	1_3mm	3	3								3	3	3		3	3	3	3	3	3			3	3	3				2	3	3		3						3
	>3mm			3					3	3	1	3		3					2			3	2	2		3	3	3	3					3				3	3

Annex 4 Traits for the species from the Grande-Cariçaie and the Ain floodplain.

Espèces	Code_sp
Berula erecta (Huds.) Coville	BERER
Callitriche sp.	CALSP
Ceratophyllum demersum L.	CERDE
Chara contraria Braun ex Kützing	CHACO
Chara globularis Thuillier	CHAGL
Chara vulgaris L.	CHAVU
Chara hispida L.	CHAHI
Elodea canadensis Michx.	ELOCA
Elodea nuttallii (Planchon) St-John	ELONU
Glyceria fluitans (L.) R. Brown	GLYFL
Groenlandia densa (L.) Fourreau	GRODE
Hippuris vulgaris L.	HIPVU
Hottonia palustris L.	HOTPA
Hydrocotyle vulgaris L.	HYDVU
Lemna minor L.	LEMOR
Lemna minuta Humb. & al.	LEMTA
Lemna trisulca L.	LEMTR
Myriophyllum spicatum L.	MYSPI
Myriophyllum verticillatum L.	MYRVE
Nasturtium officinale R. Br.	NASOF
Nitella sp.	NITSP
Nuphar lutea (L.) Sm.	NUPLU
Nymphaea alba L.	NYMAL
Potamogeton gramineus L.	POTGR
Potamogeton gr pusillus	POTPU
Potamogeton lucens L.	POTLU
Potamogeton natans L.	POTNA
Potamogeton pectinatus L.	POTPE
Potamogeton perfoliatus L.	POTPF
Potamogeton plantagineus Roem. & Schult.	POTPL
Ranunculus trichophyllus Chaix S.L.	RANTR
Riccia fluitans L.	RICFL
Rorripa amphibia (L.) Besser	RORAM
Sparganium minimum Wallr.	SPAMI
Utricularia intermedia Hayne	UTRIN
Utricularia gr. vulgaris	UTRVU
Utricularia minor L.	UTRMI
Utricularia ochroleuca R.W. Hartm.	UTROC
Veronica beccabunga L.	VERBE
Veronica anagallis-aquatica L.	VERAN
Zannichellia palustris L.	ZANPA

Annex 5 Species list with their codes and the thesis chapters in wich they appear.