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1.1. LES ÉPIDÉMIES

Le terme *épidémie* est souvent attribué à des phénomènes médicaux ou écologiques qui ont des impacts négatifs notables sur la population humaine, l'économie ou sur l'exploitation des ressources naturelles. L'édition 2011 du *Nouveau Petit Robert* de la langue française définit une épidémie comme étant une « *apparition accidentelle d'un grand nombre de cas d'une maladie infectieuse transmissible; d'un accroissement considérable d'un nombre de cas dans une région donnée au sein d'une collectivité ou encore de l'accroissement du nombre de cas de toute maladie ou phénomène anormal* » (Robert *et al.*, 2010).

Du point de vue écologique, les épidémies peuvent être définies comme étant une augmentation explosive de l'abondance d'une espèce sur une période de temps relativement courte (Berryman, 1988). Quoi qu'il en soit, le terme épidémie fait référence à un phénomène positif en ce qui concerne le nombre ou l'abondance mais négatif en ce qui a trait à sa perception ainsi que pour les impacts qui en découlent (O'Neil et Naumova, 2007).

Les épidémies créent souvent un effet de panique chez l'être humain en raison de leurs impacts potentiels sur l'économie ou la société, comme par exemple lors d'une pandémie de grippe. Chez les insectes, les épidémies de sauterelles en Afrique peuvent dévaster les cultures sur de vastes régions, alors que pour les insectes forestiers, leur alimentation sur des arbres peut réduire considérablement le volume de matière ligneuse à intérêt commercial d'une région, d'une province ou d'un pays (MacLean, 1984; Alfaro et Maclauchlan, 1992).

Dans une synthèse des principales hypothèses avancées dans la littérature scientifique pour identifier les facteurs à l'origine des épidémies d'espèces animales, Berryman (1988) a regroupé en sept catégories les théories proposées sur le sujet. Un exercice similaire a également été repris par Abbott et Dwyer en 2007. Ces catégories sont :

1. les épidémies sont causées par des changements dramatiques de l'environnement physique, notamment lors des pics de présence de taches solaires (Elton, 1924; Kerr, 1990; Myers, 1998), suite à la succession de plusieurs étés aux conditions météorologiques favorables à l'espèce – ou théorie du « *climatic release* » – (Greenbank, 1956) ou en fonction de différents facteurs environnementaux favorables – ou « *environmental forcing* » – comme par exemple les températures printanières ou l'abondance des précipitations, notamment l'hiver (Andrewartha et Birch, 1984; Hunter et Price, 1998);
2. les épidémies sont causées par des changements génétiques (Chitty, 1971; Ginzburg et Taneyhill, 1994) ou par les caractéristiques physiologiques de certains individus au sein de la population (Wellington, 1960; Christian et Davis, 1971);
3. les épidémies résultent d'interactions trophiques entre les herbivores et les plantes, ou entre les prédateurs et les proies, en produisant des cycles de

populations d'amplitude élevée sous certaines conditions (Lotka, 1925; Volterra, 1926; Nicholson et Bailey, 1935);

4. les épidémies d'herbivores sont dues à des changements qualitatifs ou quantitatifs chez les plantes hôtes, causés habituellement par des stress environnementaux (Mattson et Addy, 1975; White, 1978);
5. les épidémies sont le résultat de stratégies biologiques observées plus communément chez les espèces nuisibles opportunistes (Southwood et Commis, 1976; Rhoades, 1985);
6. les épidémies surviennent lorsque les populations d'espèces nuisibles échappent à la régulation exercée par leurs ennemis naturels (Morris, 1963; Takahashi, 1964; Holling, 1965; Isaev et Khlebopros, 1977; McCann *et al.*, 2000; Maron *et al.*, 2001);
7. les épidémies surviennent lorsque les populations surpassent les systèmes de défense de leurs hôtes (Berryman, 1982a, 1982b).

Il y a des avantages et des inconvénients liés à de telles explosions démographiques. L'augmentation de la densité des populations à des niveaux épidémiques réduit indéniablement l'espace et la nourriture disponibles pour chaque individu. De plus, les densités élevées favorisent la transmission des maladies, parasites ou parasitoïdes entre les individus. Par contre, du point de vue de l'individu, la présence d'un grand nombre de congénères réduit les risques posés par la prédation, favorise l'accroissement du territoire occupé par l'espèce lors de la migration des individus vers des sites à densité moins élevée et offre des opportunités plus nombreuses pour la reproduction (Berryman, 1986).

1.2. LES ÉPIDÉMIES D'INSECTES

Les insectes affectant la production agricole ou forestière se voient fréquemment attribuer l'étiquette de pestes ou d'insectes nuisibles (Berryman, 1986; Wallner, 1987). Ils peuvent être porteurs de maladies ou de pathogènes, ou bien être des compétiteurs pour l'utilisation des ressources. Toutefois, les effets ou impacts des épidémies d'insectes ne sont pas seulement négatifs. Les épidémies d'insectes indigènes sont des phénomènes naturels qui ont un rôle important à jouer dans la dynamique des écosystèmes (Mattson et Addy, 1975; Romme *et al.*, 1986; Schowalter *et al.*, 1986; MacLean, 1988; Haack et Byler, 1993). Selon leur intensité, elles peuvent entraîner une mortalité importante des espèces d'arbres ce qui peut entraîner une ouverture de la voûte forestière ou entraîner le déclin ou même éliminer ces espèces, jouant ainsi un rôle structurant dans l'écosystème, (Bhiry et Filion, 1996; Ellison *et al.*, 2005, Bouchard et Pothier, 2010). Au bout du compte, ceci peut avoir des répercussions sur tout l'écosystème, tant sur la végétation que sur les populations d'insectes participant à la décomposition de la litière (Eveleigh *et al.*, 2007; Cobb, 2010).

Les populations d'insectes nuisibles suivent habituellement des patrons graduels, cycliques ou éruptifs (Berryman et Stark, 1985; Wallner, 1987). Plusieurs espèces d'insectes sont épidémiques, atteignant des niveaux de population très élevés pendant une période de temps relativement courte et causant une défoliation ou une mortalité massive chez leurs espèces hôtes. Les épidémies sont séparées par des périodes, parfois longues, de faible densité d'individus (Varley *et al.*, 1973; Crawley, 1983; Berryman, 1988; Myers, 1988; Logan et Allen; 1992; Abbot et Dwyer, 2007).

Les insectes qui atteignent des niveaux de population épidémiques constituent une faible proportion de tous les insectes phytophages, étant des exceptions plutôt que la règle (Morris, 1964). Parmi ces exceptions, peu d'entre elles ont des patrons épidémiques cycliques. Des 80 espèces épidémiques de lépidoptères de l'Amérique du Nord et de l'Europe, seulement 18 ont une dynamique de population cyclique (Myers, 1993). Que les épidémies soient cycliques ou non, les insectes à l'origine d'épidémies sévères entraînant une mortalité significative de leurs espèces hôtes sont des agents de perturbation importants qui peuvent jouer un rôle clé dans la dynamique forestière; elles peuvent même initier une succession forestière (Holling, 1992).

1.2.1. LES ÉPIDÉMIES CYCLIQUES D'INSECTES

De nombreuses études ont été consacrées à la compréhension des cycles épidémiques d'insectes forestiers ravageurs (Blais, 1961, 1983; Haukioja *et al.*, 1983; Royama, 1984, 1992; Berryman, 1986, 1996; Martinat, 1987; Baltensweiler et Fischlin, 1988; Myers, 1988, 1993; Volney, 1988; Larsson *et al.*, 1993; Rossiter, 1994). Bien que les niveaux de populations soient influencés par plusieurs variables, un patron cyclique semble nécessiter la présence d'un ou plusieurs facteurs dominants, comme par exemple des conditions météorologiques particulières, des parasitoïdes en plus ou moins grande abondance, un effet maternel c'est-à-dire une plasticité transgénérationnelle, la propagation des virus, des populations de prédateurs en déclin ou en croissance, des relations hôtes-insectes particulièrement intenses, une certaine disponibilité des espèces hôtes (quantité et qualité), etc. (Haukioja *et al.*, 1983 ; Berryman, 1986, 1996; Baltensweiler et Fischlin, 1988). Plusieurs de ces facteurs peuvent interagir de différentes façons et à différents moments et être à l'origine des cycles épidémiques (Myers, 1988).

1.2.2. LE SYNCHRONISME SPATIAL DES ÉPIDÉMIES D'INSECTES

Au cours des deux dernières décennies, l'aspect spatial de la dynamique des populations a retenu de plus en plus l'attention des chercheurs, plus particulièrement la dynamique et les interactions des groupes de populations reliées entre elles (Matter, 2001, Liebhold *et al.*, 2004). Il a été observé que des populations géographiquement distinctes pouvaient fluctuer de façon synchrone (Greenman et Benton, 2001; Haynes *et al.*, 2009). Le synchronisme spatial est un phénomène courant qui a été étudié chez de nombreux animaux et insectes, dont les insectes forestiers défoliateurs (Mason, 1978; Williams et Liebhold, 1995; Myers 1998, Haynes *et al.* 2009).

En Amérique du Nord, plusieurs espèces d'insectes défoliateurs montrent un certain synchronisme spatial lors d'épidémies. C'est le cas par exemple de la spongieuse (*Lymantria dispar*) (Liebhold *et al.* 2000, Abbott et Dwyer, 2008), de la livrée des forêts (*Malacosoma disstria*) (Huang *et al.*, 2008), la tordeuse du pin gris (*Choristoneura pinus* pinus) (McCullough, 2000) et la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*) (Williams et Liebhold, 2000; Jardon, 2001). Lorsque ces insectes atteignent des niveaux de population épidémiques simultanément sur de grandes régions, ils peuvent causer des dommages considérables aux forêts.

Plusieurs mécanismes ont été proposés pour expliquer le synchronisme spatial des épidémies, notamment la stochasticité régionale et la migration. Ces deux mécanismes sont les plus généraux et ont fait l'objet de nombreuses études (Régnière et Fletcher, 1983; Williams et Liebhold, 1995; Liebhold *et al.*, 2000; McCullough, 2000; Williams et

Liebhold, 2000; Jardon, 2001) et seraient à l'origine du synchronisme observé chez les insectes forestiers défoliateurs. Ils sont expliqués dans les sections qui suivent.

1.2.2.1. LA STOCHASTICITÉ RÉGIONALE OU EFFET MORAN

L'hypothèse la plus répandue pour expliquer le synchronisme spatial est que des forces environnementales corrélées engendreraient des fluctuations synchrones de populations distinctes (Mackenzie, 1952; Moran, 1953b; Royama, 1992; Ranta *et al.*, 1995; Haydon et Steen, 1997; Liebhold *et al.*, 2004; Bjornstad *et al.*, 2008). En étudiant le cycle du lynx du Canada, Moran (1953a, 1953b) a suggéré que des populations locales d'une espèce largement répandue puissent être régionalement synchronisées par l'influence d'une perturbation commune extrinsèque, comme par exemple les conditions météorologiques. Ces oscillations de populations découleraient de perturbations stochastiques et résulteraient de processus intrinsèques dépendants de la densité. Moran (1953b) a été le premier à suggérer que les mécanismes à l'origine du synchronisme seraient différents de ceux responsables des cycles de populations. Les facteurs à l'origine de la stochasticité régionale, ou effet Moran, peuvent agir de concert rapidement pour synchroniser les fluctuations de populations disjointes (Moran, 1953b; Royama, 1992; Ranta *et al.*, 1997; Myers, 1998). L'effet Moran a été identifié comme étant un facteur important dans le synchronisme d'épidémies d'insectes forestiers (Williams et Liebhold, 1995; Myers 1998; Liebhold *et al.*, 2004).

1.2.2.2. LA MIGRATION

Le deuxième mécanisme suggéré pour expliquer le synchronisme des fluctuations des populations est la migration. Lorsque des individus émigrent d'une région à densité de population élevée vers des régions adjacentes moins denses, ils synchronisent la dynamique régionale des populations (Barbour, 1990; Holyoak et Lawler, 1996; Sutclife *et al.*, 1996; Swanson et Johnson, 1999; Buonaccorsi *et al.*, 2001). La migration des individus peut également être indépendante de la densité des populations alors qu'une fraction constante de la population migrerait à chaque génération (Ruxton et Rohani, 1999; Ylikarjula *et al.*, 2000). La migration des individus peut avoir lieu sur une brève période de temps, plus particulièrement chez les insectes, car seulement certains stades de développement ont des ailes (Royama, 1984), alors que pour d'autres espèces, la migration est plus intensive durant certaines périodes de l'année (Bjornstad *et al.*, 1999). Finalement, certaines espèces peuvent migrer de façon continuelle (Ripa, 2000). Il a été observé que le niveau de synchronisme chez les populations était supérieur après la migration qu'avant la migration (Ripa, 2000) et qu'il y aurait une relation négative entre le synchronisme et la distance de migration (Swanson et Johnson, 1999).

1.3. LES ÉPIDÉMIES DE LA TORDEUSE DES BOURGEONS DE L'ÉPINETTE

La tordeuse des bourgeons de l'épinette est un lépidoptère de la famille des Tortricidae dont la distribution naturelle est la même que celle de ses espèce hôtes, c'est-à-dire l'épinette blanche (*Picea glauca*), l'épinette noire (*Picea mariana*), l'épinette rouge (*Picea rubens*), le mélèze (*Larix laricina*) et le sapin baumier (*Abies balsamea*), son hôte de prédilection et qui est aussi le plus vulnérable à sa défoliation (Blais, 1957, 1961; Greenbank, 1963; MacLean, 1984; Harvey, 1985; Martineau, 1985; MacLean et Ostaff, 1989; Bergeron *et al.*, 1995; Nealis et Régnière, 2004). Les populations de la tordeuse atteignent des niveaux épidémiques approximativement tous les 34 ans dans l'Est du Canada et sont l'une des perturbations naturelles les plus importantes des forêts boréales de l'Amérique du Nord (MacLean, 1984; Morin et Laprise, 1990; Jardon *et al.*, 2003). Fraver et collaborateurs (2007) ont pour leur part observé un intervalle moyen de 67 ans entre les différentes épidémies de tordeuses survenues dans le nord du Maine, soit le double de l'intervalle observé dans l'Est du Canada. Ces chercheurs suggèrent que les différences entre les types de forêt et la dynamique des peuplements qui leur est associé pourraient expliquer les intervalles plus longs observés dans le nord du Maine.

Lors d'une épidémie, les premières années de défoliation entraînent la réduction de la production de pollen et de graines chez les arbres touchés (Blais, 1957; Morris, 1963). Lorsque la défoliation persiste, les arbres sous couvert meurent, puis les cimes des arbres dominants meurent graduellement. Après trois à quatre années de défoliation sévère, les arbres matures meurent également (Royama, 1984, Jardon, 2001; Nealis et Régnière, 2004). Cette mortalité permet à la régénération pré-établie de sapin baumier de constituer progressivement une nouvelle strate arborescente (Mattson et Addy, 1975; Romme *et al.*, 1986; Schowalter *et al.*, 1986; MacLean, 1988; Haack et Byler, 1993; Morin, 1994).

Selon leur intensité, les épidémies peuvent réduire temporairement la croissance individuelle des arbres, entraîner la mort des espèces hôtes de peuplements entiers ou entraîner des changements dans la composition forestière (Kneeshaw et Bergeron; 1998; Bouchard *et al.*, 2006; Bouchard et Pothier, 2010). À l'échelle régionale, les impacts des épidémies sont liés à la composition et à la structure des peuplements, qui sont elles-mêmes influencées par les perturbations survenues antérieurement (Bouchard *et al.*, 2006). Les peuplements forestiers dominés par les espèces hôtes de la tordeuse subissent une mortalité plus importante que les couverts forestiers mixtes (MacLean, 1980; MacLean et MacKinnon, 1997; Bouchard *et al.*, 2005).

L'étude des cernes de croissance des arbres hôtes de la tordeuse a permis de reconstituer l'histoire des épidémies survenues au cours des 450 dernières années (Blais, 1965; Krause, 1997; Jardon *et al.*, 2003; Boulanger et Arseneault, 2004). Dans une étude de 32 sites d'échantillonnage répartis sur 200 000 km^2 et couvrant les quatre domaines bioclimatiques occupés par la tordeuse dans les forêts du Québec, Jardon (2001) a pu retracer six périodes épidémiques s'échelonnant entre les années 1800 et 2000, soit entre 1810 et 1830, entre 1840 et 1860, entre 1870 et 1890, entre 1910 et 1920, entre 1940 et 1950, puis entre 1970 et 1980.

L'âge des arbres vivants affectés par d'anciennes épidémies de la tordeuse dépasse rarement plus de 200 ans, et c'est pourquoi Krause (1997) de même que Boulanger et Arseneault (2004) ont étudié les cernes de croissance d'épinettes utilisées lors de la construction de la charpente de bâtiments historiques tels que des églises, des vieilles habitations ou des vieilles granges. Ils ont ainsi pu détecter pour la première fois des épidémies survenues au cours des 16^e, 17^e et 18^e siècles survenues au Saguenay (1710-1716, 1754-1759) et dans le Bas Saint-Laurent (1577-1600, 1642-1648, 1678-1690, 1710-1724, 1752-1776), deux régions de l'Est du Québec.

Plusieurs hypothèses ont été émises pour expliquer la dynamique des épidémies de la tordeuse, notamment :

1. un déclenchement de nature météorologique lorsque les conditions sont favorables à la survie et à la reproduction de l'insecte (Wellington *et al.*, 1950; Greenbank, 1956);
2. un équilibre double des niveaux de populations, c'est-à-dire des niveaux faibles maintenus par les ennemis naturels et des niveaux élevés favorisé par la disponibilité en nourriture (Clark *et al.*, 1979);
3. un synchronisme de l'insecte avec le développement de peuplements hôtes matures équiens (Blais, 1985);
4. une régulation des populations par des parasitoïdes spécialistes (Royama, 1984);
5. la présence d'un pathogène omniprésent (Régnière et Lysyk, 1995);
6. des interactions tri-trophiques entre la plante hôte, l'insecte et ses ennemis naturels qui génèrent des fluctuations des niveaux de population périodiques, d'amplitude élevée, et synchronisées sur de vastes régions forestières (Cooke *et al.*, 2007).

Certaines des épidémies récentes de la tordeuse des bourgeons de l'épinette sont survenues simultanément sur de grands territoires de l'Amérique du Nord (Hardy *et al.*, 1986, Morin *et al.*, 2007). Blais (1983) et Jardon (2001) ont observé que les épidémies survenues lors du 20e siècle étaient davantage synchronisées et ont eu un impact important sur de vastes étendues de forêt comparativement aux épidémies survenues lors du 19e siècle qui n'étaient pas synchronisées à l'échelle supra-régionale et qui ont affecté des populations plus localisées (Morin *et al.*, 2007).

Deux hypothèses ont été initialement suggérées pour expliquer ce patron régional d'épidémies. La première de ces hypothèses stipule que les populations épidémiques se développent en premier dans des régions à peuplements forestiers susceptibles aux épidémies et se dispersent par la suite aux autres régions (théorie des épicentres; Hardy *et al.*, 1983). La deuxième hypothèse suppose que les fluctuations des populations locales qui oscillent à cause de facteurs intrinsèques dépendants de la densité sont synchronisées par l'exposition à une perturbation régionale commune (Royama, 1984, 1992).

Les théories actuelles sur le synchronisme spatial des épidémies de la tordeuse reposent principalement sur la dispersion des individus et l'effet Moran (Royama, 1984; Régnière et Lysyk, 1995; Williams et Liebhold, 2000; Jardon, 2001). Ces phénomènes se traduiraient par l'émergence rapide des épidémies sur de grandes régions. Jardon (2001) a aussi observé que le synchronisme variait d'une épidémie à l'autre.

Bien que les épidémies de la tordeuse des bourgeons de l'épinette survenues lors du 20e siècle puissent être synchronisées sur de grandes superficies (Royama, 1984; Candau *et al.*, 1998; Jardon *et al.*, 2003) et semblent homogènes à grande échelle, d'importantes variations locales et régionales peuvent être observées dans la fréquence, la durée et l'amplitude des épidémies (Blais, 1968; Royama, 1984), créant ainsi des niveaux variables d'impacts sur la forêt (Turner, 1952; MacLean, 1980; Bergeron *et al.*, 1995; Nealis et Régnière, 2004; Bouchard *et al.*, 2007).

1.4. DYNAMIQUE DES POPULATIONS D'INSECTES FORESTIERS RAVAGEURS AU COURS DE L'HOLOCÈNE

Afin de bien comprendre la dynamique récente des épidémies d'insectes forestiers ravageurs et d'obtenir le plus d'information possible sur leur fréquence, leur intensité et leur synchronisme, il est souhaitable de reconstituer leur histoire, et ce sur la période la plus longue possible et de la manière la plus complète qui soit. L'étude des épidémies d'insectes survenues au cours de l'Holocène peut être réalisée par l'étude des cernes de croissance d'arbres vivants (Blais, 1965, 1983; Morin et Laprise, 1990; Morin, 1998; Ryerson *et al.*, 2003; Morin *et al.*, 2007), de subfossiles (Simard, 2003) ou composant la charpente de vieux bâtiments (Krause, 1997; Boulanger et Arseneault, 2004). Il est également possible de les étudier par le biais des traces laissées par ces perturbations dans les archives naturelles que sont les humus épais, les dépôts tourbeux ou les sédiments lacustres (Simard *et al.*, 2002, 2006).

1.4.1. RECONSTITUTIONS DENDROÉCOLOGIQUES

Plusieurs longues chronologies d'épidémies d'insectes ont pu être réalisées à partir de cernes d'arbres vivants ou subfossiles, notamment pour la tordeuse des bourgeons de l'épinette, la tordeuse occidentale de l'épinette (*Choristoneura occidentalis*), la tordeuse du mélèze (*Zeiraphera diniana*), la tenthrède du mélèze (*Pristiphora erichsonii*) et le papillon de pandore (*Coloradia pandora*). La plupart de ces études permettent de remonter de 300 à 450 ans dans le passé (Swetnam et Lynch, 1989; Jardon *et al.*, 1994; Weber et Schweingruber, 1995; Ryerson *et al.*, 2003; Fraver *et al.*, 2007; Büntgen *et al.*, 2009). Certaines études ont toutefois pu retourner encore plus loin en arrière, soit plus de

600 ans dans le cas du papillon de pandore (Speer *et al.*, 2001) et près de 1200 ans pour la tordeuse du mélèze (Esper *et al.*, 2007).

Les études de Swetnam et Lynch (1989), de Ryerson et collaborateurs (2003), de même que de Weber et Schweingruber (1995) indiquent que les intervalles entre les épidémies de la tordeuse occidentale survenues dans le sud du Colorado et au Nouveau-Mexique lors des 350 dernières années étaient très variables et qu'il n'y a pas eu de changement notable au niveau de la sévérité des épidémies de l'insecte. Swetnam et Lynch (1989) ont noté une augmentation du synchronisme des épidémies survenues dans la deuxième moitié du 20^e^ siècle. Ils attribuent cette augmentation à des changements dans la structure d'âge et la composition forestière découlant de l'exploitation forestière et de la lutte contre les feux. Speer et collaborateurs (2001) attribuent également la diminution de l'activité du papillon de pandore dans l'ouest des États-Unis entre 1920 et 1980 à des interventions humaines en forêt. Ils ont également observé une grande variabilité dans les intervalles entre les épidémies de cet insecte, qui fluctuaient entre 9 et 156 ans. De plus, il n'y aurait pas eu de changement dans le synchronisme ou la sévérité des épidémies lors du 20^e siècle.

Dans la plus longue reconstitution dendrochronologique d'épidémies d'insectes publiée à ce jour, Esper et collaborateurs (2007) ont observé que le cycle épidémique de la tordeuse du mélèze dans les Alpes européennes a été très régulier au cours des 1200 dernières années, soit tous les 9,3 ans, et ce jusqu'au début des années 1980. Un cycle similaire a également été observé par Büntgen *et al.* (2009), soit d'une durée de 8 à 9 ans pour les 300 dernières années. Ces cycles seraient restés les mêmes en dépit du réchauffement des températures observés pendant le Moyen-Âge de même que lors du refroidissement des températures observé lors du Petit Âge glaciaire, survenu entre 1550 et 1860. Toutefois, aucune épidémie de la tordeuse du mélèze ne seraient survenues dans les Alpes européennes depuis 1981. Esper et collaborateurs (2007) suggèrent que l'absence d'épidémie de cet insecte serait attribuable à une période de réchauffement climatique régional exceptionnel à l'échelle du dernier millénaire, indiquant la vulnérabilité de ce système écologique dans le contexte actuel de changements climatiques.

1.4.2. L'APPORT DE LA PALÉOÉCOLOGIE DANS L'ÉTUDE DES ÉPIDÉMIES D'INSECTES

La paléoécologie, plus particulièrement l'analyse macrofossile, permet de retracer plusieurs centaines, voir plusieurs milliers d'années d'information sur les épidémies d'insectes (Davis et Hoskins, 1980; Fillion et Quinty, 1993; Bhiry et Filion, 1996; Simard *et al.*, 2002, 2006; Jasinski et Payette; 2005; Filion *et al.*, 2006; Lavoie *et al.*, 2009). Les conditions d'accumulation des grains de pollen et des macrofossiles végétaux et animaux prévalant dans les tourbières ou les sédiments lacustres facilitent la conservation de ces indicateurs de perturbations. Il est ainsi possible de reconstituer la dynamique à court, moyen et long termes de ces milieux récepteurs ainsi que des peuplements forestiers environnants (Barber, 1993; Chambers et Charman, 2004; Anderson *et al.*, 2010; Colpron-Tremblay et Lavoie, 2010).

Grâce aux méthodes paléoécologiques, on a pu associer le déclin de la pruche nord-américaine (*Tsuga canadensis*), qui a débuté il y a 5400 ans, à des épidémies de la tordeuse des bourgeons de l'épinette et de l'arpenteuse de la pruche (*Lambdina* *fiscellaria*). Dans ce cas, ce sont des capsules céphaliques de larves et des feuilles broutées trouvées dans des dépôts tourbeux des basses terres du Saint-Laurent, au Québec, qui ont fourni les indices en faveur de l'hypothèse d'un lien déclin – épidémies d'insectes (Bhiry et Filion, 1996). Plus récemment, l'apport de l'analyse pollinique pour détecter les épidémies du dendroctone de l'épinette (*Dendroctonus rufipennis*) a pu être validé par une étude à haute résolution d'une section de sédiments récoltée dans un petit étang des montagnes Rocheuses du Colorado (Anderson *et al.*, 2010). Les chercheurs ont démontré que ce type d'analyse pourrait être appliqué sur une plus longue échelle temporelle et permettrait de reconstituer l'histoire des épidémies de ce coléoptère au cours de l'Holocène.

La paléoécologie a également un rôle clé à jouer dans l'étude des épidémies anciennes de la tordeuse des bourgeons de l'épinette, notamment pour confirmer ou réfuter l'hypothèse de Blais (1965) et de Baskerville (1975) à l'effet que la relation cyclique entre les épidémies de la tordeuse des bourgeons de l'épinette et la régénération des peuplements de sapin baumier à partir de leurs banques de semis serait relativement stable depuis plusieurs milliers d'années, soit depuis la fin de la dernière époque glaciaire. Les plus longues chronologies réalisées pour retracer les épidémies de la tordeuse témoignent de l'équilibre entre l'insecte et ses hôtes, notamment le sapin. Ces chronologies ont démontré que suite au passage d'une épidémie, les peuplements touchés se régénèrent pour former de nouveaux peuplements, qui seront à leur tour touchés par le passage de nouvelles épidémies (Jardon, 2001; Fraver *et al.*, 2007; Morin *et al.*, 2007). Lavoie et Filion (2001) ont émis l'hypothèse que les chutes répétées de grains de pollen de sapin et d'épinette observées depuis plus de 4000 ans à l'île d'Anticosti seraient attribuables à des épidémies de la tordeuse des bourgeons de l'épinette ou de l'arpenteuse de la pruche. Lavoie et collaborateurs (2009) ont pu confirmer par la suite cette hypothèse en détectant des restes de ces deux insectes correspondant aux chutes de grains de pollen de sapin.

Ces études n'ont toutefois pas permis de caractériser la fréquence, l'intensité ou le synchronisme des épidémies de ces insectes comparativement aux reconstitutions dendrochronologiques. Par ailleurs, la faible résolution temporelle des analyses paléoécologiques permet difficilement de se prononcer sur les cycles épidémiques des insectes forestiers ravageurs (Lavoie et Filion, 2001; Simard *et al.*, 2002).

1.5. IMPACTS DES CHANGEMENTS CLIMATIQUES SUR LA DYNAMIQUE DES POPULATIONS D'INSECTES RAVAGEURS

Les prévisions actuelles à l'égard des changements climatiques indiquent que l'augmentation de la température se poursuivra au cours des prochaines années (IPCC, 2007), se traduisant entre autres en Amérique du Nord par des hivers et des printemps plus chauds. Ces changements pourront avoir des impacts significatifs sur la dynamique des insectes forestiers ravageurs, notamment si le développement, la survie, la reproduction et le mouvement des populations d'insectes sont favorisés (Williams et Liebhold, 1995; Volney et Fleming, 2000).

Plusieurs chercheurs prévoient que les changements climatiques modifieront significativement tous les aspects du comportement épidémique des insectes forestiers ravageurs, dont leur distribution (Williams et Liebhold, 1995; Ungerer *et al.*, 1999) et qu'il y aura une augmentation de l'intensité et de la fréquence des épidémies (Bylund, 1999; Logan *et al.*, 2003). Les changements climatiques pourraient également contribuer à synchroniser les épidémies de différents insectes (Myers, 1998). À l'opposé, une rupture attribuable aux changements climatiques semble être survenue dans le cycle épidémique de la tordeuse du mélèze dans les Alpes européennes au début des années 1980 (Esper *et al.*, 2007; Büntgen *et al.*, 2009).

Au Québec, la modification du régime des précipitations se traduisant par une réduction des précipitations pourra avoir un impact sur les épidémies de la tordeuse si les périodes de sécheresse, favorisant le développement et la survie des larves, sont plus importantes et que l'intervalle entre les feux en forêt boréale augmente (Bergeron et Leduc, 1998). Les régions où les changements climatiques entraîneront un cycle de feux plus long pourront subir plus de mortalité due aux épidémies de la tordeuse des bourgeons de l'épinette comparativement aux régions où le cycle des feux sera plus court (Bergeron et Leduc, 1998). Des périodes de sécheresse plus importantes entraînerait une augmentation du stress hydrique chez les arbres hôtes de la tordeuse ce qui pourrait favoriser la survie et la reproduction de la tordeuse et qui pourrait atteindre des niveaux de population plus importants.

Puisque les épidémies d'insectes forestiers ravageurs peuvent causer une mortalité importante des arbres sur de vastes superficies, une modification de la dynamique des épidémies pourraient avoir des répercussions importantes sur la gestion des ressources forestières, notamment sur les programmes de contrôle des populations d'insectes et sur les modèles prédictifs pour évaluer les prélèvements. Ces changements pourraient également affecter la résilience des écosystèmes, le cycle des nutriments, de même que les activités récréatives (Fleming et Volney, 1995; Anderson *et al.*, 2010).

1.6. OBJECTIFS

L'objectif principal de cette thèse est de reconstituer l'histoire des épidémies de la tordeuse des bourgeons de l'épinette survenues au Saguenay au cours de l'Holocène dans des secteurs où la dynamique récente des épidémies est bien documentée. Les objectifs secondaires sont *i*) de démontrer le potentiel de l'utilisation des crottins de la tordeuse pour reconstituer l'histoire récente des niveaux de population de cet insecte, *ii)* de vérifier si la dynamique des épidémies est restée la même lors des 8 000 dernières années, *iii*) de déterminer s'il y a eu des changements dans l'intensité des signaux épidémiques reconstitués par la paléoécologie au courant des derniers siècles et *iv*) d'établir si les épisodes épidémiques retracées dans les différents sites étudiés étaient synchronisés au courant de l'Holocène.

L'atteinte de ces objectifs permettra d'améliorer les connaissances sur la dynamique des épidémies de la tordeuse et de mettre en lumière les changements qui ont pu survenir lors des derniers siècles, suite à l'exploitation et l'aménagement des forêts par l'être humain par exemple.

1.7. HYPOTHÈSES DE RECHERCHE

La thèse comporte trois hypothèses générales.

1) *Les épidémies de la tordeuse survenues au cours de l'Holocène ont laissé des traces dans les dépôts tourbeux des peuplements de sapins et d'épinettes touchés.*

La découverte de crottins de plus de 1 500 ans dans des humus épais de l'archipel de Mingan (Simard *et al.*, 2002) témoigne de leur fort potentiel d'indicateur macrofossile pour retracer les épidémies. Afin de tester cette hypothèse, de petites tourbières situées en forêt boréale au Saguenay dans des secteurs où l'histoire récente des épidémies est bien documentée ont été sélectionnées pour une étude détaillée des preuves macrofossiles indicatrices d'épidémies d'insectes du passé.

2) *Il existe une forte correspondance entre les reconstitutions d'épidémies effectuées à partir de crottins et celles effectuées à partir d'autres indices.* Cette étude comparera plusieurs indicateurs permettant de reconstituer des épidémies d'insectes, sur une échelle de quelques siècles, afin de démontrer le potentiel ou les faiblesses respectives de chaque méthode d'analyse.

3) *Les périodes épidémiques sévères sont des épisodes rares au cours de l'Holocène et sont plus localisés que ceux observés depuis le début du 20^e^ siècle dans l'Est du Québec.*

Blais (1983) et Jardon (2001) ont observé un changement dans la dynamique des épidémies de la tordeuse des bourgeons de l'épinette au début du 20^e^ siècle. La fréquence des épidémies n'aurait pas changé mais leur intensité aurait augmenté et elles seraient davantage synchronisées sur de grands territoires. Les interventions humaines et une modification de la fréquence des feux pourraient être à l'origine de ce changement de dynamique. Ces conclusions ont été contestées par Boulanger et Arseneault (2004) qui n'ont pas observés de changements dans la fréquence ou le synchronisme des épidémies lors des 450 dernières années. Bien que la présente thèse ne permette pas d'évaluer si la fréquence des épidémies a changé au cours de l'Holocène, la comparaison de l'historique des épidémies des quatre tourbières à l'étude permettra de déterminer s'il y a eu des changements dans le synchronisme des épidémies lors des 8000 dernières années dans la région étudiée.

CHAPITRE 2. VALIDATION OF SPRUCE BUDWORM FECES AS A PROXY TO RECONSTRUCT RECENT INSECT OUTBREAKS

2.1. ABSTRACT

A small ombrotrophic peatland located in a balsam fir – black spruce forest in the Saguenay region (Quebec, Canada), disturbed by spruce budworm (*Choristoneura fumiferana*) outbreaks, was studied to validate the potential of budworm feces as proxies for the reconstruction of the history of epidemics. With the help of ^{210}Pb dating, the outbreaks detected in two peat profiles and one humus section were associated with those observed in tree-ring chronologies. The well-documented outbreaks of the 1950's and the 1970's were detected in the peat and humus profiles, as well as in a tree-ring chronology constructed with trees growing near the peatland. For the detection of older outbreaks, like the ones of the end of the 19th and beginning of the 20th centuries, some differences were observed between the profiles and published tree-ring chronologies. Macrofossil analyses suggest five recent outbreaks compared to only three for tree-ring analyses. Several factors may explain those differences, notably trees too young to sustain a dense population of spruce budworm larvae, so less severely affected. The discrepancies observed between the outbreak records reconstructed using different techniques may also be the result of a variable macrofossil input, or local differences in the intensity of outbreaks. This study showed that the results obtained with macrofossil analysis and dendrochronology are complementary; combined together, these two methods give a more complete history of spruce budworm outbreaks at a particular site.

2.2. INTRODUCTION

Defoliating insects play a major role in forest dynamics and may have a significant impact on forest harvesting by killing a large number of trees; this explains why a lot of attention has been paid to the study of the history of outbreaks. Spatial and temporal approaches can be used to reconstruct outbreak history or insect population fluctuations. Tools like egg mass or larvae counts, pheromone-bait traps and defoliation maps are used at a spatial scale to evaluate insect population levels and the spatio-temporal dynamics of defoliation (Brown, 1970; Kettela, 1983; Royama, 1984; Elkinton and Liebhold, 1990; Myers, 2000; Royama *et al.*, 2005; Buntgen *et al.*, 2009). Remote sensing is also used to monitor the spread of insect defoliation (Radeloff *et al.*, 1999; Cairns *et al.*, 2008). These survey methods often cover only one or a few epidemics of an insect, depending on the length of outbreak cycles or time elapsed between outbreaks, if they are not cyclic. They provide useful information on population abundance. However, methods like defoliation mapping are of limited usefulness for detecting changes at low population densities, so they may provide wrong information on the rate of change between endemic and epidemic levels (Régnière, 1985).

Long temporal studies of outbreak dynamics rely mainly on dendrochronological methods. Tree-ring analyses are used to identify and date insect outbreaks (Swetnam and Lynch, 1989; Morin *et al.*, 1993; Ryerson *et al.*, 2003; Nishimura and Laroque, 2010), to measure tree growth losses caused by insect defoliation (Maclean, 1984; Alfaro and Maclauchlan, 1992; Jardon *et al.*, 1994; Muzika and Liebhold, 1999), or to study forest regeneration after a large disturbance (Wickman, 1980; Morin, 1994, Man and Rice, 2010). A few hundred years of outbreak history can be reconstructed with tree rings, but trees sampled are often survivors which may have sustained less damage than the trees killed by the insects during an outbreak. As a result, the information obtained from tree-ring analyses probably may underestimates the extent and severity of past outbreaks (Régnière and Lysyk, 1995). Also, the first year of defoliation may be inaccurately detected by tree-rings studies due to the time-lag between the first year of insect damage and the first year of tree-ring growth reduction near the base of host trees (Krause and Morin, 1995*a*, 1995*b*, 1999; Simard and Payette, 2003).

In eastern North America, spruce budworm (*Choristoneura fumiferana* [Clem.]) is one of the major defoliating insects disturbing coniferous forests. Recurrent outbreaks reduce the growth or kill vast areas of balsam fir (*Abies balsamea* [L.] Mill.) and spruce (*Picea* spp.) forests. Several studies were dedicated to the understanding of the spatial and temporal dynamics of spruce budworm outbreaks. The mapping of budworm defoliation between 1909 and 1981 illustrates the spread of outbreaks in eastern Canada (Brown, 1970; Kettela, 1983; Hardy *et al.*, 1986), while several dendrochronological studies have contributed to the reconstruction of about three hundred years of epidemics (Blais, 1965; Morin and Laprise, 1990; Krause, 1997; Jardon *et al.*, 2003, Boulanger and Arseneault, 2004).

On a longer temporal scale, macrofossil analysis helped to reconstruct the fluctuations in spruce budworm abundance during the Holocene (Bhiry and Filion, 1996; Jasinski and Payette, 2005; Simard *et al.*, 2002, 2006). Spruce budworm feces give information on the past insect abundance on a millennium time scale, but it is not clear whether this indicator provides reliable, and possibly different, information on outbreaks, considering the slow accumulation of the peat material in which the feces are extracted (Simard *et al.*, 2002, 2006).

In order to reconstruct recent spruce budworm outbreaks and to confirm the potential of feces as a proxy for outbreaks on a longer time scale, we compared the recent outbreak history of a small ombrotrophic peatland in Québec (Canada) reconstructed using macrofossil analysis and tree-ring chronologies. We hypothesized that any outbreaks during the last two centuries would have left distinct traces in peat and humus material – as clear as those detected in tree-ring chronologies – and that combined with ^{210}Pb dating, paleoecology can provide additional and reliable information on recent spruce budworm outbreaks of a region.

0.3. STUDY AREA

The study area is located in the Mont Valin region, approximately 100 km north of Saguenay, in the province of Quebec, Canada (Figure 2.1). It is included in the balsam fir (Abies balsamea [L.] Mill.) – white birch (Betula papyrifera Marsh.) and in the balsam fir – black spruce (Picea mariana [Mill.] B.S.P.) ecological regions (Thibault, 1987). The landscape is mountainous and the area lies on Precambrian crystalline rocks (Rowe, 1972). The major disturbances affecting the forests of the area are logging, fire and spruce budworm outbreaks.

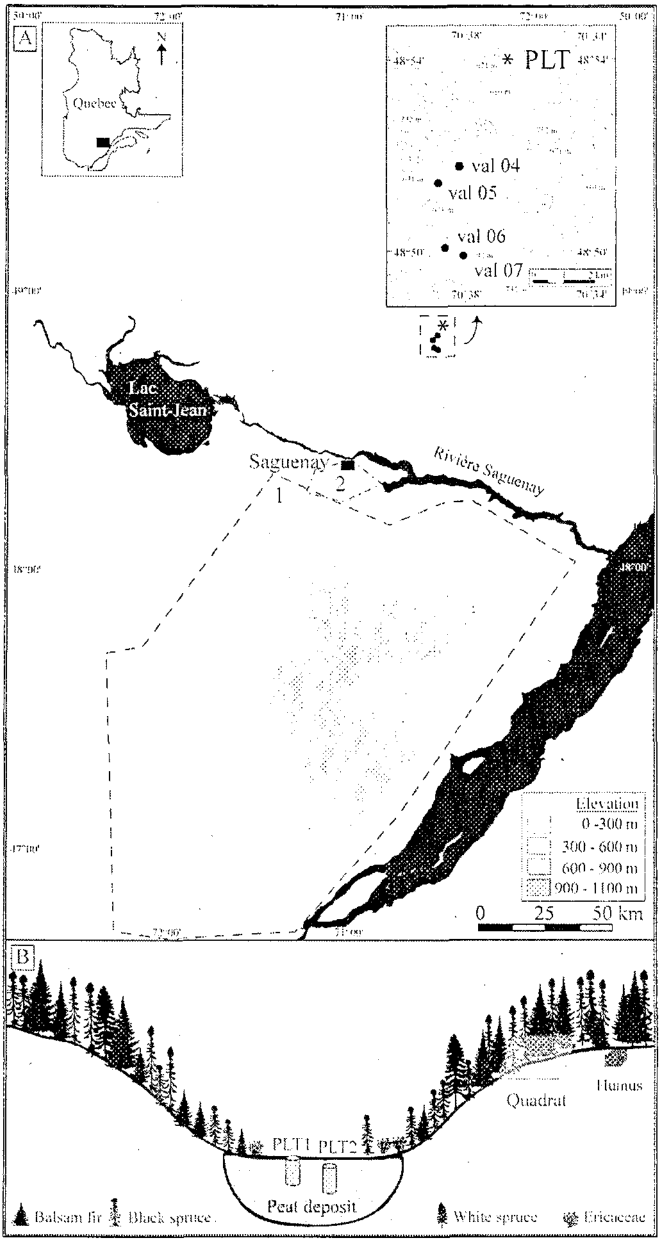

Figure 2.1A) Location of the PLT study site (Saguenay region, Quebec, Canada; macrofossil and tree-ring analyses), along with the position of Morin (1994, 1998) sites val 04, val 05, val 06 and val 07 (tree-ring analyses). Areas 1 and 2 represent the study areas of Blais (1965) and Krause (1997), respectively (tree-ring analyses). B) Schematic representation of the PLT study site, with the approximate position of the PLT1 and PLT2 peat cores, of the PLT humus section, and of the quadrat delineated to collect samples for a tree-ring analysis.

A small ombrotrophic peatland of approximately 0.02 ha, (PLT: 48° 54' 07" N, 70° 36' 35" W, 645 m above sea level) was selected for this reconstruction of spruce budworm outbreaks (Figure 2.1). This peatland is surrounded by a dense forest composed of 65% of black spruce and 35% of balsam fir, with some white spruce (*Picea glauca* [Moench] Voss), trees species that are susceptible to spruce budworm outbreaks. Data available on recent fire history of the study site do not reveal any fire since 1972 (Ministère des Ressources naturelles et de la Faune du Québec, personal communication, 2005). Recent spruce budworm outbreaks were registered in the area in 1914, 1952 and 1978; these years correspond to the lowest radial tree growth during the epidemics recorded in tree-ring chronologies (Morin, 1994, 1998).

0.4. METHODS

Macrofossil reconstruction of spruce budworm outbreak history was conducted on the first 40 cm of two peat cores (PLT1, PLT2) and on one humus section (20 × 20 × 21 cm, down to the mineral soil). The PLT1 peat core was extracted approximately 5 m from the forest edge surrounding the peatland. It was the closest location possible due to the configuration of the peatland, fallen trees on the ground and buried trees in the peat. The PLT2 core was extracted approximately 3 m from PLT1, i.e., 8 m from the forest edge. The humus section was extracted from the soil under the canopy, approximately 50 m from the peat cores, on the top of a hill (Figure 4.1). A Coûteaux corer (Coûteaux, 1962) with a 10-cm diameter was used to sample peat, while a hand saw and a small shovel were used to extract the humus section.

The three soil profiles were wrapped in plastic and transported to the laboratory where they were kept frozen until further manipulations. They were cut into continuous

1-cm thick samples and placed in labeled bags. The samples were washed gently with water, and the material collected by 2.0, 1.0 and 0.5 mm mesh sieves was examined at 60× under a binocular microscope. Spruce budworm feces found in the samples were identified according to Simard *et al.* (2002, 2006). Feces are often characteristic in size and form for larvae of different ages and species (Morris, 1949; Fridén, 1958). Spruce budworm feces are small brown cylinders composed of conifer leave fragments mixed with organic matter. Their size varies from 0.8 to 1.1 mm in width, and from 1.6 to 3.2 mm in length, respectively. To make sure that the feces found in the peat profiles were produced by spruce budworm and not by another insect species, they were compared to feces 1) of spruce budworm larvae reared in laboratory and feeding on balsam fir and black spruce leaves, 2) collected on the ground in the Saguenay region during the last spruce budworm outbreak, and 3) collected in a site presently affected by moderate spruce budworm defoliation. The feces found in the peat profiles were also compared to reference feces of four other defoliating insects found in the boreal forest of Québec, e.g, the hemlock looper (*Lambdina fiscellaria fiscellaria* [Guen.]), the eastern blackheaded budworm (*Acleris variana* [Fern.]), the yellowheaded spruce sawfly (*Pikonema alaskensis* [Rohwer]) and the Swaine jack pine sawfly (*Neodiprion swainei* Midd.). Larvae of these four species were reared in laboratory to obtain feces. They all showed important differences from the spruce budworm fecal pellets. Their shape was approximately the same (cylinder), but their color and proportions were different (Simard *et al.* 2002, 2006).

Twelve peat samples per profile and ten samples of humus were submitted to ^{210}Pb dating. Based on the radioactive decay series of ^{238}U, ^{210}Pb dating (Goldberg, 1963, Appleby and Oldfield, 1978) allows for radiometric dating of peat deposits over the past 150–200 years (Turetsky *et al.*, 2004). The total 210Pb pool in peat has a supported 210Pb component produced within the peat via radioactive decay of ^{222}Rn that never diffused to the atmosphere; and an unsupported ^{210}Pb component derived from ^{222}Rn that first diffused into the atmosphere and subsequently decayed to ^{210}Pb. Unsupported ^{210}Pb is removed from the atmosphere via wet deposition and dry fallout and later deposited onto the earth's surface. In undisturbed peat, the unsupported 210Pb activity is highest in young surface deposits and decrease in older, deeper material as a result of radioactive decay (Appleby and Oldfield 1983). By quantifying the unsupported 210Pb inventory from the surface to a depth where unsupported 210Pb is undetectable, it is possible to calculate the age-depth relations for a peat deposit (Turetsky *et al.*, 2004).

Ages were calculated according to a constant rate of supply model (CRS model), and a second order polynomial model was used to describe the age vs. depth relationship of the profiles. The CRS model assumes a constant supply of ^{210}Pb to the surface of a vertically aggrading soil, sediment or peat deposit. It allows accurate dating despite temporal variations in sediment or accumulation rates. This model is appropriate for dating peat cores, particularly in ombrotrophic peatlands that only receive atmospheric inputs of ^{210}Pb (Turetsky *et al.*, 2004). Fragments of wood, leaves and seeds extracted from the PLT1 peat core at a 37-cm depth were also dated by the accelerator mass spectrometry radiocarbon method. The conventional radiocarbon date was converted to a calendar age according to Stuiver *et al.* (1998).

In order to validate the recent spruce budworm outbreak history reconstructed with macrofossil analysis, a tree-ring chronology was built from 40 balsam fir trees, the preferential host species of spruce budworm (dbh > 3 cm), contained in a 20 × 20 m quadrat located in the forest surrounding the peatland near the extraction site of the humus section (Figure 2.1). One wood core per tree was extracted 30 cm above the ground with a Pressler borer. Usual dendrochronological techniques were used for the sanding, dating and measuring of the cores, which was done with a precision of 0.01 mm (Swetnam *et al.*, 1985; Cook and Kairiukstis, 1990). Two cores had to be discarded due to inexplicable irregularities, so 38 raw series were visually cross-dated on a light table and with the COFECHA software to validate the dating and localize missing tree-rings (Holmes, 1997). All raw chronologies were standardized with the ARSTAN program (Cook and Holmes, 1999) to remove the long-term age-related growth trend. Standardization was realized by dividing each raw series with a cubic smoothing spline with a 50% frequency response of 50 years. A mean standardized chronology was then built by averaging all 38 series according to the calendar years of tree-ring formation. Past spruce budworm outbreaks were visually identified by comparing tree growth reductions of the chronology with published regional chronologies, which were based on comparisons with growth curves of non-host species such as jack pine (*Pinus banksiana* Lamb.) and white birch (Morin, 1994, 1998; Krause and Morin, 1995a). In addition to this chronology, the recent spruce budworm outbreak history reconstructed by macrofossil analysis was also compared with three other tree-ring chronologies realized by Blais (1965, Figure 2.1 area 1) Morin (1994, 1998, Figure 2.1, val 04, val 05, val 06 and val 07) and Krause (1997, Figure 2.1, area 2) near the study site. For Blais (1965) and Krause (1997) chronologies, only the outbreaks that occurred after 1800 were considered for this comparison.

2.5. RESULTS

0.5.1. RADIOMETRIC ACTIVITY

The unsupported ^{210}Pb activity decreased from the surface to the bottom of the profiles. The maximum values observed for unsupported ^{210}Pb activity PLT1, PLT2 and PLT humus were respectively 46.94, 22.01 and 36.27 dpm/g. The ^{210}Pb activity reached background levels between depth 20 and 29 cm. The age vs. depth relationships goes back to 1800 AD, and the coefficients of the polynomial regressions for the age vs. depth relationships are highly significant (Figure 4.2). Istotopic ^{210}Pb concentrations found in the two peat profiles and in the humus section indicated stratigraphic continuity.

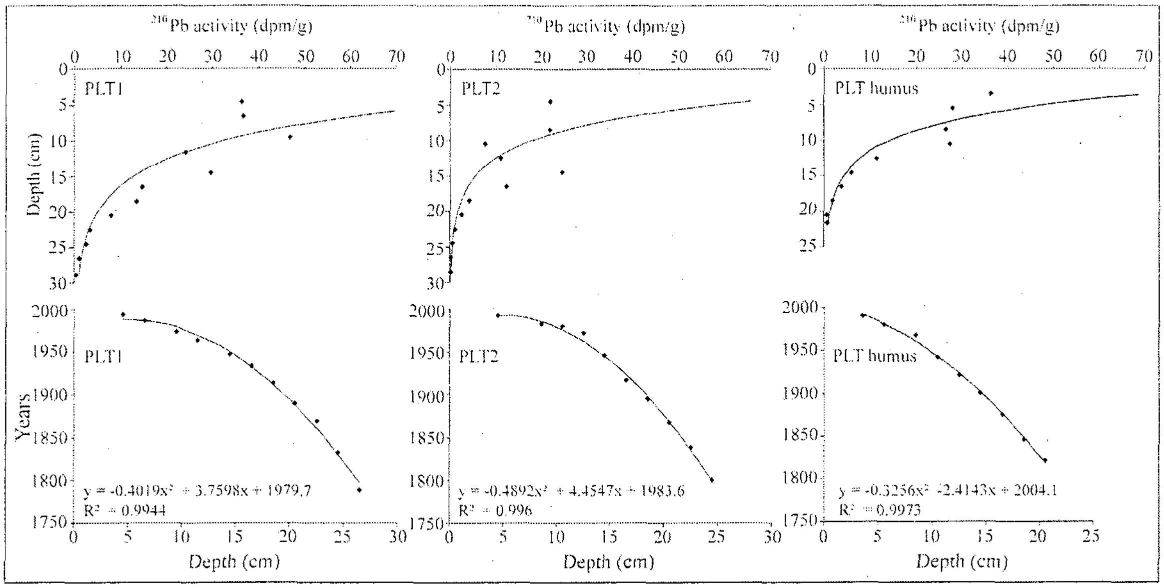

Figure 2.2 Maximum unsupported ^{210}Pb activity and age vs. depth relationships of the PLT1 and PLT2 peat cores, and of the PLT humus section, respectively. Age models and R^2 are also shown.

0.5.2. SPRUCE BUDWORM FECES ABUNDANCE

Abundant spruce budworm feces were extracted in the top 25 cm of the PLT1 peat core, and throughout the PLT2 core and the PLT humus section (Figure 2.3). Distinct peaks of feces were observed in PLT1 around 9, 14 and 20 cm, which correspond to the years 1972, 1947–1952 and 1884–1897, respectively (Figure 2.4). Two other peaks, less distinct, may also be outlined at 4 cm (1994) and 16 cm (1920–1939). Peaks were also observed in PLT2 in the first centimetre, around 4, 8, 14, 24, and 32 cm, which can be associated with the years 1998–2000, 1994, 1984–1988, 1940–1950, 1827–1845 and 1800–1809, respectively.

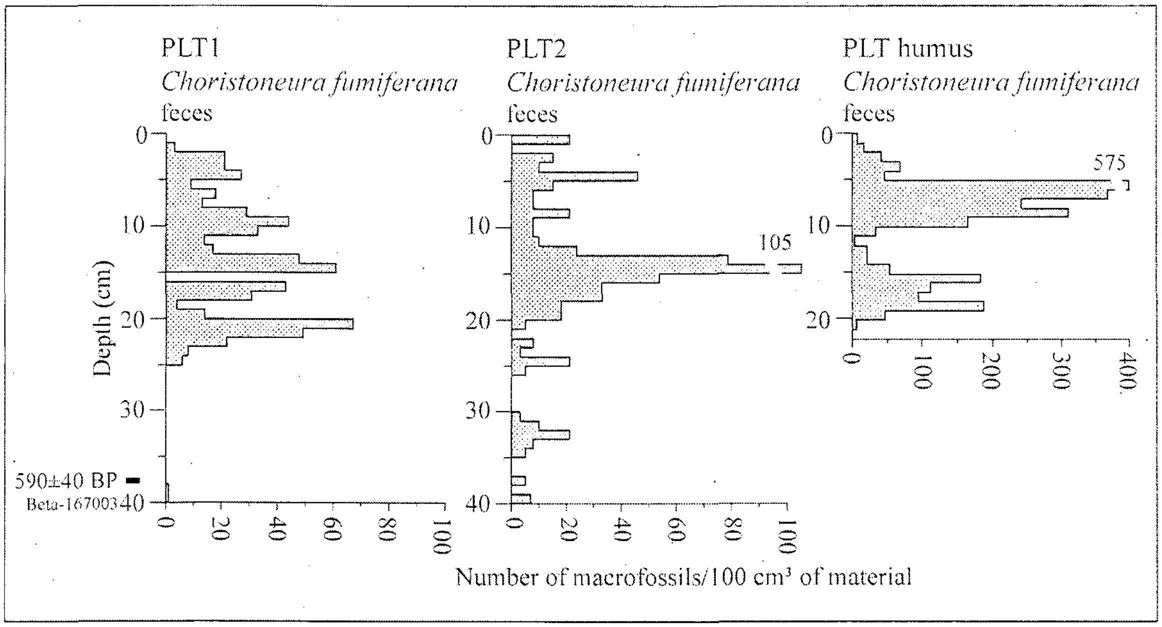

Figure 2.3 Abundance of spruce budworm (*Choristoneura fumiferana*) feces vs. depth found in the PLT1 and PLT2 peat cores, and in the PLT humus section

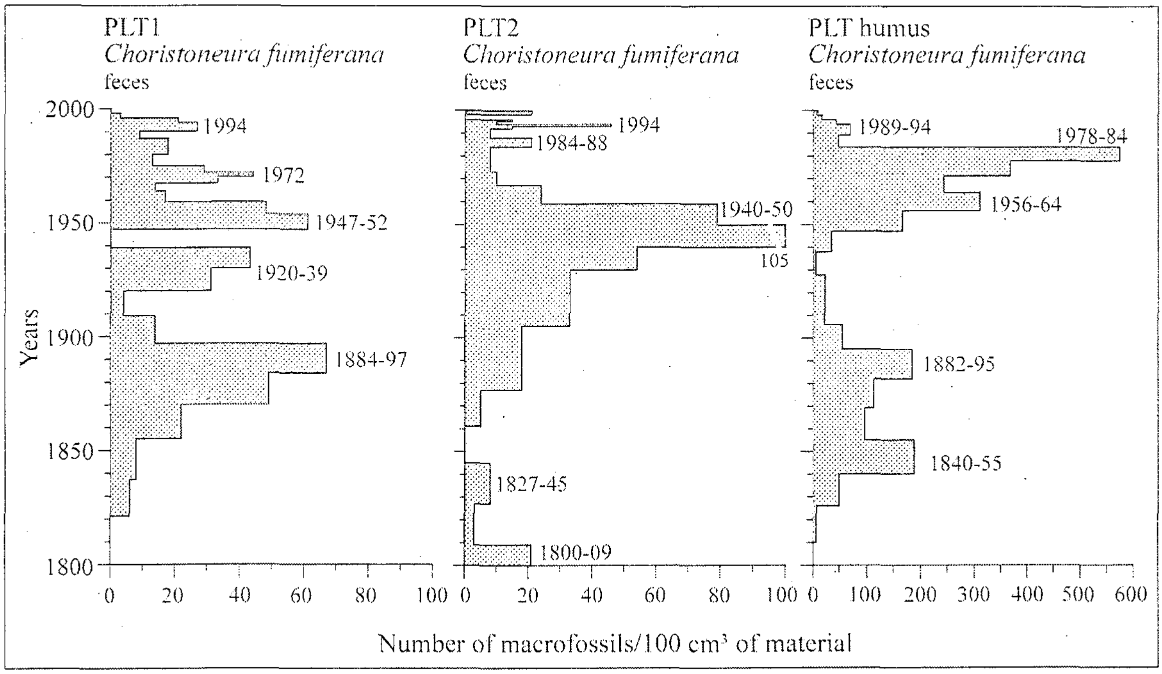

Figure 2.4 Spruce budworm (*Choristoneura fumiferana*) feces abundance through time for the PLT1 and PLT2 peat cores, and for the PLT humus section.

The PLT humus section showed peaks of spruce budworm feces at, 5, 8, 15 and 18 cm, which corresponds to the years 1978–1984, 1956–1964, 1882–1895 and 1840–1855, respectively. A smaller and less distinct peak can also be observed at 3 cm, corresponding to the years 1989–1994.

0.5.3. TREE-RING CHRONOLOGY

The balsam fir tree-ring chronology of the PLT site went back to 1838, but the majority of the sampled trees were approximately 100 years old. Three periods of spruce budworm outbreaks were identified in the tree-ring reconstruction, i.e., between 1912 and 1931, between 1940 and 1955, with a local temporary growth restart around 1945, and between 1975 and 1981 (Figure 2.5). Other regional tree-ring chronologies (Figure 2.6) covered a period of three hundred years, and showed several tree growth reductions associated with spruce budworm outbreaks.

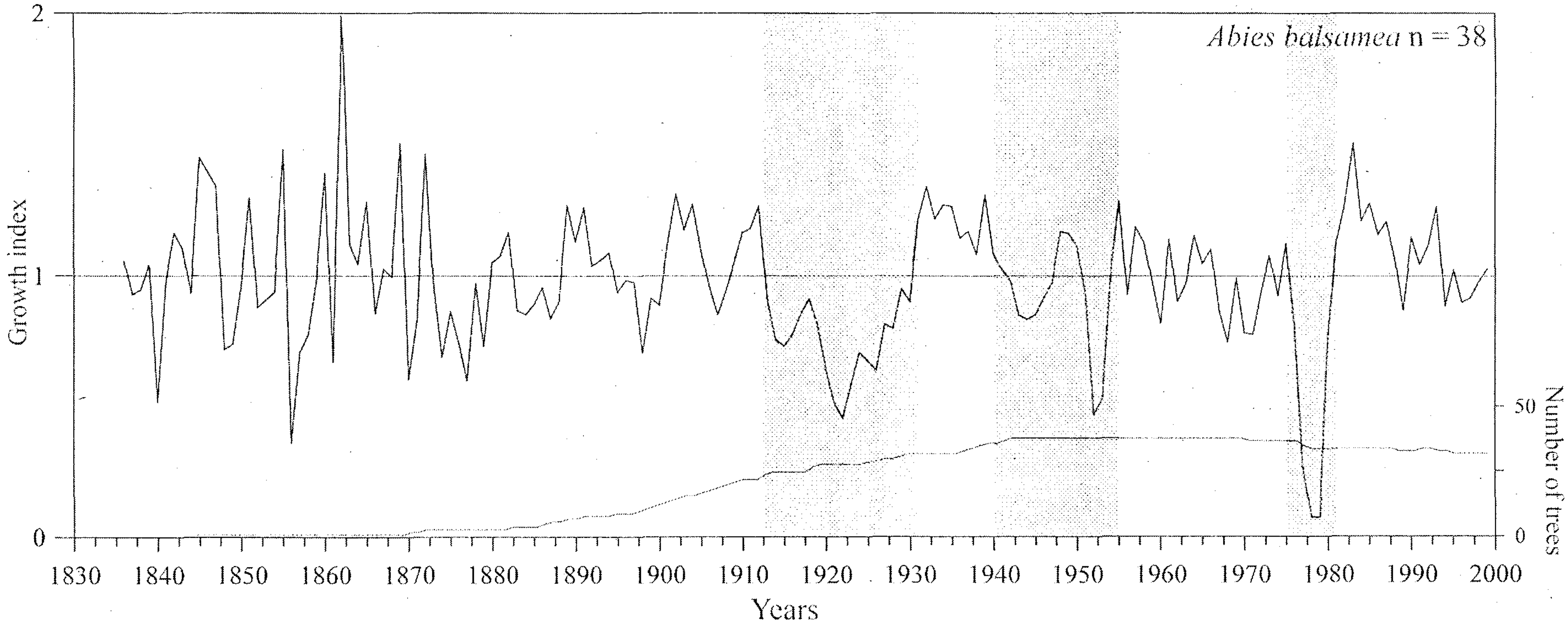

Figure 2.5 Standardized tree-ring chronology of balsam fir (*Abies balsamea*) trees sampled in the PLT study site. The shaded areas represent spruce budworm outbreaks that affected the study area.

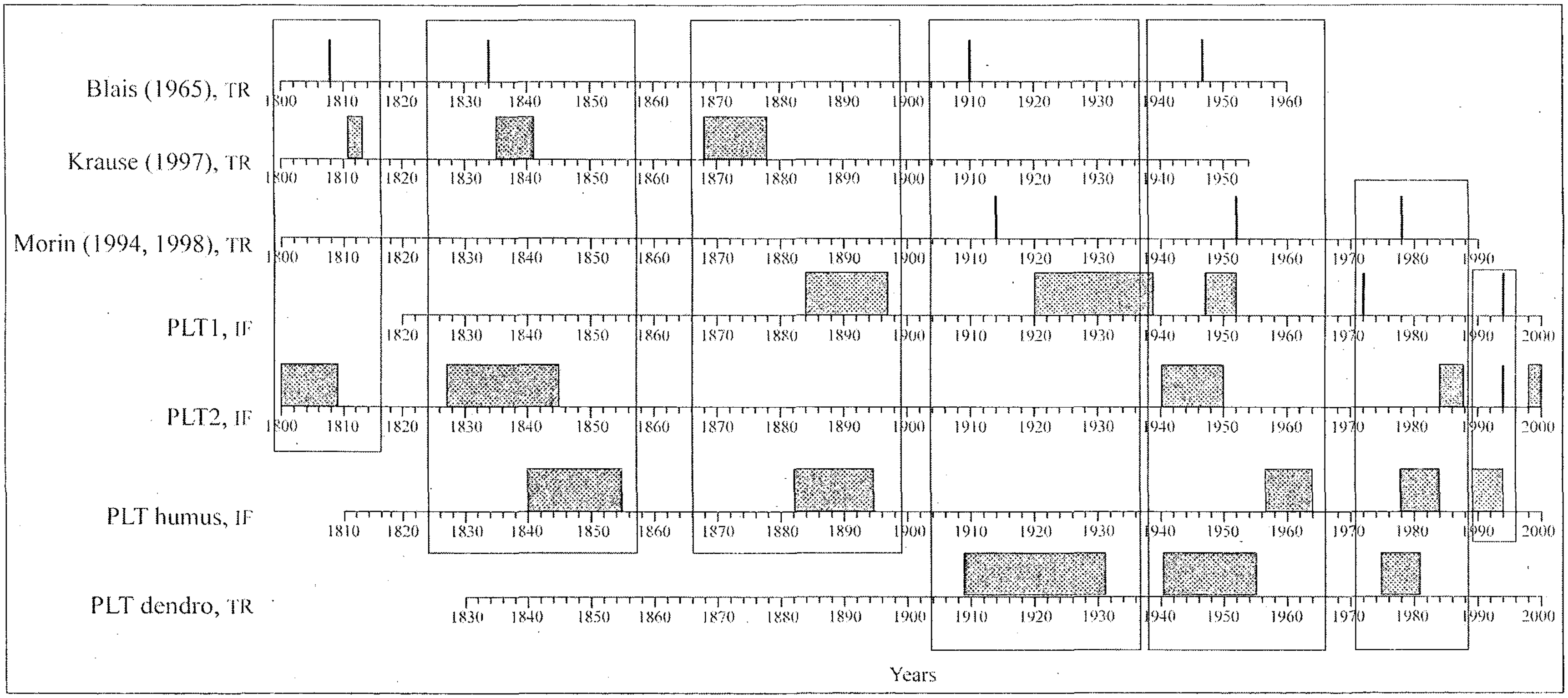

Figure 2.6 Spruce budworm (*Choristoneura fumiferana*) outbreaks (shaded areas) identified near the study area with tree-rings (TR) or with insect feces (IF). For Blais (1965) and Krause (1997) studies, only the outbreaks that occurred after 1800 were considered. Vertical lines represent narrow rings associated with an outbreak; the empty boxes represent periods of growth reduction or spruce budworm feces abundance associated with outbreaks.

0.6. DISCUSSION

A reconstruction of the history of spruce budworm outbreaks for a particular site is usually based on tree-ring analyses. Paleoecology has been used to detect past insect population fluctuations at a multi-millennial time scale but not to reconstruct recent outbreaks. In this study, several distinct peaks of feces were detected near the surface of two peat profiles and one humus section, allowing the testing of the accuracy of macrofossil analyses and their potential for recent and long-term spruce budworm outbreak reconstructions. By using the CRS model of ^{210}Pb dating, it has been possible to associate these recent peaks of spruce budworm feces to known outbreaks previously documented by dendrochronological studies (Figure 2.6).

The two well-documented outbreaks of the 1950's and 1970's were detected in the two peat profiles and in the humus section. They were also detected in the tree-ring chronology built for this project. The dates obtained varied between 1972 and 1988 for the last outbreak, and between 1940 and 1964 for the previous one. These dates are similar to those extracted from published tree-ring chronologies (Figure 2.6). The differences observed between the years may be due to the fact that some studies used single years to identify outbreaks, while others used time intervals. Also, the differences may be attributable to the precision of the methods used for dating. In fact, for dendrochronological records, there may be a lag between the occurrence of defoliation and the production of a narrow ring associated to the defoliation, or between the end of the growth suppression and the increase in ring width to pre-outbreak levels(Krause and Morin, 1995a), whereas for macrofossil analyses, one centimetre of peat material may represent several years.

The detection of older outbreaks differed between the peat and humus profiles and the PLT tree-ring chronology, especially for the outbreak that occurred at the beginning of the 20th century. This outbreak was only detected in the PLT1 peat core and the PLT tree-ring chronology, i.e, between 1920 and 1939, and between 1912 and 1930, respectively. It left no distinct trace in the PLT2 peat core and the PLT humus section. Also, the outbreak that occurred at the end of the 19th century was recorded in the PLT1 peat core and in the PLT humus section, but not in PLT2 core or the tree-ring chronology. This suggests that spruce budworm feces give insights about some outbreaks that are difficult to obtain using conventional tree-ring series, especially if the trees are suppressed or too young during the epidemic to sustain a dense population of feeding larvae, or if all the suitable trees were killed and no survivors remain for future tree-ring reconstructions. The raw data used to build the tree-ring chronology (not shown in this chapter) indicate trees started to grow again at the end of the 19th century. The trees were probably established following the previous outbreak, so they were probably too young to sustain important populations of feeding larvae at that time. Moreover, they were in the understory of the forest, so the growth reduction was probably difficult to detect in the tree-rings. The use of black spruce instead of balsam fir for the tree-ring chronology might have given a longer chronology since black spruce lives longer and is less susceptible to spruce budworm then balsam fir.

One additional outbreak was detected in PLT2 and PLT humus between 1827 and 1855. That outbreak was also registered by Blais (1965) and by Krause (1997). Finally PLT2 is the only profile in which we have detected the outbreak at the beginning of the 19th century between 1800 and 1809. This outbreaks is however outside of the reliability of the dating method. Blais (1965) and Krause (1997) also detected that outbreak respectively in 1808 and between 1811 and 1813. In addition, small peaks of feces were detected in PLT1, PLT2 and PLT humus around 1994 and 1998. These recent peaks correspond to the light defoliation observed by the Ministère des Ressources naturelles et de la Faune, who is monitoring the activity of spruce budworm in the province (Ministère des Ressources naturelles et de la Faune, 2005a, 2005b)

Overall, with the use of spruce budworm feces, we were able to detect all of the recent documented spruce budworm outbreaks with feces retrieved in the peat cores and/or the humus monolith. None of the dendrochronological series or the macrofossils records were able to detect all outbreaks. Spruce budworm outbreaks are not homogenous at the local or regional level. There might be some patches of unaffected forest or varying levels of outbreak intensity across an area (Bouchard et al, 2006; Lavoie *et al.*, 2009), which can explain why an outbreak is registered at one site and not another. PLT1 and PLT2 did not register the same outbreaks. PLT1 registered the outbreaks of the 1890's, 1920's, 1950's and 1970's, while PLT2 registered the older outbreaks, at the beginning of the 1800's and in the 1830's, and the recent ones, in the 1950's and the 1970's. The differences that were observed between the number of peaks of feces and the dates obtained for the two peat profiles may be attributable to the fact that PLT1 was collected closer to the forest edge than PLT2, so their macrofossil inputs were probably different. Also, the ability of peat to record a forest disturbance at a given point decreases as the distance to the forest margin increases (Pitkänen *et al.*, 2001). The further the core is collected from the forest edge, the smaller is the probability that macrofossil pieces from trees or from the disturbance affecting the trees will be accumulated in the soil. Temporal differences between cores may be attributable to the ^{210}Pb dating method. There is an increasing error in the CRS data with depth; it becomes large for dates near 100 years because of the uncertainty involved in estimating the small amount of ^{210}Pb contained in older sediment (Appleby *et al.*, 1988; Turner and Delorme, 1996). ^{210}Pb dating usually constructs a continuous reliable dating record extending back to no more than about 150 years.

0.7. CONCLUSION

We demonstrated the reliability of spruce budworm feces as indicators of recent outbreaks by validating the macrofossil reconstructions with published chronologies. We were able to detect five outbreaks with feces compared to only three with the tree-ring chronology built for this project. The trees of the study area were relatively young and only a few of the trees used to build the tree-ring chronology were more than one hundred years old. Macrofossil analyses combined to ^{210}Pb dating may be less precise in time and space than tree-ring chronologies, but they offer the possibility to go back further in time, and to delineate outbreaks that would not be detectable with other means in certain circumstances. Both methods have strengths and weaknesses. Both indicators (feces, tree rings) should be used together in order to retrieve as much information as possible on spruce budworm outbreaks. The cost of 210Pb dating, approximately 100.00 $ per sample, should be taken in consideration when choosing the method.

0.8. AKNOWLEDGEMENTS

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CHAPITRE 3. A MILLENIAL-SCALE RECONSTRUCTION OF SPRUCE BUDWORM ABUNDANCE IN SAGUENAY, QUEBEC, CANADA

Simard, I. Morin, H. and Lavoie, C. «A millennial-scale reconstruction of spruce budworm abundance in Saguenay, Québec, Canada», *The Holocene*, vol. 16, n°1, 2006, p.31-37.

3.1. ABSTRACT

A high-resolution macrofossil analysis was conducted to reconstruct spruce budworm abundance in an 8600-year old peatland in Saguenay, Québec, Canada. Abundant spruce budworm (*Choristoneura fumiferana* [Clem.]) feces recovered in the peat profile suggested endemic and epidemic presence of the insect in the study site since 8240 cal. BP. Important variations in the abundance of feces were observed, and two exceptional periods of insect activity were delineated, from 6815 to 6480 cal. BP and during the 20th century. Lepidoptera head capsules were also found in the Lac des Îlets peat profile. They were less abundant and more fragmented and decomposed than spruce budworm feces, but they offered complementary information on insect activity. The long-term perspective achieved with this macrofossil analysis strongly suggests that intense periods of spruce budworm activity were rare events during the Holocene.

3.2. INTRODUCTION

Disturbances such as fire and insect outbreaks have a major influence on the dynamics of boreal ecosystems, more particularly on forest composition and structure (Payette, 1992; Bergeron *et al.*, 1998; McCullough *et al.*, 1998). Insect outbreaks have been studied worldwide to understand their impacts on forest dynamics. Dendroecological and paleoecological techniques have been used to reconstruct insect outbreak history (Elkinton and Liebhold, 1990; Veblen *et al.*, 1991, 1994; Swetnam and Lynch, 1993). Spruce budworm (*Choristoneura fumiferana* [Clem.]) has been widely studied in this respect because it is the main insect affecting coniferous forests in eastern North America (Hardy *et al.*, 1986). Periodic increases in budworm populations to epidemic levels cause extensive mortality and growth reduction in balsam fir (*Abies balsamea* [L.] Mill.) and black spruce (*Picea mariana* [Mill.] B.S.P.) populations (Blais, 1983; Miller and Rusnock, 1993). Using tree rings, it is possible to reconstruct three to four hundred years of spruce budworm activity (Blais, 1965, 1983; Morin and Laprise, 1990; Morin *et al.*, 1993; Morin, 1994, 1998; Krause, 1997). However, the time frame of tree-ring studies is limited by the age of trees, and it is rare to find living balsam fir or black spruce older than 300 years. A millennial-scale perspective is nevertheless essential to achieve a better understanding of natural disturbance cycles and to evaluate the impacts of recent forest management strategies.

A long-term perspective can be achieved with the help of paleoecological proxies. Most paleoecological reconstructions of insect outbreaks used head capsules as indicator of the presence of the insect. By using head capsules of hemlock looper (*Lambdina fiscellaria fiscellaria* [Guen.]) and hemlock needles showing chewing damage as indicators, Bhiry and Filion (1996) were able to associate the mid-Holocene hemlock decline in eastern North America with phytophagous insect activity. Head capsules were also tentatively used to reconstruct spruce budworm outbreaks (Davis *et al.*, 1980), but they were too scarce and fragmented to provide a valuable long-term history of insect infestations. Spruce budworm feces recovered from thick boreal forest humus were also used as a paleoecological indicator to reconstruct recent outbreak history. The discovery of 1500-year old feces in thick humus deposits suggests that this proxy could be used for the long-term reconstruction of insect outbreaks (Simard *et al.*, 2002). The objective of this research was to reconstruct spruce budworm outbreaks and vegetation history of an 8600-year old ombrotrophic peatland in Saguenay, Québec, Canada.

3.3. STUDY AREA

The study area is located in the Laurentides Wildlife Reserve (48°11’50”N, 71°14’34”W, 120 m a.s.l.), approximately 30 km south of Saguenay, Québec, Canada (Figure 3.1). It is included in the Laurentides – Onatchiway forest region (Rowe, 1972) and the balsam fir – white birch (*Betula papyrifera* Marsh.) ecological region 8e (Thibault, 1987). The relief is undulating to mountainous and the area lies on Precambrian crystalline rocks (Rowe, 1972). Regional weather conditions at the study area for AD 1961 – 1990 (Bagotville station A, 48°20’N, 71°00’W, 159 m a.s.l.) are characterized by a mean annual temperature of 2.2 °C and mean annual precipitation of 930 mm, 37% falling as snow (Environnement Canada, 1993). The main natural disturbances affecting the forests of the Laurentides Wildlife Reserve are spruce budworm outbreaks and fires. The most recent spruce budworm outbreaks affecting the study area were registered around AD 1748, 1808, 1834, 1910, 1947 and 1972 (Blais, 1965; Lussier *et al.*, 2002). The fire history of the study area is not known. The study site is located in the forested area of the Lac des Îlets peatland, approximately 500 m away from the open ombrotrophic part of the peatland, in a dense black spruce stand growing on a thick peat deposit (Figure 3.1). The vegetation is dominated by black spruce and mosses, mainly *Sphagnum* spp. and *Pleurozium schreberi* (Brid.) Mitt.

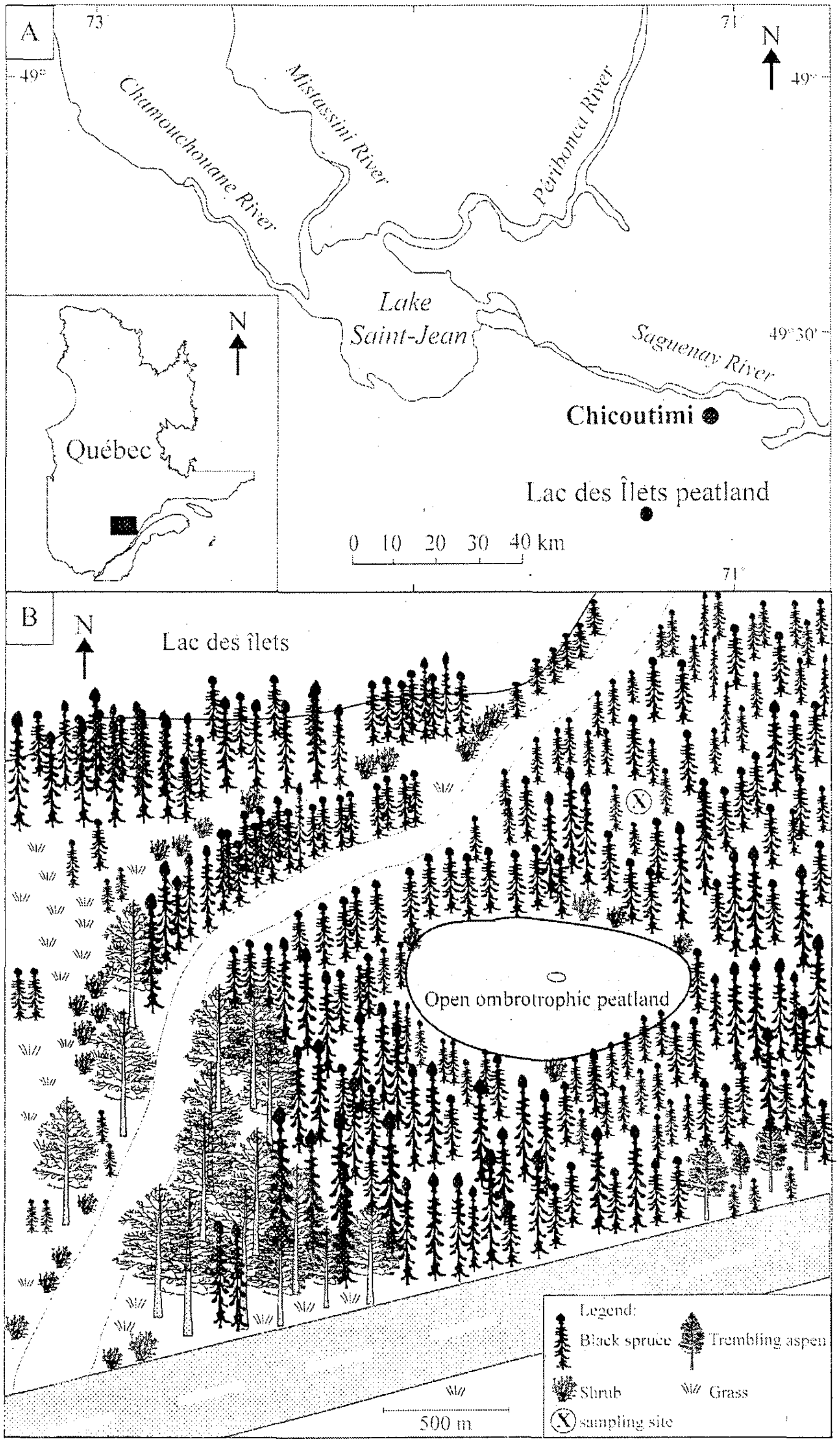

Figure 3.1 Localization of the Lac des Îlets peatland (Saguenay, Québec, Canada) (A) and schematic representation of the study site (B).

3.4. METHODS

A 258-cm core, covering the entire peat deposit and the upper part of the underlying clay deposit, was extracted in the forest area of the peatland. The first 40 cm of the profile were extracted with a shovel (10 × 10 × 40-cm monolith). A Coûteaux corer (Coûteaux, 1962) with a 10-cm diameter was used to sample peat from 40 to 207 cm. The bottom part of the core (207 – 258 cm) was sampled using a 4.5-cm diameter side-wall peat corer (Jowsey, 1966). The peat was wrapped in plastic and aluminum foil and placed in plastic tubes for transportation to the laboratory where it was kept frozen.

The entire profile was cut into continuous 1-cm thick slices for macrofossil analysis. No chemical treatment was applied to the samples. Samples were washed through a series of sieves (2, 1, 0.5-mm meshes). Macrofossils recovered (charcoal, spruce budworm feces, Lepidoptera head capsules, vascular plant, moss and other animal remains) were identified and counted at 60× under a binocular microscope. Plant macrofossils were identified using Montgomery (1977) and Lévesque *et al.* (1988) illustrated guides. A reference collection of seeds, fruits, leaves and stems was also used to identify macrofossils. Nomenclature follows Marie-Victorin (1995) for vascular plants, except Farrar (1996) for trees, and Anderson *et al.* (1990) for mosses. Spruce budworm feces (Figure 2.2) were identified according to Simard *et al.* (2002). They were compared to reference feces 1) of spruce budworm produced by reared larvae feeding on balsam fir and black spruce trees, 2) of spruce budworm collected on the ground during the last outbreak, and 3) collected in a site presently affected by moderate defoliation by spruce budworm. The feces found in the peat profile were also compared to reference feces of four other defoliating insects found in boreal forests of Québec: hemlock looper

(*Lambdina fiscellaria fiscellaria* [Guen.]), eastern blackheaded budworm (*Acleris variana* [Fern.]), yellowheaded spruce sawfly (*Pikonema alaskensis* [Rohwer]) and Swaine jack pine sawfly (*Neodiprion swainei* Midd.). Larvae of these four species were also reared in laboratory to obtain feces. When there was a doubt regarding their identification, they were labelled "unidentified" feces.

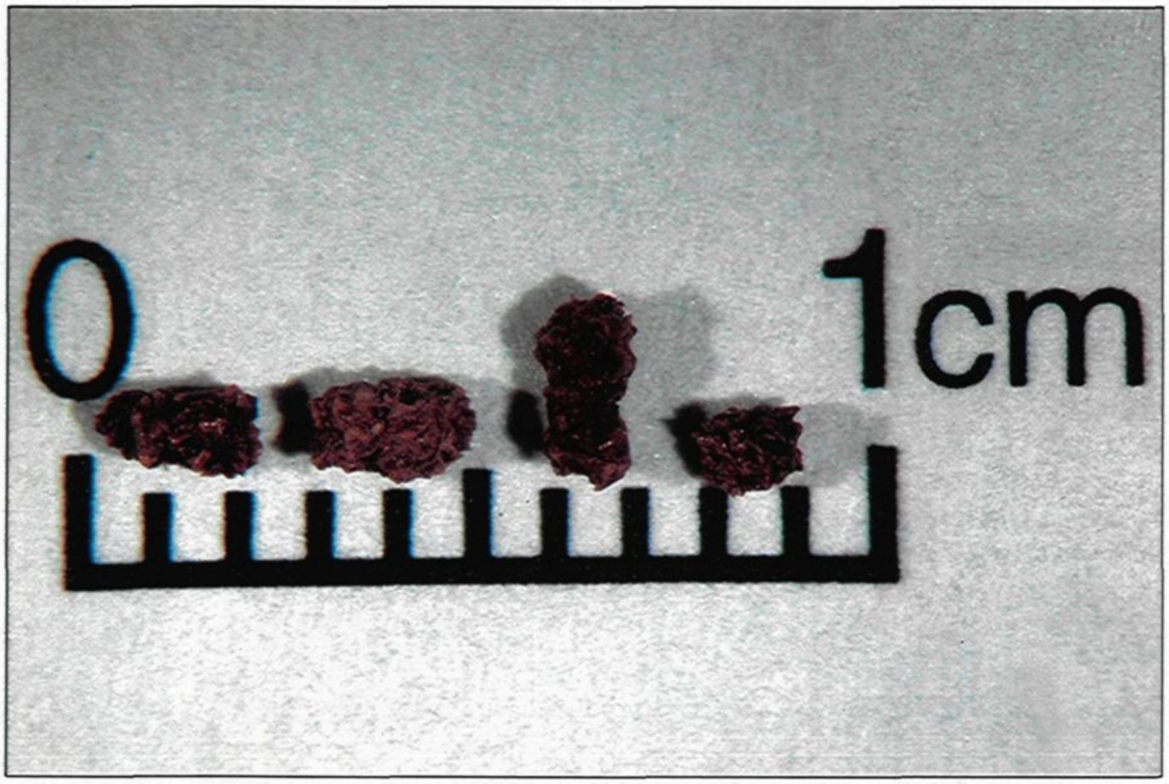

Figure 3.2 Recent spruce budworm feces.

Volumes and data were standardized to obtain the number of pieces corresponding to a uniform sampling volume of 100 cm^3. When moss and *Sphagnum* stems were too numerous in a fraction to be easily counted ($n > 200$), the number of stems contained in a sub-sample of 0.3 g was counted. The real number of stems was then extrapolated for the total weight of the fraction. Once the macrofossil analyses completed, plant remains were extracted from five samples (76 – 77, 102 – 103, 151 – 152, 212 – 213 and 257 – 258 cm) for accelerator mass spectrometry radiocarbon dating. Calibrated radiocarbon dates (Stuiver *et al.*, 1998) were used to calculate the peat accumulation rate by linear interpolation. Macrofossil zones were delineated according to changes observed in the relative abundance of taxa and species composition throughout the peat profile.

3.5. RESULTS

3.5.1. PEAT ACCUMULATION RATE AND STRATIGRAPHY

Plant material in the basal section of the soil profile was dated 8600 cal. BP (Table 3.1, Figure 3.3). The basal section (258 – 236 cm) was composed of lacustrine clay containing mollusk shells (Figure 3.3). The clay was overlaid by 34-cm of brown gyttja. Peat accumulation was initiated about 7700 cal. BP. The peat accumulation rate was relatively constant between 8600 and 5185 cal. BP, varying from 0.44 to 0.67 mm/year (Figure 3.3). The peat accumulation curve suggests a very slow accumulation rate during the last 5000 years, but it is likely that part of the surface (0 – 80 cm) peat material was burned and lost because of the intense fire activity that occurred during this period as suggested by the important numbers of charcoal fragments in the top 80 cm.

Tableau 3.1 Radiocarbon dates of Lac des Îlets peatland (Saguenay, Québec, Canada).

Depth (cm)	Laboratory number	Conventional radiocarbon age (BP)	Calibrated age (cal. BP)	Material used for datation
76-77	Beta-159827	4540±40	5185	Leaves, seeds and wood fragments
102-103	Beta-161780	4920±50	5665	Leaves and wood fragments
151-152	Beta-159828	5950±50	6775	Leaves, seeds and wood fragments
212-213	Beta-159829	7120±50	7925	Leaves, seeds and wood fragments
257-258	Beta-159830	7830±50	8600	Leaves and seeds

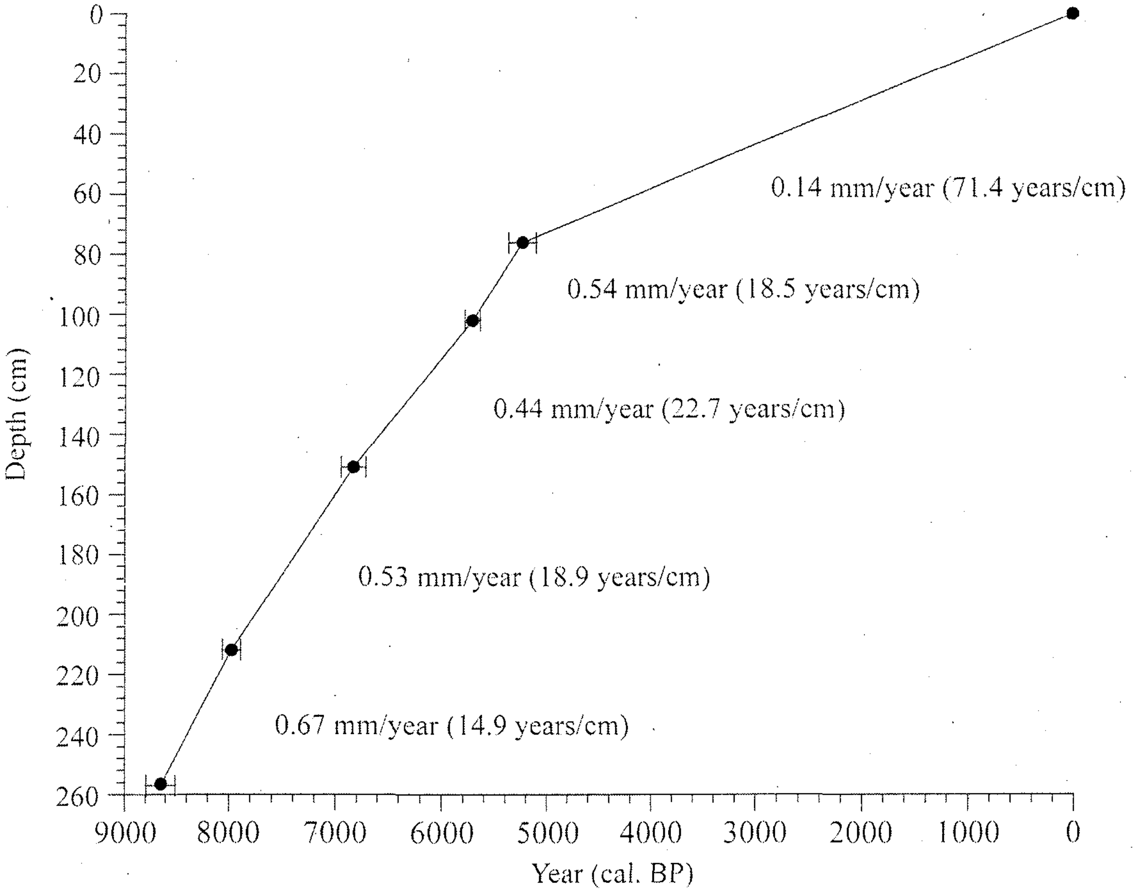

Figure 3.3 Peat accumulation rate for the Lac des Îlets peatland (Saguenay, Québec, Canada). Horizontal bar: 2 sigma calibrated age range.

3.5.2. VEGETATION RECONSTRUCTION

According to changes observed in species composition through the Lac des Îlets profile (Figure 3.4, Table 3.2), six macrofossil zones were delineated to reconstruct vegetation history. Between 8600 and 8287 cal. BP (Zone I), the study site was a small lake. The vegetation composition was dominated by trees and aquatic plants. Abundant macrofossil remains of organisms like Bivalva spp. and Gasteropoda spp. were observed in that zone. Macrofossil Zone II (8287 to 7873 cal. BP – shallow pond stage) is characterized by the disappearance of Bivalva and Gastropoda shells and a rise in the number of ericaceous shrub, sedge and moss remains. Abundant charcoal fragments were recovered in that section of the profile. A transition from pond to minerotrophic peatland was observed in Zone III (7873 to 6850 cal. BP). A first important decrease in tree macrofossils abundance occurred at the beginning of this period, while mosses, ericaceous shrubs and sedge species were abundant. The vegetation history of Zone IV (6850 to 5609 cal. BP) reflects a transition from minerotrophic to ombrotrophic peatland with a second drastic decline in tree composition and abundance. A major decrease in the abundance of ericaceous shrub and sedge remains was also registered in Zone VI, whereas abundant *Sphagnum* spp. and *Pleurozium schreberi* (BSG.) Mitt. stems were recovered. Between 5609 to 269 cal. BP (Zone V), the study site was an open ombrotrophic peatland. Abundant charcoal fragments were retrieved in that zone, while plant macrofossil remains were very scarce. Macrofossil Zone VI (269 cal. BP to present) corresponds to the treed ombrotrophic stage of the Lac des Îlets peatland. *Picea mariana*, ericaceous shrubs and mosses dominated the vegetation during that period. The highest number of charcoal fragments of the Lac des Îlets peatland was observed at 14 cm.

Errata: The head capsules found in the study site were all from larvae of Bibionidae, a family of Diptera that lives underground and contributes to the decomposition of dead organic material. This identification was made after the publication of the manuscript.

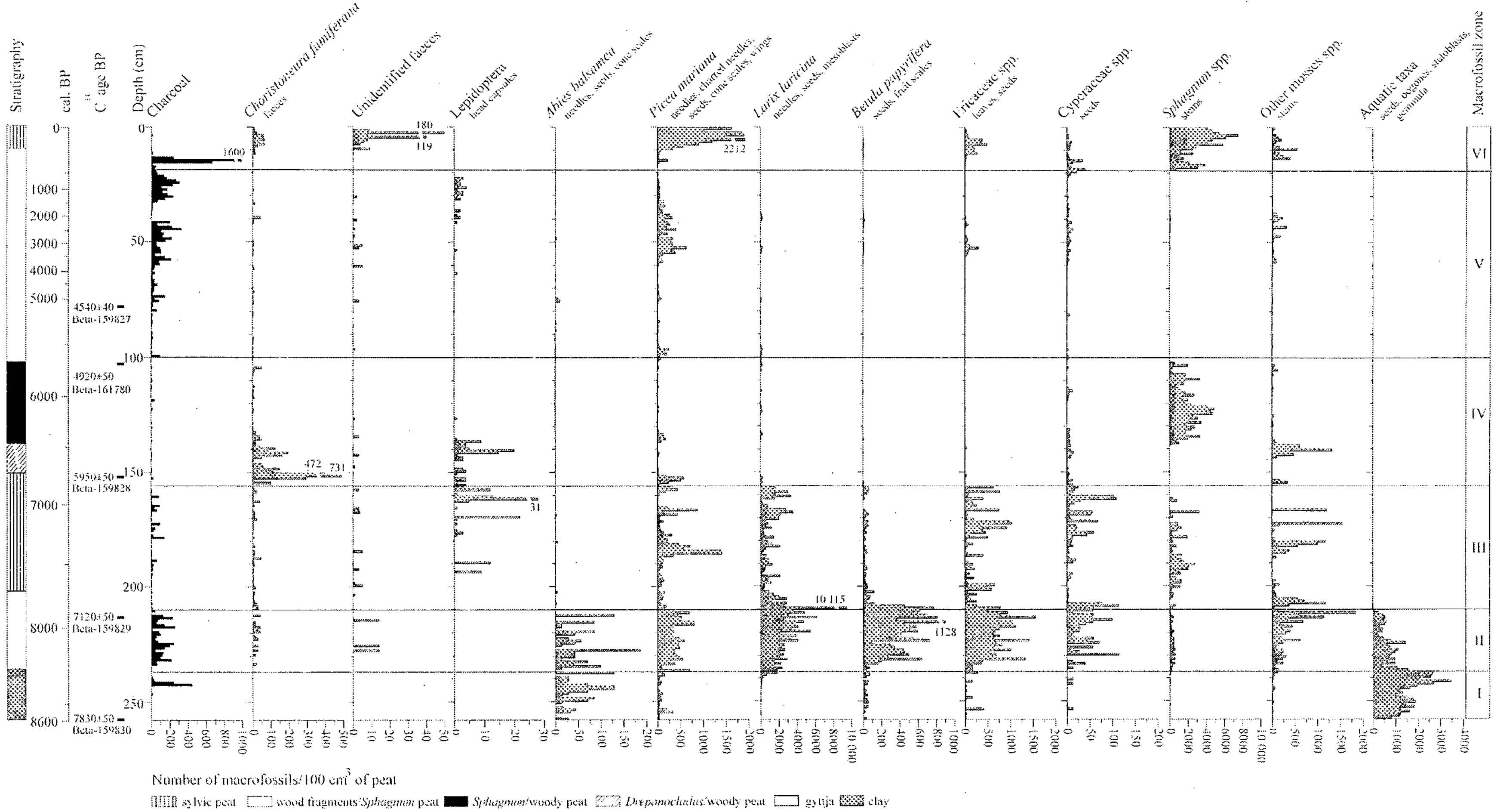

Figure 3.4 Macrofossil diagram (selected taxa) for the Lac des Îlets peatland (Saguenay, Québec, Canada).

Tableau 3.2 Dominant species and developmental stages of the Lac des Îlets peatland observed for each macrofossil zone.

Macrofossil zone	Depth (cm)	Age (cal. BP)	Dominant species	Developmental stage
VI	0-18	0 - 269	*Picea mariana*, *Carex trisperma*, *Sphagnum* spp., *Pleurozium schreberi*, *Kalmia angustifolia*, *Rhododendron groenlandicum*	Treed ericaceous peatland
V	18-100	269-5609	*Picea mariana*, *Carex trisperma*, *Pleurozium schreberi*, ericaceous shrubs	Ombrotrophic peatland
IV	100-156	5609-6850	*Picea mariana*, *Carex trisperma*, *Carex disperma*, *Viola* spp., *Sphagnum* spp, *Pleurozium schreberi*	Transition from a minerotrophic to an ombrotrophic peatland
III	156-210	6850-7873	*Picea mariana*, *Larix laricina*, Cyperaceae spp., *Chamaedaphne calyculata*, *Calla palustris*, *Hypericum virginicum*, *Menyanthes trifoliata*, *Myrica gale*, *Sparganium* spp., *Sphagnum spp.*, *Tomenthypnum falcifolium*, *Drepanocladus* spp.	Transition from a pond to a treed minerotrophic peatland
II	210-237	7873-8287	*Chara* spp., *Naja flexilis*, *Potamogeton* spp., *Abies balsamea*, *Betula papyrifera*, *Larix laricina*, *Picea mariana*, *Chamaedaphne calyculata*, *Myrica gale*, *Drepanocladus* spp., *Pleurozium schreberi*	Shallow pond
I	237-258	8287-8600	Bivalva spp., Gasteropoda spp., *Daphnia* spp., *Chara spp.*, *Naja flexilis*, *Potamogeton* spp. Porifera spp., *Abies balsamea*, *Betula papyrifera*, *Picea mariana*	Small lake

3.5.3. SPRUCE BUDWORM MACROFOSSIL ABUNDANCE

Spruce budworm feces started accumulating in the study site about 8240 cal. BP (Figure 3.4). The feces were observed throughout the peat profile, but were particularly abundant around 150 cm (6775 cal. BP), 140 cm (6550 cal. BP), and in the surface peat layer corresponding approximately to the last two centuries. A few Lepidoptera head capsules were also collected in the peat core, but were too altered or fragmented to be correctly identified to the species level. Peaks in head capsules were observed near 170, 160, 140 and 30 – 20 cm, which sometimes corresponded with but was most often out of phase with the peaks in spruce budworm feces. No head capsules were recovered in the surface (20 cm) peat layer.

3.6. DISCUSSION

3.6.1. DEVELOPMENT OF THE LAC DES ÎLETS PEATLAND AND VEGETATION HISTORY

The major changes observed in the vegetation composition of the Lac des Îlets site (Table 3.2) are the result of the typical transition occurring in a peatland environment: from lake to a pond, to a minerotrophic peatland followed by an ombrotrophic peatland (Zobel, 1988; Kuhry *et al.*, 1993; Hu and Davis, 1995; Hughes and Dumayne-Peaty, 2002). The vegetation succession was mainly induced by autogenic processes, including peat buildup, oligotrophication and acidification, mediated by the peatland ecosystem itself (Kuhry *et al.*, 1993). The most drastic changes observed in the abundance of tree macrofossil remains are also attributable to the autogenic evolution of the peatland. The first important reduction of the number of tree macrofossils occurred around 7800 cal. BP. *Abies balsamea* disappeared from the study site while the abundance of the other tree species greatly diminished. The second major tree decline occurred around 6800 cal. BP. The decline of tree species like *Larix laricina* and *Betula papyrifera* is probably attributable to the thickness of the peat deposit, which was respectively 50-cm (7800 cal. BP) and 100-cm (6800 cal. BP) thick; tree roots no longer had access to the nutrients from the underlying mineral soil (Montague and Givnish, 1996; Lavoie *et al.*, 2001). Tree macrofossils declines were also observed at similar depths in other peatlands of eastern Québec (Lavoie *et al.,* 2001; Zimmermann and Lavoie, 2001). However, the decline in the number of *Picea mariana* remains did not occur to the same degree as the other tree species. Furthermore, the present-day black spruce stand is growing on a 237-cm thick deposit, suggesting that the thickness of the peat deposit does not prevent the establishment and growth of the species. On the other hand, the decline in the number of black spruce macrofossils coincided with an exceptional peak of spruce budworm feces around 6800 cal. BP, suggesting that insect activity may have had a major influence on the vegetation structure of the peatland.

3.6.2. SPRUCE BUDWORM ABUNDANCE

Spruce budworm feces were recovered in almost the entire peat core, suggesting endemic or epidemic presence of the insect at the study site since 8240 cal. BP. This is the earliest recorded date of spruce budworm presence in North America. Important variations in the abundance of feces were observed in the Lac des Îlets peat profile, with two periods of presumably intense spruce budworm activity (Figure 3.4). The first peak, which also yielded the highest number of spruce budworm feces, was registered between 6815 and 6480 cal. BP. This exceptional period of spruce budworm activity occurred while balsam fir (*Abies balsamea*), the preferred host species of spruce budworm, was absent from the study site, although it was probably present in the forests surrounding the peatland. The high number of feces in an ecosystem without fir (the Lac des Îlets peatland) suggests that the presence of a high population of spruce budworm larvae feeding on a secondary host (*Picea mariana)* (Stillwell, 1956; Blais, 1981, 1984; Mattson *et al.*, 1988). Such phenomenon was observed during recent high intensity outbreaks.

The second period of high spruce budworm activity in the Lac des Îlets peatland was observed in the top 15 cm of the profile, corresponding approximately to the spruce budworm outbreaks that occurred in the Laurentides Wildlife Reserve during the last two centuries (Blais, 1965; Lussier *et al.*, 2002). The dates of those six outbreaks cannot be precisely established using the feces distribution. The peat accumulation rate was too low during that period and outbreaks too frequent to allow the formation of distinct layers of spruce budworm feces. The rest of the feces distribution fluctuated more or less regularly but never reached the abundance described for the two periods of high budworm activity. Not every outbreak can occur in a single location even with dendrochronological techniques. So it is possible that some outbreaks were missed. Nevertheless, the feces distribution suggests that intense periods of spruce budworm activity were rare events during the Holocene in the boreal zone. They may indicate important changes in the dynamics of spruce budworm outbreaks. Low fire activity, associated with other factors like the presence of susceptible stands and weather conditions favorable to larval development, were possibly responsible for the major spruce budworm outbreaks that occurred in the Lac des Îlets peatland between 6815 and 6480 cal. BP and during the last century (Greenbank, 1956; Pilon and Blais, 1961; Lucuik, 1984; Blais, 1985; Bergeron and Archambault, 1993; Bergeron and Leduc, 1998). Conversely, the absence or the low abundance of susceptible stands may have contributed to less budworm activity between 5000 and 2000 cal. BP.

Feces are a new paleoecological proxy of the presence of spruce budworm. Lepidoptera head capsules were also used to reconstruct outbreak history (Davis *et al.*, 1980; Filion *et al.*, 1998). In the Lac des Îlets peat profile, feces were much more abundant than head capsules. Feces were also better preserved and easier to identify. Noticeable mismatches were observed between peaks of spruce budworm feces and those of head capsules. In addition, no head capsules were collected in the upper 15 cm of the core, corresponding to the outbreaks that occurred during the two last centuries in the study area. Consequently, spruce budworm feces appear to be a more suitable paleoecological indicator for reconstructing past outbreaks. Feces are often characteristic in size and form for larvae of different ages and species (Morris, 1949; Fridén, 1958). The identification of feces indicates the presence of the insect *in situ* and may be the only apparent clue to identify the defoliator (Morris, 1942). However, head capsules should not be discarded as paleoecological indicators for insect defoliation. A few of the peaks in Lepidoptera head capsules found in the Lac des Îlets peat core were observed where no or few spruce budworm feces were recovered. Those peaks may represent spruce budworm activity that was not clearly detected in the feces reconstruction. It appears that in order to collect as much information as possible on spruce budworm activity, both head capsules and feces should be used simultaneously as complementary indicators of the presence of the insect.

3.7. CONCLUSION

This study showed that spruce budworm was endemic in the Lac des Îlets peatland over the last 8240 years. Furthermore, the long-term perspective achieved with this macrofossil analysis strongly suggests that very intense periods of spruce budworm activity were exceptional events during the Holocene in the study area. Outbreaks are natural phenomena, but human interventions and a change in fire frequency might have modified the forest structure and increased the abundance of spruce budworm during the 20th century. Fire recurrence may also have had an impact on spruce budworm activity, as the two major defoliation periods at the study site occurred while fire activity was low. Low fire recurrence might have favored the development of mature host stands highly susceptible to spruce budworm outbreaks. The link between fire and spruce budworm outbreaks should be investigated more thoroughly in order to obtain more information on the dynamics of the boreal forest. A possible relation between warm weather conditions and intense periods of spruce budworm activity should also be investigated since the highest abundances of spruce budworm feces were observed during the two warmest periods of the Holocene, i.e., between 7000 and 6000 cal. BP and during the 20th century (Richard, 1994, 1998; Sawada *et al.*, 1999).

3.8. ACKNOWLEDGEMENTS

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CHAPITRE 4. HOLOCENE DYNAMICS OF SPRUCE BUDWORM POPULATION ABUNDANCE IN THE BOREAL ZONE OF EASTERN CANADA

4.1. ABSTRACT

Most data available on insect outbreak history are fragmented or cover a relatively short time period. Here we provide the first reliable millennium-long reconstruction of the activity of an epidemic insect species. The Holocene history of spruce budworm (*Choristoneura fumiferana* [Clem.]) abundance in the Saguenay region (Quebec, Canada) was reconstructed with indicators that were well-preserved in peat material, i.e., spruce budworm feces, spruce budworm head capsules and zonal disks of *Lophodermium piceae* (Fckl.) Hoehn., a needle fungus found on senescent spruce and fir trees. The omnipresence of spruce budworm feces in the peat cores suggests an endemic presence of the insect for the last 8200 years. Important periods of spruce budworm activity never previously detected were registered between 8200 and 7700, around 7310, between 6700 and 6300, and approximately around 5800, 4800, 1900, 1600, 1500 and 1000 cal. BP. Some of these periods were apparently very intense but most were recorded only at a single site. Conversely, two of the last three outbreaks of the 20th century were detected at all sites, suggesting that recent outbreaks were more widespread and synchronous than those that occurred during most of the Holocene epoch. Insect outbreaks probably influenced the relative abundance of black spruce or balsam fir trees but did not compromise their regeneration, which indicates a relatively stable insect-host relationship during the Holocene. Recent modifications in the boreal forest structure and composition may have,

however, changed these dynamics by favouring the development of large outbreaks.

4.2. INTRODUCTION

Insect outbreaks are major disturbances in forest ecosystems, particularly in coniferous forests where many native species reduce growth or kill trees across large areas (Mattson and Addy, 1975; Pickett and White, 1985; Cappuccino, 1995; Speer *et al.*, 2001; Duchesne and Ouimet, 2008). Several defoliators like forest Lepidoptera undergo cyclic population fluctuations reaching outbreak levels on a more or less regular basis (Wallner, 1987; Berryman, 1996; Jardon *et al.*, 2003). Some species even demonstrate spatial synchrony in the timing of their outbreaks across large geographic areas as a result of mechanisms like dispersal or regional stochasticity, referred to as the Moran effect (Régnière and Lysyk, 1995; Myers, 1998; Liebhold and Kamata, 2000; Williams and Liebhold, 2000; Bjornstad *et al.*, 2008). The cyclical recurrence of outbreaks has been documented for several defoliating insects. However, not all defoliating insect species have cyclical population fluctuations. Of the 80 Lepidoptera outbreak species present in Europe and North America, only 18 can be considered as 'cyclic' (Myers, 1988; 1998). Some species have relatively short and regular cycles (ca. 7 – 11 years), like the larch budmoth (*Zeiraphera diniana* Guénée) and the gypsy moth (*Lymantria dispar* L.), while others have longer and more variable cycles (ca. 18 – 41 years), like the pandora moth (*Coloradia pandora* Blake) and the western spruce budworm (*Choristoneura occidentalis* Freeman) (Baltensweiler *et al.*, 1977; Weber, 1997; Liebhold *et al.*, 2000; Swetnam and Lynch, 1993; Speer *et al.*, 2001).

Most historical data available on outbreaks are fragmented or cover a relatively short time period. Egg or larval counts and defoliation maps give the most precise information on population densities and the spatial distribution of outbreaks, but they rarely extend over more than 40 to 70 years, i.e., only a few outbreaks of a species. Dendrochronological data extend the record of epidemics to a few hundred years (Blais, 1965; Swetnam and Lynch, 1993; Weber and Schweingruber, 1995; Krause, 1997; Boulanger and Arsenault, 2004). However, little is known about outbreaks that occurred prior to the last two centuries, especially in North America where few historical data exist (Morin *et al.*, 1993, 2007). Therefore, ecologists must rely on paleoecological indicators to reconstruct the long-term outbreak history of defoliating insects.

Spruce budworm (*Choristoneura fumiferana* [Clem.]) is one of the most important and profusely studied defoliating insects in North America, periodically affecting millions of hectares of spruce and fir forests when reaching outbreak levels, i.e., approximately every 35 years (Royama, 1984; MacLean, 1988; Jardon *et al.*, 2003). Despite their economic impact on the forest industry, spruce budworm epidemics are natural phenomena which allow advance balsam fir (*Abies balsamea* [L.] Mill.) regeneration to recruit to the mature fir overstory (MacLean, 1988). It has been suggested that the relationship between the defoliator and the regeneration of old-growth balsam fir forest has been relatively stable for several thousands of years (Baskerville, 1975; Blais, 1983; Volney and Hirsch, 2005; Bouchard *et al.*, 2006). The last two to three hundred years of spruce budworm outbreaks are well documented by entomological (Royama, 1984; Royama *et al.*, 2005; Hardy *et al.* 1986) and dendrochronological studies (Blais, 1965; Krause, 1997; Morin, 1998). In eastern Canada, and more particularly in the province of Quebec, eight outbreaks have occurred since the 18th century (Blais, 1983; Morin and Laprise, 1990; Jardon *et al.*, 2003; Boulanger and Arsenault, 2004) and a new outbreak is currently active in the province (Louis Morneau, ministère des Ressources naturelles et de la Faune, personnal communication, 2010).

A change in spruce budworm dynamics was observed at the beginning of the 20th century (Blais, 1983; Jardon, 2001). While outbreak frequency has not changed, there has been an increase in severity and a greater synchrony of outbreaks across large areas. This change has been attributed to human impact on forest ecosystems (Blais, 1983) as well as to a decrease in fire frequency, resulting in the development of extensive balsam fir stands, the preferred host of the spruce budworm (Jardon, 2001; Morin *et al.*, 2007). However, Boulanger and Arseneault (2004) suggested that neither the frequency nor the synchrony of outbreaks in eastern Quebec have changed during the last 450 years in eastern Québec, but their study did not cover a vast territory. More than ever long-term reconstructions of spruce budworm outbreaks are needed to put the outbreaks of the last 200 years in perspective. In this chapter, we reconstructed the 8200-year history of spruce budworm abundance in eastern Quebec primarily using spruce budworm feces as paleoecological indicators. We also studied the variation in spruce budworm activity during the Holocene period, and verified if all the important periods of spruce budworm abundance were registered in all the study site indicting possible synchrony at a regional scale in the boreal zone before the 19th century. We hypothesized that periods of intense spruce budworm activity were rare phenomenon during the Holocene and were probably more localized than those that occurred during the last 100 years in eastern Quebec.

4.3. STUDY AREA

The study area was located in the Saguenay region, Quebec, Canada (48°12' – 48°57'N, 70°26' – 71°14'W; Figure 4.1), in a sector greatly affected by spruce budworm outbreaks during the 20th century (Morin and Laprise, 1990; Morin, 1994, 1998). This area is included in the Laurentides – Onatchiway region of the boreal forest of Canada (Rowe 1972), specifically in the balsam fir – white birch (*Betula papyrifera* Marsh.) and in the balsam fir – black spruce (*Picea mariana* [Mill.] B.S.P.) ecological regions (Thibault, 1987). The topography is mountainous and the area lies on Precambrian crystalline rocks (Rowe, 1972). The deglaciation of the area occurred around 10 200 BP (Richard, 1977). A study of the post-glacial vegetation conducted near the sampling sites (Kénogami, 48°22'N, 71° 34'W) revealed that black spruce forests appeared around 8000 BP, whereas the establishment of balsam fir – white birch forests occurred around 7400 BP (Richard, 1977).

After a detailed survey of most small peatlands surrounded by balsam fir and black spruce stands in the Mont-Valin and Chicoutimi area, four ombrotrophic peatlands were selected for their high potential of capture of the macrofossil rain produced by outbreaks (Figures 4.1 and 4.2). The study sites were located in regions highly disturbed by recent and well-documented spruce budworm outbreaks. The forest cover of ILETS and NEX was dominated by black spruce whereas that of PLT and VALIN was composed by 65% of black spruce and 35% of balsam fir. Three of the peatlands were located north of the Saguenay River in the Mont-Valin area (NEX, PLT, VALIN), whereas the fourth site (ILETS) was located south of the river in the Laurentides Wildlife Reserve. There was less than 100 km between ILETS and NEX, the NEX, PLT and VALIN sites were small open bogs dominated by moss species and ericaceous shrubs. ILETS had a thick peat deposit covered by a dense black spruce stand located approximately 500 m from an open bog.

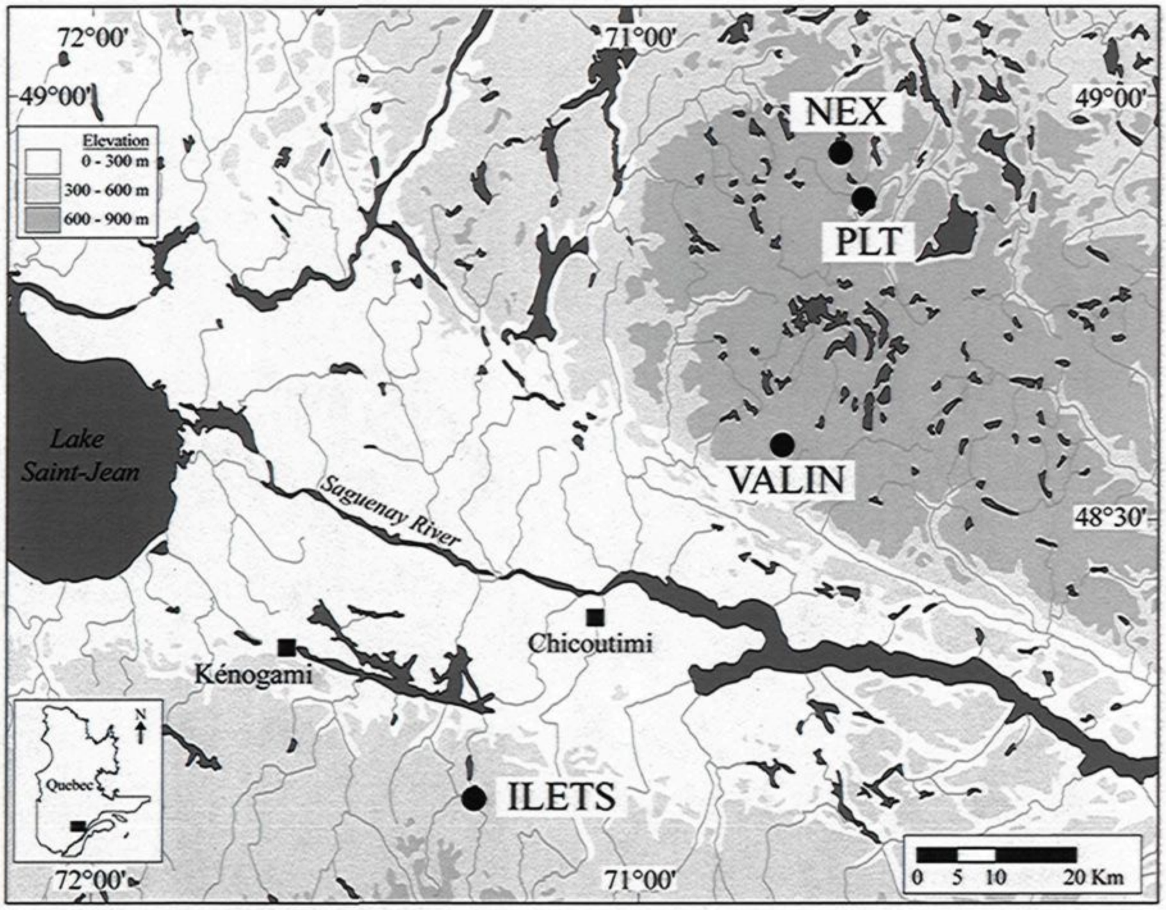


Figure 1 Location of the four study sites in Saguenay, Quebec, Canada.

The major recent disturbances of the forests of the study area are logging, fire and spruce budworm outbreaks. Available data on the recent fire history of the study area go back to 1972 (Ministère des Ressources naturelles et de la Faune du Québec, personal communication, 2005). No fires were recorded in the study sites since 1972. Dendrochronological analyses conducted at ILETS allowed the detection of a major fire prior to 1972, i.e., around AD 1922 (unpublished dendrochronological data conducted during this project and Gagnon, 1989). Tree-ring data also indicate that recent spruce budworm outbreaks disturbed the forests of the Laurentides Wildlife Reserve around AD 1710, 1755, 1811, 1838, 1914, 1952 (Blais, 1965) and 1978 (Lussier *et al.*, 2002), whereas published tree-ring chronologies of the forests of the Mont-Valin detected spruce budworm outbreaks in AD 1914, 1952 and 1978 (Morin, 1994, 1998). The year with the lowest radial growth associated with insect defoliation was used to identify these outbreaks.

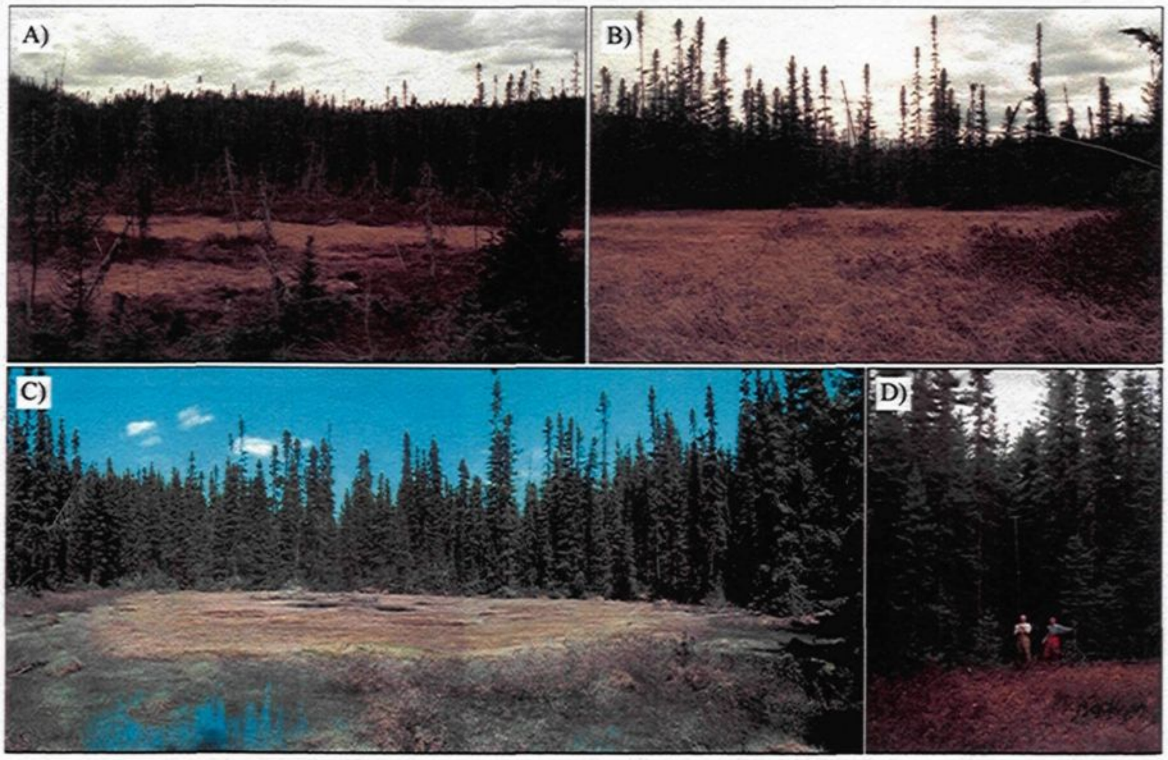


Figure 4.2 Ombrotrophic peatlands of the Saguenay region (Quebec, Canada) selected for spruce budworm outbreak reconstructions: A) VALIN, B) NEX, C) PLT, and D) ILETS.

4.4. METHODS

One peat core was extracted from each of the four peatlands. NEX, PLT and VALIN cores were collected as close as possible to the forest surrounding the peatlands in order to obtain direct evidence of past fires and spruce budworm activity. The ILETS core was retrieved from a thick peat deposit covered by a dense black spruce stand. A Coûteaux corer with a 10-cm diameter (Coûteaux, 1962) was used to extract the surface (2 m) peat deposit. When the peat deposit was deeper, a side-wall peat corer with a 4.5-cm diameter (Jowsey, 1966) was used to extract a core from the rest of the deposit. Peat cores were wrapped and transported in plastic tubes to the laboratory and kept frozen to prevent fungal development. The cores were cut into continuous 1-cm thick slices and placed in labeled bags. The samples were washed gently through a series of sieves (2, 1, 0.5-mm meshes). The material collected was dried at ambient air temperature and examined at 60× magnification under a binocular microscope.

Spruce budworm feces were the principal paleoecological indicator used to reconstruct insect activity as they provide direct evidence of the presence of the insect. Feces are often characteristic in size and form for larvae of different ages and species (Morris, 1949; Fridén, 1958). Spruce budworm feces are small brown cylinders composed of conifer leaves fragments mixed with organic matter (Figure 4.3). Their size varies from 0.8 to 1.1 mm in width, and from 1.6 to 3.2 mm in length, respectively. To make sure that the feces found in the peat profiles were produced by spruce budworm and not by another insect species, they were compared to feces 1) of spruce budworm larvae reared in the laboratory and feeding on balsam fir and black spruce leaves, 2) collected on the ground in the Saguenay region during the last spruce budworm outbreak, and 3) collected in a site presently affected by moderate defoliation by spruce budworm. The feces found in the peat profiles were also compared to reference feces of four other defoliating insects found in the boreal forest of Québec, i.e., hemlock looper (*Lambdina fiscellaria fiscellaria* [Guen.]), eastern blackheaded budworm (*Acleris variana* [Fern.]), yellowheaded spruce sawfly (*Pikonema alaskensis* [Rohwer]) and Swaine jack pine sawfly (*Neodiprion swainei* Midd.). Larvae of these four species were reared in laboratory to obtain feces. They all showed important differences from the spruce budworm fecal pellets. Their shape was approximately the same (cylinder), but their colour and proportions were different.

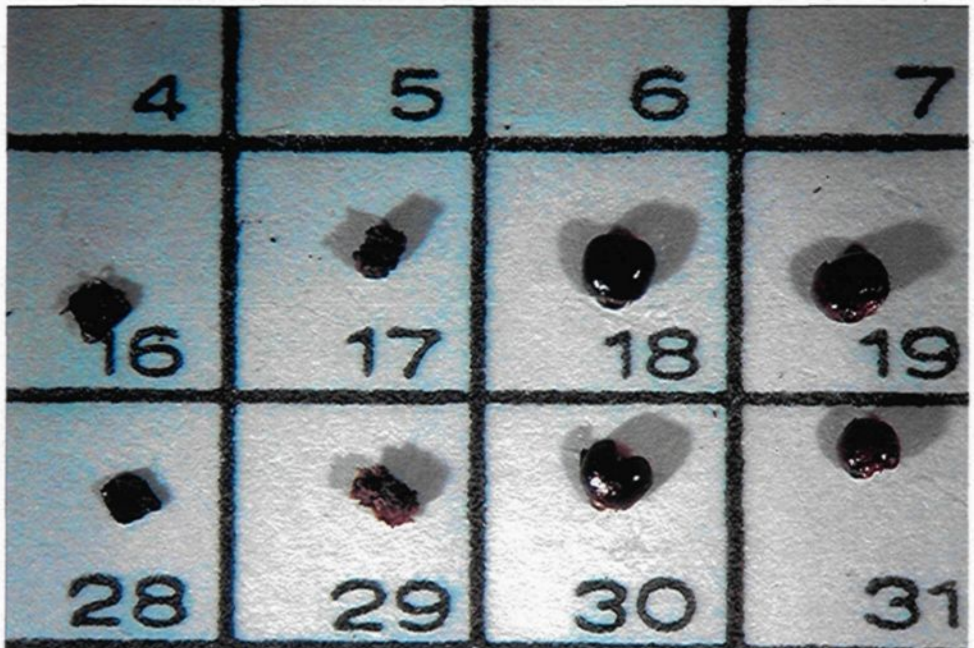


Figure 4.3 Photo of spruce budworm feces (17, 29), zonal disks of *Lophodermium picea* (16, 28), spruce budworm head capsules (18, 30) and Bibionidae head capsules (19, 31).

Head capsules (Filion *et al.*, 1998; Payette *et al.*, 2000) were used as a complementary indicator to validate or complement the feces reconstruction of spruce budworm activity. The identification of spruce budworm head capsules was based on the same criterions used by Bhiry and Filion (1996). These criteria were 1) the presence of six stemmata (eyes), distributed along an oval shape on both sides of the capsules, 2) a cervical triangle with a 'v' shape that connects to the front, and 3) the position of setae on the front (Figure 4.3). Reference head capsules of spruce budworm, hemlock looper, eastern blackheaded budworm, yellowheaded spruce sawfly and Swaine jack pine sawfly were also used to identify the capsules found in the samples. Unidentified head capsules were sent for identification to experts at the Canadian National Collection of Insects, Arachnids and Nematodes (Agriculture and Agri-food Canada). Finally, zonal disks from *Lophodermium piceae* (Fckl.) Hoehn. (Figure 4.3), a needle fungus found on senescent spruce and fir species, were also used as a proxy for spruce budworm epidemics (Jasinski and Payette, 2005, 2007). These disks are formed by several layers of hyphae and melanised parenchyma cells (Gourbière *et al.*, 1986) and were linked to forest decline due to spruce budworm (Jasinski and Payette, 2007). The fungus was also associated with drought and stressed trees.

The identification and counts of charcoal fragments, spruce budworm feces, needle zonal disks and head capsules were conducted for every centimeter of the four peat profiles. Plant macrofossils were identified at every centimeter for ILETS and PLT. It appeared that a high resolution analysis of plant macrofossils was unnecessary to attain the objectives of this study. Consequently, a lower resolution (one sample of 1 cm every 5 cm) was used for

NEX and VALIN, especially because these sites were less affected by spruce budworm and fire. Additional plant macrofossil analyses were conducted on the first 16 cm of NEX and at the bog-fen transitions of NEX and VALIN (respectively 100 – 105 cm and 80 – 85 cm) to obtain more precise information about vegetation composition changes at these levels. Illustrated guides (Montgomery, 1977; Lévesque *et al.*, 1988) and a reference collection were used to identify plant macrofossils. Spruce budworm feces were identified according to Simard *et al.* (2002). Data were standardized to obtain the number of macrofossil remains corresponding to a uniform sampling volume of 100 cm^3. Moreover, when moss stems were too abundant ($n > 200$) to be easily counted within a fraction, the number of stems contained in a sub-sample of 0.3 g was counted and later extrapolated for the total weight of the fraction. The delineation of macrofossil zones was qualitatively made according to changes observed in the abundance of taxa and in species composition. Nomenclature follows Marie-Victorin (1995) and Hinds (2000) for vascular plants and Anderson *et al.*, (1990) for mosses.

Plant remains and wood fragments were extracted for radiocarbon dating, with the accelerator mass spectrometry method, from the basal sections of the cores and at specific depths where charcoal pieces or spruce budworm feces were particularly abundant. Conventional radiocarbon dates were converted to calendar ages according to Stuiver *et al.* (1998). A second order polynomial model was used to describe the age-versus-depth relationship in each of the study sites in order to find approximate ages of historical events such as fires and peaks of insect activity. The basal radiocarbon date of VALIN (155 – 156 cm, 5440 cal. BP) had to be excluded from the polynomial model as a result of temporal compression observed in the bottom section of the core; it greatly reduced the reliability of the model. Instead, a linear interpolation was calculated between 122 and 156 cm to extrapolate ages. Similarly, a linear interpolation was used in the top 40 cm of ILETS since the important temporal compression in that section of the profile compromised the validity of the polynomial model.

4.5. RESULTS

4.5.1. PEAT STRATIGRAPHY

The four peat profiles differed in thickness and age (Table 3.1, Figure 4.4). The ILETS core was thicker and 2000 to 3000 years older than the other cores. The NEX, PLT and VALIN profiles had similar peat thicknesses, but the age of their basal sections differed. Peat accumulation rates also differed among the four study sites (Figure 4.4). Two important hiatuses or time compressions were observed: one at ILETS between 4800 cal. BP and ca. AD 1922, and the other at VALIN between 5440 and 1700 cal. BP. Abundant charcoal fragments were retrieved from the top 80 cm of the ILETS peat core (Figure 4.4) suggesting that part of the peat material was probably burned. The temporal compression observed in the bottom 30 cm of the VALIN peat core can be explained by the low peat accumulation rate associated with the pond stage at the site.

Tableau 4.1 Accelerator mass spectrometry radiocarbon dates of the studied peatlands.

Site	Depth (cm)	Laboratory number	Conventional radiocarbon age (BP)	Calibrated age (cal BP)	Material used for dating
ILETS	39-40	Beta-205599	4310±60	4962	Buds, cone scales, leaves, seeds, wood fragments
ILETS	76-77	Beta-159827	4540±40	5185	Leaves, seeds, wood fragments
ILETS	102-103	Beta-161780	4920±50	5665	Leaves, wood fragments
ILETS	151-152	Beta-159828	5950±50	6775	Leaves, seeds
ILETS	187-188	Beta-205606	6350±50	7305	Charcoals, leaves, seeds, wood fragments
ILETS	212-213	Beta-159829	7120±50	7925	Leaves, seeds, wood fragments
ILETS	257-258	Beta-159830	7830±50	8600	Leaves, seeds
NEX	48-49	Beta-205601	1850±40	1790	Charcoals, leaves, seeds, wood fragments
NEX	77-78	Beta-180661	3800±60	4195	Leaves, seeds, wood fragments
NEX	120-121	Beta-171213	5130±40	5850	Leaves, seeds, wood fragments
NEX	152-153	Beta-171214	5700±40	6545	Leaves, seeds, wood fragments
PLT	37-38	Beta-167003	590±40	590	Leaves, seeds
PLT	57-58	Beta-167004	1610±60	1490	Leaves, seeds
PLT	73-74	Beta-205602	1770±40	1690	Leaves, seeds, wood fragments
PLT	82-83	Beta-205603	1850±40	1790	Cone scales, leaves, wood fragments
PLT	90-91	Beta-167005	2020±40	1970	Leaves, seeds, wood fragments
PLT	118-119	Beta-205607	3010±40	3205	Buds, cone scales, leaves, seeds, wood fragments
PLT	138-139	Beta-159831	4400±40	5085	Leaves, seeds, wood fragments
VALIN	51-52	Beta-205604	1020±40	945	Leaves, seeds, wood fragments
VALIN	93-94	Beta-180662	1600±40	1480	Leaves, seeds, wood fragments
VALIN	122-123	Beta-205605	1720±40	1630	Leaves, seeds, wood fragments
VALIN	155-156	Beta-171215	4740±40	5440	Leaves, seeds, wood fragments

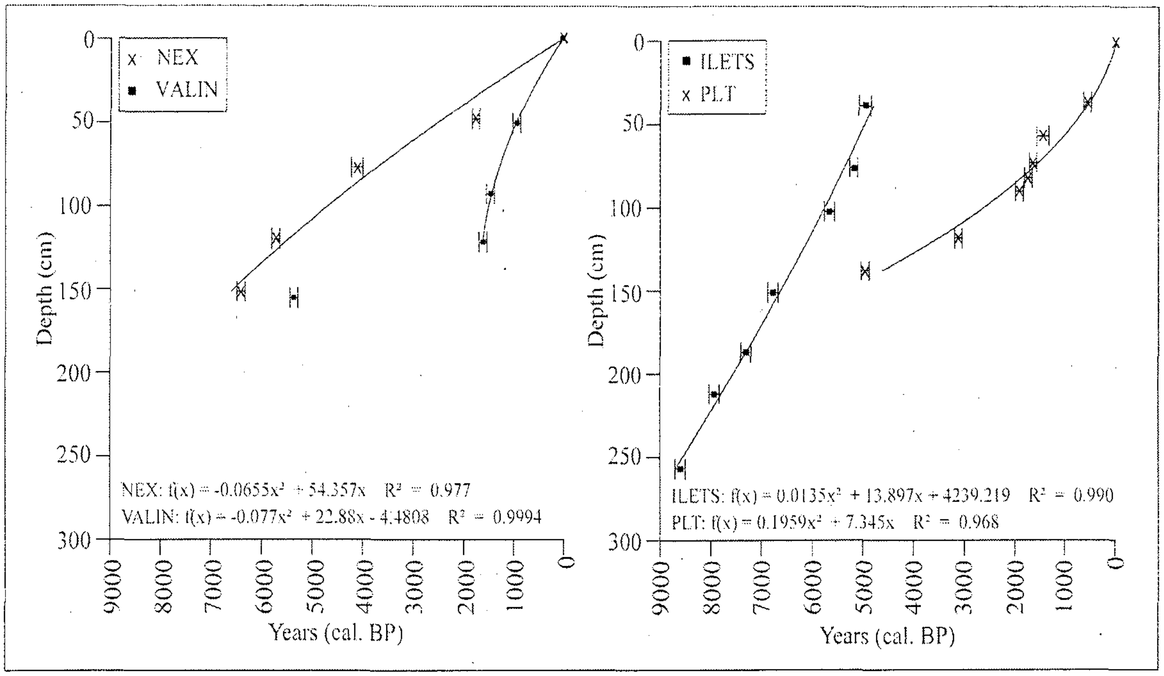


Figure 4.4 Age-versus-depth curves of the four study sites (Saguenay, Quebec, Canada) based on calibrated radiocarbon dates. Horizontal bar: 2 sigma calibrated age range. Age models and R^2 are shown.

4.5.2. SITE DEVELOPMENT AND VEGETATION HISTORY

In most cases, the autogenic development of the peatlands, i.e., the transition from pond to fen, to bog, explained the major changes in species composition and abundance that were detected in the peat cores (Figures 4.5 and 4.6). The most drastic variations noted in the vegetation history of the four sites were related to the tree and moss assemblages. Tree cover was mainly dominated by black spruce (Figure 4.5). Balsam fir, tamarack (*Larix laricina* [Du Roi] K. Koch) and white birch macrofossil remains were also abundant during the pond and fen stages of the sites. *Drepanocladus* spp. and *Tomenthypnum falcifolium* (Ren. ex Nichols) Tuom. were the dominant mosses of the fen stages, but later declined rapidly, whereas *Sphagnum* species were the most abundant Bryophyta found during the bog stages of the peatlands. In addition, various Ericaceae and Cyperaceae species were important components of the vegetation. Macrofossils of ericaceous shrubs like *Chamaedaphne calyculata* L. Moench, *Andromeda glaucophylla* (Link.) and *Vaccinium oxycoccos* L. were abundant during the fen stages, while numerous remains of *Kalmia* spp. and *Rhododendron groenlandicum* (Oeder) Kron & Judd were identified in the bog stages of the sites, especially in peat samples located near the surface. The fen and rich bog stages were also characterized by abundant Cyperaceae seeds (*Carex disperma* Dewey, *Carex trisperma* Dewey, *Carex oligosperma* Michx.).

4.5.3. SPRUCE BUDWORM MACROFOSSIL AND HEAD CAPSULES ABUNDANCE

Spruce budworm feces were recovered from the four peat cores (Figures 4.5 and 4.7). After a visual examination of the feces distribution, important peaks of feces were identified at the four study sites, particularly in the top 20 cm of the cores, corresponding approximately to the last two centuries. Other peaks in feces distribution were observed at ILETS between 8200 and 7700, around 7310, between 6700 and 6300 and around 5800 and 4800 cal. BP. Peaks were also found at VALIN (1500 and 960 cal. BP) and PLT (1900 and 1600 cal. BP). Moreover, several periods of absence or of very low abundance of feces were detected at all sites, for instance between 4800 and 200 cal. BP at ILETS, between 3200 and 1200 cal. BP at NEX, between 5440 and 2000 cal. BP at VALIN, and between 1050 and 300 cal. BP at PLT. Unidentified feces were also found in the profiles; their shape, size and color sufficiently differed from spruce budworm feces to be labelled as other than budworm. They were often observed at the same depths as spruce budworm feces but they also formed important peaks at other levels when spruce budworm feces were absent or scarce like at NEX (95 – 93 cm) and VALIN (54 – 52 cm).

Head capsules were also found in all four peatlands (Figure 4.5). Of all the head capsules found in the four peat profiles, only three were from spruce budworm. One was an unidentifiable Lepidoptera head capsule, but the vast majority of head capsules was from Bibionidae (Figure 4.5), a family of Diptera that live underground and contributes to the decomposition of dead organic material.

4.5.4. ZONAL DISKS OF *LOPHODERMIUM PICEAE*

Many zonal disks of black spruce needles associated with the endophyte fungus *Lophodermium piceae* were found in the four peat cores (Figures 4.5 and 4.7). They were particularly abundant at ILETS and PLT. Some major peaks of disks coincided with peaks of spruce budworm feces or charcoal fragments. Still, discrepancies between peaks of feces and peaks of disks were observed in all cores.

4.5.5. CHARCOAL

Numerous charcoal fragments were counted in the four peat cores (Figure 4.7), with an almost continuous charcoal input at ILETS, NEX and PLT. Important periods of fire activity were observed at the four sites, particularly at ILETS (8200 – 7700 cal. BP, 5800 – 4800 cal. BP, 3600 cal. BP – ca. AD 1922). The important peak of charcoal observed in ILETS at 13 cm was produced during the 1922 fire documented by Gagnon (1989).

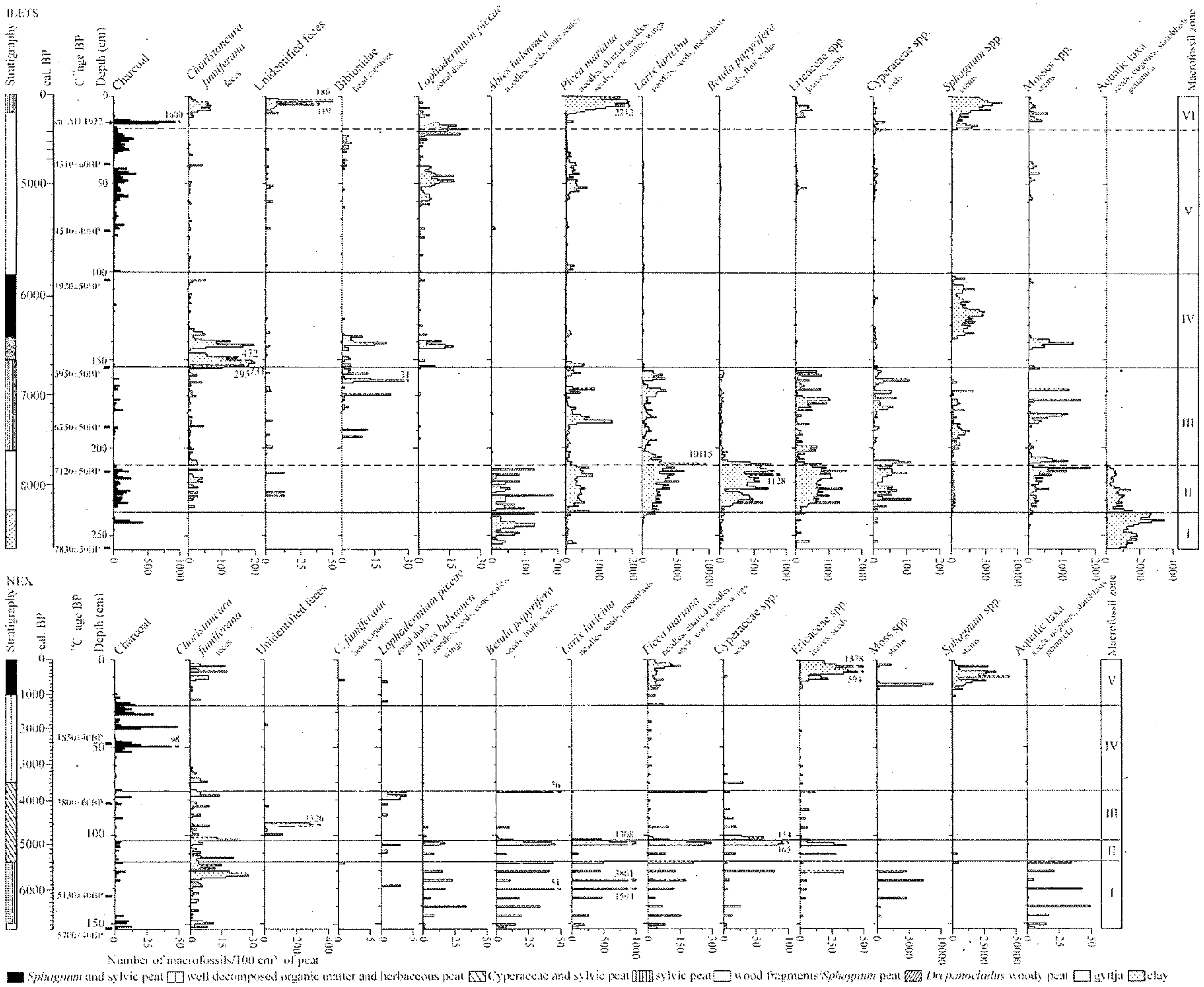
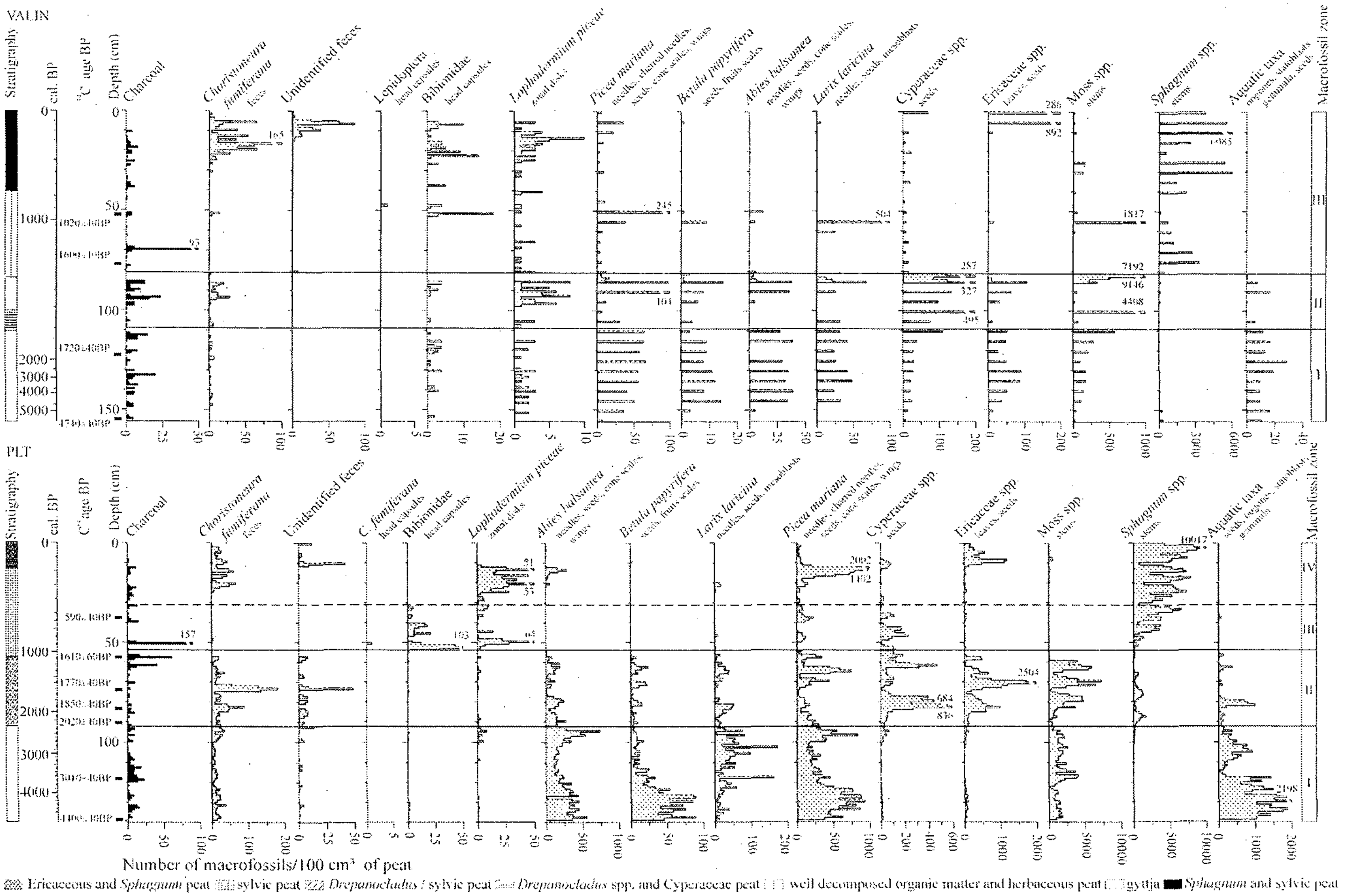


Figure 4.5 Macrofossil diagrams (selected taxa) of the four study sites (Saguenay, Quebec, Canada).



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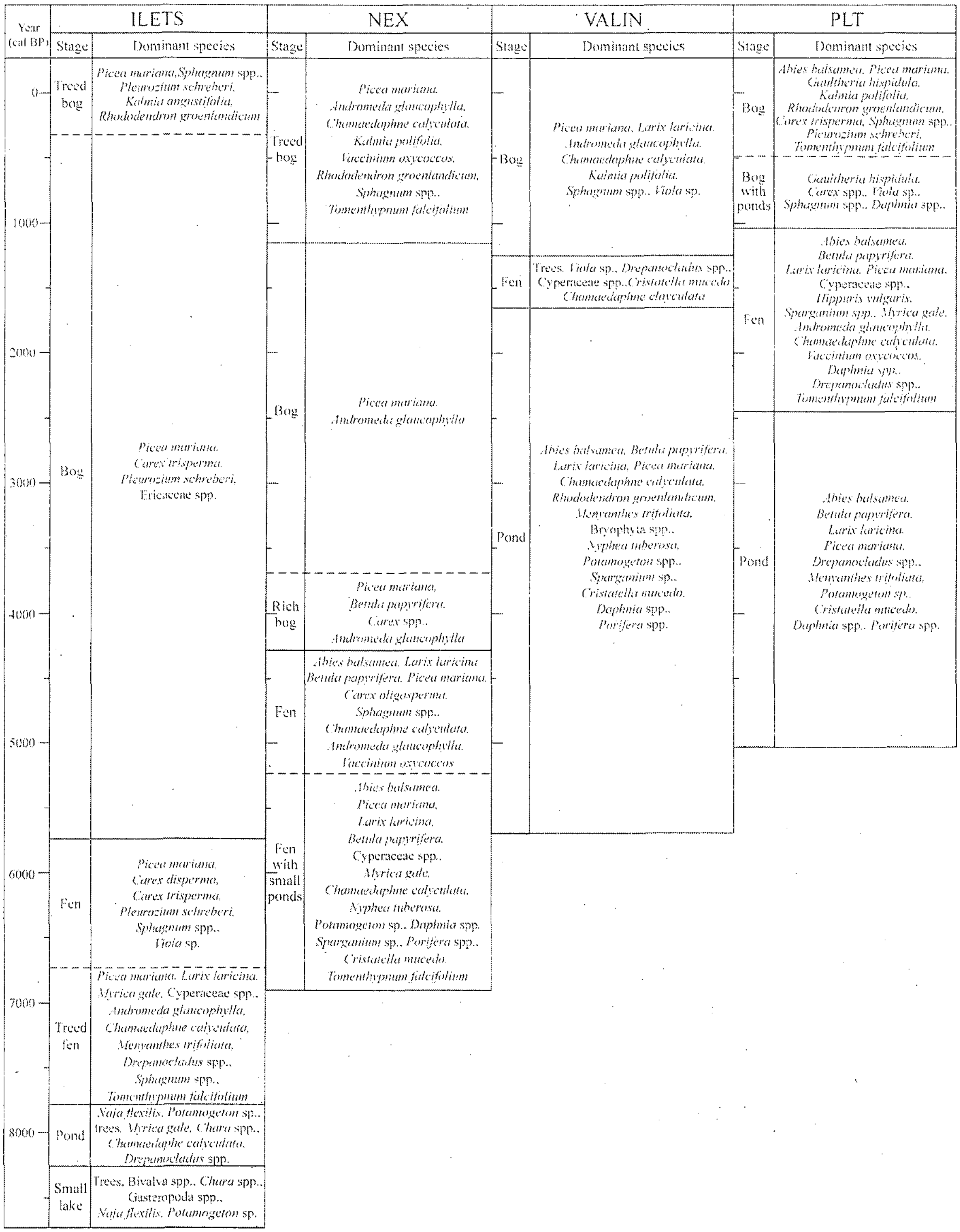

ILETS	
Stage	Dominant species
Treed bog	*Picea mariana,Sphagnum* spp., *Pleurozium schreberi,* *Kalmia angustifolia,* *Rhododendron groenlandicum*
Bog	*Picea mariana.* *Carex trisperma.* *Pleurozium schreberi,* Ericaceae spp.
Fen	*Picea mariana,* *Carex disperma,* *Carex trisperma.* *Pleurozium schreberi.* *Sphagnum* spp., *Viola* sp.
Treed fen	*Picea mariana. Larix laricina.* *Myrica gale,* Cyperaceae spp., *Andromeda glaucophylla,* *Chamaedaphne calyculata,* *Menyanthes trifoliata,* *Drepanocladus* spp., *Sphagnum* spp., *Tomenthypnum falcifolium*
Pond	*Naja flexilis. Potamogeton* sp., trees, *Myrica gale, Chara* spp., *Chamaedaphe calyculata.* *Drepanocladus* spp.
Small lake	Trees, Bivalva spp., *Chara* spp., Gasteropoda spp., *Naja flexilis. Potamogeton* sp.

NEX	
Stage	Dominant species
Treed bog	*Picea mariana.* *Andromeda glaucophylla,* *Chamaedaphne calyculata.* *Kalmia polifolia.* *Vaccinium oxycoccos.* *Rhododendron groenlandicum,* *Sphagnum* spp., *Tomenthypnum falcifolium*
Bog	*Picea mariana.* *Andromeda glaucophylla*
Rich bog	*Picea mariana,* *Betula papyrifera.* *Carex* spp., *Andromeda glaucophylla*
Fen	*Abies balsamea. Larix laricina* *Betula papyrifera. Picea mariana.* *Carex oligosperma.* *Sphagnum* spp., *Chamaedaphne calyculata.* *Andromeda glaucophylla.* *Vaccinium oxycoccos*
Fen with small ponds	*Abies balsamea.* *Picea mariana,* *Larix laricina,* *Betula papyrifera.* Cyperaceae spp., *Myrica gale,* *Chamaedaphne calyculata.* *Nyphea tuberosa.* *Potamogeton* sp., *Daphnia* spp. *Sparganium* sp., *Porifera* spp., *Cristatella mucedo.* *Tomenthypnum falcifolium*

VALIN	
Stage	Dominant species
Bog	*Picea mariana, Larix laricina.* *Andromeda glaucophylla.* *Chamaedaphne calyculata.* *Kalmia polifolia.* *Sphagnum* spp., *Viola* sp.
Fen	Trees. *Viola* sp., *Drepanocladus* spp., Cyperaceae spp.,*Cristatella mucedo* *Chamaedaphne calyculata*
Pond	*Abies balsamea, Betula papyrifera.* *Larix laricina, Picea mariana.* *Chamaedaphne calyculata.* *Rhododendron groenlandicum.* *Menyanthes trifoliata,* Bryophyta spp., *Nyphea tuberosa,* *Potamogeton* spp., *Sparganium* sp., *Cristatella mucedo.* *Daphnia* spp., *Porifera* spp.

PLT	
Stage	Dominant species
Bog	*Abies balsamea. Picea mariana.* *Gaultheria hispidula.* *Kalmia polifolia.* *Rhododeuron groenlandicum.* *Carex trisperma, Sphagnum* spp., *Pleurozium schreberi,* *Tomenthypnum falcifolium*
Bog with ponds	*Gaultheria hispidula.* *Carex* spp., *Viola* sp., *Sphagnum* spp., *Daphnia* spp.,
Fen	*Abies balsamea.* *Betula papyrifera.* *Larix laricina. Picea mariana.* Cyperaceae spp., *Hippuris vulgaris.* *Sparganium spp., Myrica gale.* *Andromeda glaucophylla.* *Chamaedaphne calyculata.* *Vaccinium oxycoccos.* *Daphnia spp.*, *Drepanocladus* spp., *Tomenthypnum falcifolium*
Pond	*Abies balsamea.* *Betula papyrifera.* *Larix laricina.* *Picea mariana.* *Drepanocladus* spp., *Menyanthes trifoliata,* *Potamogeton sp.*, *Cristatella mucedo.* *Daphnia* spp., *Porifera* spp.

Figure 4.6 Developmental stages and dominant species through time at the four peatlands (Saguenay, Quebec, Canada).

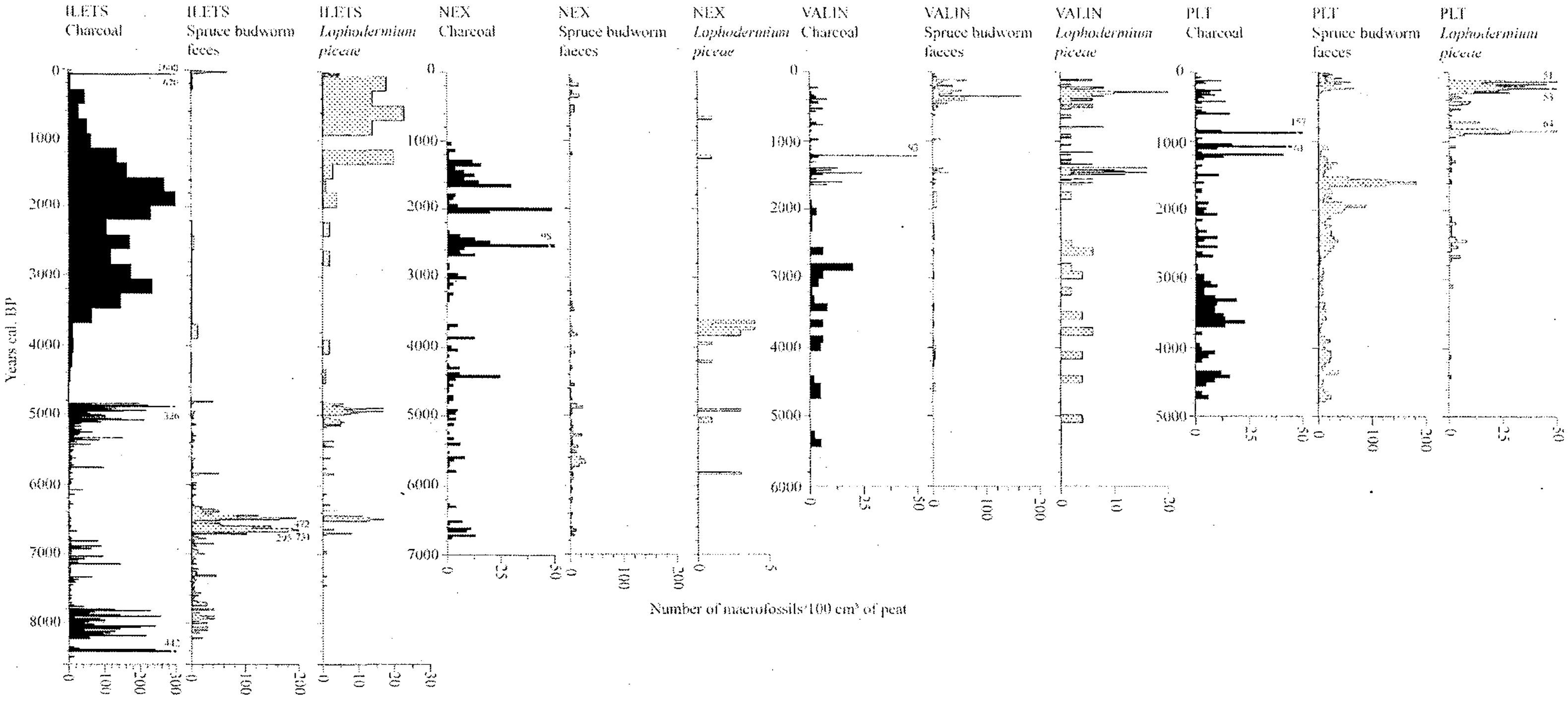

Figure 4.7 Charcoal fragments, spruce budworm feces, and zonal disks of *Lophodermium piceae* through time for the four study sites (Saguenay, Quebec, Canada).

4.6. DISCUSSION

4.6.1. RECONSTRUCTION OF PERIODS OF HIGH SPRUCE BUDWORM ACTIVITY

To our knowledge, this study is the first reliable multiple millennium-long reconstruction of the activity of an epidemic insect species. For this reconstruction of the history of spruce budworm activity, we considered that a high number of feces corresponded to a period of a high abundance of the insect associated with severe tree defoliation, although the conservation conditions prevailing during the accumulation of the peat material may also have influenced the abundance of feces. Previously undetected periods of intense spruce budworm activity in the boreal forest during the Holocene were identified using spruce budworm feces: between 8200 and 7700, around 7310, between 6700 and 6300, and approximately around 5800, 4800, 1900, 1600, 1500 and 1000 cal. BP. Outbreaks that occurred during the last two centuries were also clearly detected in PLT, VALIN and NEX, but the ILETS profile was the only site to clearly registered the 1978 outbreak due to important temporal compression in the first 40 cm of the profile. The black spruce stand of ILETS originated from the 1922 fire (Gagnon, 1989), which correspond to the peak of charcoal observed at 13 cm in the profile. The trees were probably too young in 1952 to be seriously affected by spruce budworm (Morin, 1993).

Head capsules and zonal disks were tentatively used to support the history reconstructed with spruce budworm feces. However, feces were the more reliable to reconstruct a multi millennium-long spruce budworm abundance than the other paleoecological indicators used and there validity to reconstruct recent outbreak was demonstrated in chapter 2. Moreover, they were more abundant and better preserved than head capsules or *Lophodermium piceae* zonal disks; their alteration did not significantly increase with depth. A high number of feces were found near the soil surface of all sites, but larger amounts were found deeper in the peat. Furthermore, peaks of feces were more numerous than peaks of disks or head capsules. Very few spruce budworm head capsules were found in the four profiles, and, surprisingly, none in the surface peat samples corresponding to the period covering the 19th and 20th century spruce budworm outbreaks. A spruce budworm history reconstructed solely using head capsules would have failed to detect the most recent and well documented outbreaks. Zonal disk were the most abundant at the same depth of important peaks of charcoal or feces, indicating the senescence of trees due to fire or outbreaks, and confirming periods of spruce budworm outbreaks. However, the disks were also abundant in ILETS during the last 2 000 years suggesting that the black spruce stands were stressed or affected by dieses or dying. Head capsules and fungal disks are fragile, so they are less likely to remain well preserved in peat material. Much more peat material is required to obtain enough spruce budworm head capsules and *Lophodermium piceae* zonal disks to construct a reliable history of the activity of the insect. Sieves with smaller mesh (250 – 180 μm) are also probably required to retain head capsules of smaller larval stages. Studying head capsules and zonal disks is consequently time consuming as compared to feces for the particular case of spruce budworm.

It is noteworthy that the distinct peak of spruce budworm feces detected at ILETS around 5800 cal. BP (4920 ± 50 BP) corresponds to a documented period of high abundance of head capsules of spruce budworm in southern Quebec (4910 ± 90 BP; Bhiry and Filion, 1996), and with a documented period of high abundance of microlepidoptera head capsules in northern Maine (ca. 4800 BP; Anderson *et al.*, 1986). This period corresponds to the hemlock (*Tsuga canadensis* L. [Carr.]) decline in eastern North America, which has been attributed to defoliation by hemlock looper and spruce budworm (Filion and Quinty, 1993; Bhiry and Filion, 1996).

The low time resolution of paleoecological analyses and the temporal compression of the peat material do not allow the detection of all the periods of intense spruce budworm activity, especially when they are too close in time and, consequently, do not permit the calculation of the duration of outbreak cycles. Moreover, since only one peat core was collected at each site, other periods of insect activity may have been missed. In addition, fire may have compromised the detection of feces by burning peat material (ILETS). Fire may also have played a significant role in spruce budworm activity. Fleming *et al.* (2002) observed that areas frequently affected by spruce budworm outbreaks exhibit low fire frequency, suggesting that fire may prevent the development of extensive mature forests more susceptible to spruce budworm outbreaks. Our results indicate that all major peaks of spruce budworm feces occurred when fire activity was low, while conversely, feces occurrence was very low during periods of intense fire activity. So we hypothesized that forests frequently affected by fire would be less severely affected by spruce budworm outbreaks, because fire prevents the development of extensive mature forests more susceptible to spruce budworm outbreaks. Their detection in tree-rings chronologies or in macrofossil assemblages would be more difficult if the budworm populations were lower compared to the population levels during periods of low fire frequency and high spruce budworm activity.

Periods of high spruce budworm activity were not only found when black spruce and/or balsam fir macrofossil remains were present in the samples, which suggests that the paleoecological reconstructions were probably not much influenced by the presence of host trees directly in the sampling sites. However, host trees had to be present nearby, at the marge of the peatlands or close in the forest surrounding the peatlands, in order to feed the larvae since lateral transportation of feces by wind is probably limited to the same distance as macroscopic charcoal, i.e., a few meters (Clark *et al.*, 1998; Ohlson and Tryterud, 2000; Carcaillet *et al.*, 2001).

4.6.2. IMPACT OF SPRUCE BUDWORM AND FIRE ON VEGETATION

The vegetation history of the study sites was mainly influenced by the autogenic development (peat build up, oligotrophication, acidification) of the peatlands. This is a natural phenomenon commonly observed in peatlands of Europe and North America (Kuhry *et al.*, 1993; Lavoie *et al.*, 2001; Hughes and Dumayne-Peaty, 2002). Fen to bog transitions had major impacts on tree composition and abundance resulting in an important decrease of macrofossil remains of balsam fir, white birch and tamarack (ILETS around 6740 cal. BP, NEX around 4860 cal. BP, VALIN around 1550 cal. BP, PLT around 1030 cal. BP). The increasing thickness of the peat deposits was probably responsible for this decline, because it reduces root access to mineral soil nutrients (Montague and Givnish 1996; Lavoie *et al.*, 2001). Black spruce was also affected by this change in the trophic regime, but the abundance of macrofossil remains later increased at all sites.

Because of the strong influence of autogenic processes, it is difficult to identify a clear impact of fire and spruce budworm on vegetation composition or abundance by macrofossil analysis. Fire and insect outbreaks may have induced fluctuations in the relative abundance of balsam fir and black spruce trees. Balsam fir, the preferred host of spruce budworm, was able to maintain its presence in the study sites until the fen-bog transition occurred, despite evidence of high spruce budworm activity at ILETS (8200 – 7800 cal. BP), NEX (6800 – 4860 cal. BP) and PLT (4800 – 1000 cal. BP). This supports the hypothesis of Baskerville (1975) and MacLean (1988) that spruce budworm and balsam fir forests form a relatively stable ecological system that undergoes fluctuations in population abundance in the absence of other catastrophic events.

4.6.3. HAS SPRUCE BUDWORM ACTIVITY CHANGED DURING THE HOLOCENE?

Several entomologists and dendroecologists have suggested that spruce budworm outbreaks occurred almost periodically at an average interval of 35 years (Swain and Craighead, 1924; Blais, 1965; Royama, 1984; Jardon *et al.*, 2003) during the last 300 years, and probably also during most of the Holocene epoch (Baskerville, 1975; Blais, 1983). Our own results suggest that abundance of the insect considerably fluctuated during in the Holocene, and that important changes in the dynamics of spruce budworm populations occurred through time.

The omnipresence of spruce budworm feces in the four peat cores suggests an endemic presence of the insect for the last 8200 years. However, prior to the last 200 years, periods of high spruce budworm activity were rare and local, although some periods may have been very intense at a particular site. The fact that the outbreaks of the last 200 years were detected in three of the sites, – a phenomenon not detected in the profiles during the Holocene in the boreal zone – may suggests that recent outbreaks were regional more intense and widespread than those that occurred during the rest of the Holocene epoch in the boreal zone, suggesting some synchrony across the region. This is in agreement with the dendrochronological studies of Blais (1983) and Jardon (2001) showing an increase in intensity and synchrony of spruce budworm outbreaks during the 20th century. Blais (1983) suggested that fire suppression, logging and the use of pesticides increased the abundance of balsam fir across large regions, and thus increased the vulnerability of forests to spruce budworm. Jardon (2001) and Morin *et al.* (2007) proposed that the reduction in fire frequency since the end of the 19th century observed in the southern part of the boreal forest (Bergeron and Archambault, 1993) also favored the development of mature fir forests critical for the development of virulent outbreaks.

In conclusion, spruce budworm dynamics appear to have change during the last 200 years. This may be the result of forest structure modifications. Paleoecological studies of boreal peatlands allow us to go back further in time and to retrace major spruce budworm outbreaks activity never detected before. However, the temporal resolution of peat profiles is not precise enough to estimate an outbreak frequency. Further work should be dedicated to the calibration of spruce budworm feces production and conservation in peat, gyttja, or humus. Such work would possibly give a better idea of outbreak intensity or spruce budworm population density.

4.7. AKNOWLEDGEMENTS

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CHAPITRE 5. CONCLUSION GÉNÉRALE

5.1. LES PRINCIPAUX RÉSULTATS DE LA RECHERCHE

L'histoire récente des épidémies de la tordeuse des bourgeons de l'épinette est bien connue au Québec. Les informations sont toutefois incomplètes ou inexistantes lorsque l'on remonte à plus de 300 ans dans le passé. Afin de repousser les limites temporelles auxquelles sont contraintes les analyses dendrochronologiques et les relevés de population d'insectes ou de défoliation, une approche paléoécologique a été retenue dans cette thèse, plus particulièrement la recherche d'indicateurs macrofossiles du passage des épidémies. Quatre petites tourbières situées au Saguenay entourées de sapinières et de pessières touchées par les épidémies récentes de la tordeuse ont été sélectionnées pour leur potentiel élevé au niveau de l'accumulation et de la conservation de la pluie macrofossile associée aux épidémies.

Dans un premier temps, la comparaison des épidémies identifiées dans un même site d'étude à partir de deux sections de tourbe et d'une section d'humus avec celles identifiées par des cernes de croissance d'arbres a permis de valider le potentiel des crottins de la tordeuse des bourgeons de l'épinette comme indicateur d'épidémies récentes. Il a ainsi été possible de retracer avec les crottins les mêmes périodes épidémiques que celles identifiées par Blais (1965), Morin (1994, 1998) et Krause (1997) (Chapitre 2). Les analyses macrofossiles ont même permis de détecter plus d'épidémies que les analyses dendrochronologiques, pouvant ainsi pallier à certaines lacunes de la dendrochronologie, notamment le fait que les arbres étudiés sont souvent des survivants des épidémies, donc ayant subi moins de dommages et enregistrant moins distinctement le signal des épidémies.

Il a été possible de reconstituer 8 200 ans d'histoire d'épidémies à l'aide des crottins de la tordeuse identifiés dans la tourbière du lac des Îlets (Chapitre 3). Seulement deux périodes lors desquelles les populations de la tordeuse étaient élevées ont été enregistrées, soit entre 7 000 et 6 000 cal. BP et lors du 20^e siècle, ce qui suggère que les épidémies sévères étaient des phénomènes rares lors de l'Holocène dans la région boréale, du moins à l'échelle locale dans cette région.

Certains épisodes de défoliation par la tordeuse jamais identifiées auparavant ont été détectés dans les quatre tourbières à l'étude, soit entre 8200 et 7700, vers 7310, entre 6700 et 6300, et approximativement vers 5800, 4800, 1900, 1600, 1500 et 1000 cal. BP (Chapitre 4). La plupart de ces épidémies n'ont été enregistrées que dans un seul des quatre sites étudiés, alors que deux des trois épidémies survenues au cours du 20^e siècle ont été détectées dans tous les sites. Cela suggère que les épidémies récentes étaient plus répandues dans la zone boréale étudiée et possiblement davantage synchronisées que celles qui sont survenues au cours de la majeure partie de l'Holocène dans ce secteur. Cette étude ne permet toutefois pas de statuer avec certitude sur le synchronisme des épidémies de la zone boréale. Un plus grand nombre de sites répartis sur un plus grand territoire et de préférence couvrant une échelle temporelle similaire aurait permis de conclure plus adéquatement sur un synchronisme des épidémies plus important au cours des 200 dernières années. Ce travail offre toutefois une piste de réflexion intéressante à explorer. Blais (1983) et Jardon (2001) proposent qu'un changement important dans la dynamique récente des épidémies de la tordeuse puisse être à l'origine du synchronisme des épidémies récentes. Blais (1983) a suggéré que les interventions humaines dans les écosystèmes forestiers soient à l'origine de ces changements. La coupe à blanc, la protection contre les feux, l'utilisation de pesticides contre la tordeuse et la plantation massive d'épinettes blanches auraient favorisé le développement de peuplements de sapins et d'épinettes rendant l'écosystème forestier plus vulnérable aux épidémies. Jardon (2001) fournit pour sa part une autre explication. Le changement de dynamique résulterait de la diminution de la fréquence des feux depuis la fin du Petit Âge glaciaire, diminution de fréquence observée notamment au sud de la forêt boréale. Le changement de la fréquence des feux est également proposé par Bergeron et Dansereau (1993) pour expliquer la mise en place d'une forêt âgée dominée par les espèces hôtes de la tordeuse au début du 20^e siècle, forêt qui aurait été affectée sévèrement par l'épidémie du début du siècle. Jardon (2001) rapporte que cette épidémie aurait ensuite été responsable de la mise en place de forêts de sapins et d'épinettes sur de grandes superficies. Le maintien de cette structure aurait été favorisé par la suite par le passage de nouvelles épidémies ainsi que par les pratiques forestières. Il est possible que les épidémies sévères détectées dans la zone boréale étudiée dans le cadre de ce projet, résultent d'un débordement d'épidémies plus sévères encore ayant affecté la zone de forêt mélangée plus au sud. Cette zone offre une composition et une structure forestière plus propices au développement et à la survie de la tordeuse des bourgeons de l'épinette, permettant d'atteindre des niveaux de population élevés lors d'épidémies sévères, lorsque les conditions météorologiques et les ressources alimentaires sont adéquates.

Cette thèse aura également permis de supporter l'hypothèse de Blais (1965) et de Baskerville (1975) à l'effet qu'il y aurait un équilibre relativement stable entre la régénération des sapinières et les épidémies de la tordeuse. À l'échelle locale, les épidémies semblent avoir influencé l'abondance relative de l'épinette noire et du sapin baumier sans compromettre leur régénération.

5.2. LIMITES À LA RECONSTITUTION DES ÉPIDÉMIES DE LA TORDEUSE DES BOUREGONS DE L'ÉPINETTE PAR LA PALÉOÉCOLOGIE

Bien que la paléoécologie permette de repousser les limites temporelles de la reconstitution des épidémies de la tordeuse, certaines contraintes liées à l'analyse macrofossile et au développement des tourbières restreignent toutefois les avantages de cette méthode d'analyse. En plus de nécessiter de nombreuses heures de laboratoire pour tamiser les échantillons de tourbe et identifier les macrofossiles végétaux et animaux, la résolution temporelle obtenue est considérablement moindre que celle obtenue par la dendrochronologie en raison des taux relativement bas d'accumulation de sol organique observés dans les tourbières étudiées. Cette faible résolution ne permet pas de déterminer si la fréquence des épidémies a changé au cours de l'Holocène. L'étude des varves de petits lacs, où chaque couche de sédiment représente une année d'accumulation, permettrait peut-être de palier à cette contrainte. Toutefois, des résultats non présentés dans le cadre de cette thèse provenant de deux petits lacs des Monts-Valin, n'ont pas permis d'obtenir un signal épidémique aussi clair que celui obtenu dans les petites tourbières à l'étude.

Les petites tourbières entourées de sapinières et de pessières sont des sites propices à la reconstitution de l'histoire des épidémies de la tordeuse par l'analyse macrofossile. Les processus autogéniques régissant le développement des tourbières ne permettent cependant pas de déterminer par cette méthode d'analyse, pour tout l'Holocène, si les épidémies ont eu des impacts sur la composition forestière car le couvert arborescent des tourbières disparaît lorsque l'épaisseur de la tourbe ne permet plus aux racines des arbres d'être en contact avec le sol minéral sous-jacent (Montague et Givnish, 1996; Lavoie *et al.*, 2001). L'analyse pollinique des échantillons prélevés permettrait de contourner cette difficulté, mais fournirait un portrait de la strate arborescente régionale plutôt que locale en l'absence d'arbres poussant sur la tourbe épaisse.

Relativement peu de capsules céphaliques de la tordeuse ont été observées dans les sections de tourbe comparativement au nombre élevé de crottins. Afin d'obtenir plus de capsules céphaliques, il faudrait augmenter le volume des échantillons prélevés, de même qu'utiliser des tamis à mailles plus étroites (100, 125, 125 µm), ce qui permettrait de récolter les capsules des stades larvaires plus petits. Les capsules céphaliques et les crottins de la tordeuse sont toutefois complémentaires car dans certains sites, quelques capsules de la tordeuse ont été observées alors qu'aucun crottin n'était présent. Était-ce dû à une meilleure conservation des capsules à ce moment, au hasard de la des pièces macrofossiles?

5.3. RELATIONS ENTRE LES ÉPIDÉMIES, LES FEUX ET LES CHANGEMENTS CLIMATIQUES

Certains chercheurs ont proposé l'existence d'un lien entre la fréquence des feux et celle des épidémies de la tordeuse (Fleming *et al.*, 2002). Il a été suggéré que les régions fréquemment affectées par des épidémies auraient une fréquence de feu faible, puisque le feu empêcherait le développement de peuplements matures sensibles aux épidémies de la tordeuse sur de grandes superficies. Les principaux pics de crottins de la tordeuse détectés dans cette thèse l'ont été lorsque l'abondance des restes de charbons de bois était faible. Jardon (2001) rapporte également que la réduction de la fréquence des feux observée à la fin du 19^{e} siècle – début du 20^{e} siècle pourrait être à l'origine du développement de grandes sapinières vulnérables aux épidémies de la tordeuse.

Un lien peut également être établi entre des conditions climatiques plus chaudes et des périodes épidémiques importantes. Les plus grandes abondances de crottins ont été observées durant les deux périodes les plus chaudes de l'Holocène, soit entre 7 000 et 6000 cal. BP et au 20^{e} siècle (Richard, 1994; Sawada *et al.*, 1999). Dans une perspective d'adaptation aux changements, cette question mérite d'être approfondie car selon les projections climatiques établies pour les forêts boréales du Canada, les conditions pourraient y être plus sèches et plus chaudes au cours du 21^{e} siècle (Fleming et Volney, 1995). Puisque la survie et la reproduction des insectes herbivores sont meilleures lorsque leurs hôtes subissent un stress hydrique, ces conditions sèches et chaudes pourraient favoriser l'accroissement des populations de ravageurs forestiers (Mattson et Haack, 1987; Fleming et Volney, 1995; Logan *et al.*, 2003).

5.4. IMPLICATIONS POUR LA GESTION DES FORÊTS

La gestion écosystémique des ressources forestières tend à reproduire les impacts des perturbations naturelles, plus particulièrement celles des feux (Cyr *et al.,* 2009; Long, 2009), afin d'en maintenir la diversité biologique et la viabilité des écosystèmes. Cette gestion repose entre autres sur les connaissances acquises sur les perturbations naturelles des 200 à 300 dernières années, alors que la présente étude donne une perspective plurimillénaire d'histoire épidémique. La thèse suggère que les périodes épidémiques sévères, telles que celles observées lors du 20^e siècle, seraient des événements exceptionnels à l'échelle de l'Holocène dans la forêt boréale. Il serait intéressant de voir si ces nouvelles données pourraient être intégrées à la gestion des essences résineuses. Cela pourrait entraîner une révision à la baisse du volume de bois pouvant être coupé afin de maintenir la régénération des forêts de la zone boréale, ce calcul se basant seulement sur les perturbations survenues lors du 20^e siècle.

L'arrivée éventuelle au Québec d'un insecte exotique défoliateur des essences résineuses, tel que le typographe européen de l'épinette (*Ips typographus*) ou le longicorne brun de l'épinette (*Tetropium fascum*), pourrait changer la donne et modifier complètement la dynamique des perturbations naturelles de la forêt boréale. Une telle menace existe déjà pour certains arbres feuillus du Québec avec l'introduction récente de l'agrile du frêne (*Agrilus planipennis*) et avec la venue éventuelle du longicorne asiatique (*Anoplophora glabripennis*) qui est présent en Ontario et aux États-Unis. L'arrivée d'insectes exotiques envahissants devra être considérée dans la gestion des essences feuillues et résineuses afin d'assurer la régénération et la persistance, et ce, dans un contexte d'adaptation aux changements climatiques.

5.5. PERSPECTIVES DE RECHERCHE

Cette thèse de doctorat a permis d'acquérir des connaissances sur plus de 8 200 ans d'histoire des épidémies de la tordeuse. Elle soulève des questions et permet d'identifier quelques pistes de recherche. Notamment est-il possible de déterminer un seuil quantitatif d'indicateurs macrofossiles identifiant avec certitude une épidémie ? Il serait intéressant d'identifier et de quantifier les différents facteurs influençant la déposition et la capture des crottins de la tordeuse dans les tourbières. Est-ce que la phase de développement de la tourbière peut influencer la conservation des crottins? En outre, il serait intéressant de comparer le potentiel d'enregistrement et de conservation d'indicateurs épidémiques des lacs à celui des petites tourbières. L'étude des sédiments lacustres permettrait d'obtenir plus d'information sur la dynamique forestière en éliminant les contraintes associées aux processus de développement autogéniques des tourbières. Des analyses polliniques complémentaires pourraient également contribuer à l'étude des perturbations affectant la zone boréale et pourraient également fournir plus d'informations sur les peuplements forestiers entourant les sites d'étude. Par ailleurs, il serait intéressant de vérifier si la période épidémique intensive survenue au milieu de l'Holocène au lac des Îlets a aussi été enregistrée dans d'autres régions du Québec touchées par les épidémies récentes de la tordeuse et de vérifier par le fait même si les épidémies étaient synchronisées ou non à l'échelle de la province. L'hypothèse d'un débordement des épidémies sévères de la zone de forêt mélangée méridionale vers la forêt boréale, moins susceptible mérite d'être approfondie en comparant des profils plurimillénaires provenant de la forêt mélangée et de la forêt boréale. Les impacts des feux et des changements climatiques sur la dynamique des épidémies de la tordeuse devraient être étudiés plus en détail, de même que les interactions possibles entre la tordeuse et d'éventuels nouveaux insectes ou maladies affectant les essences résineuses du Québec. Il serait intéressant de tester l'hypothèse de débordement des épidémies de la zone de forêt mélangée vers la zone boréale en étudiant des profils de tourbes dans les deux zones.

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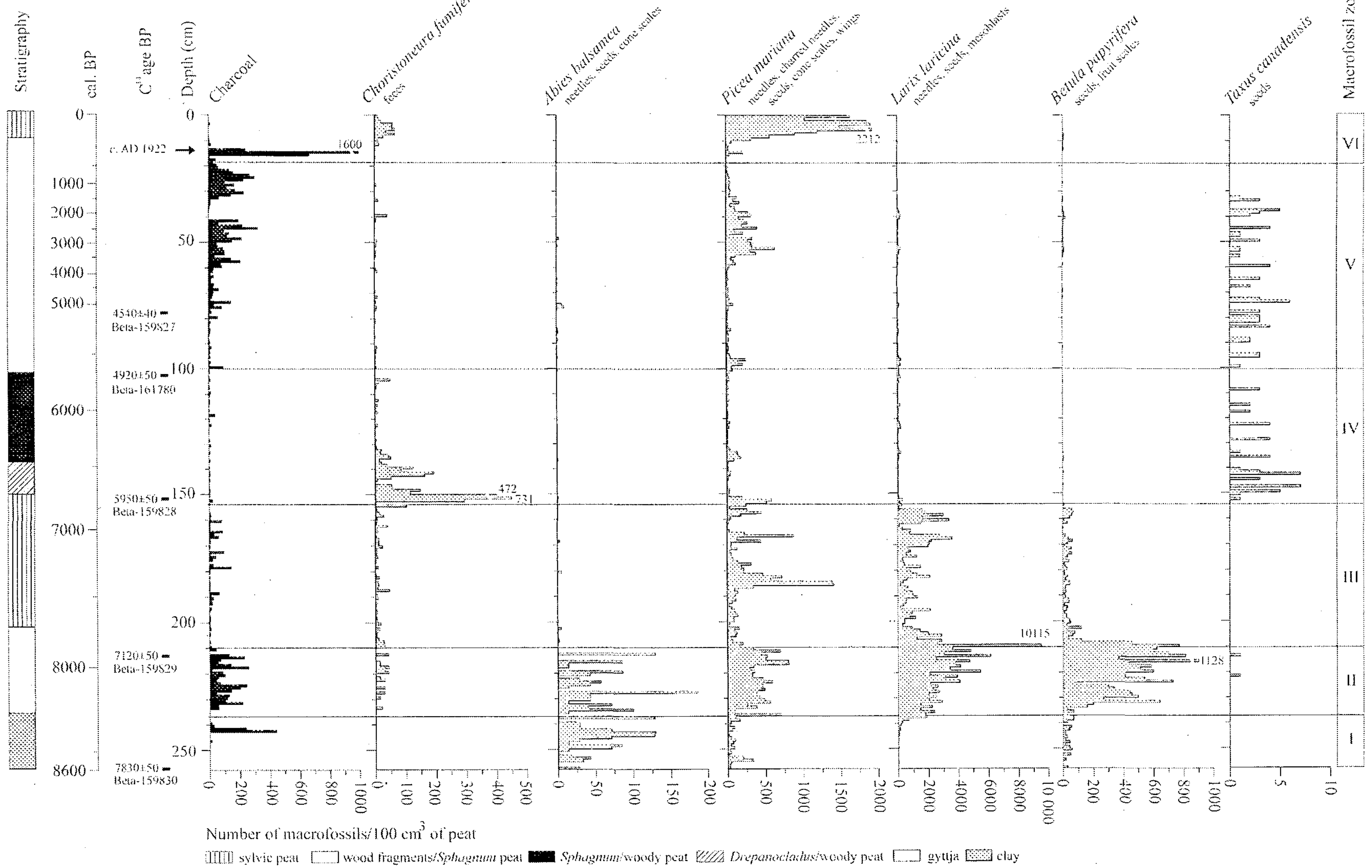
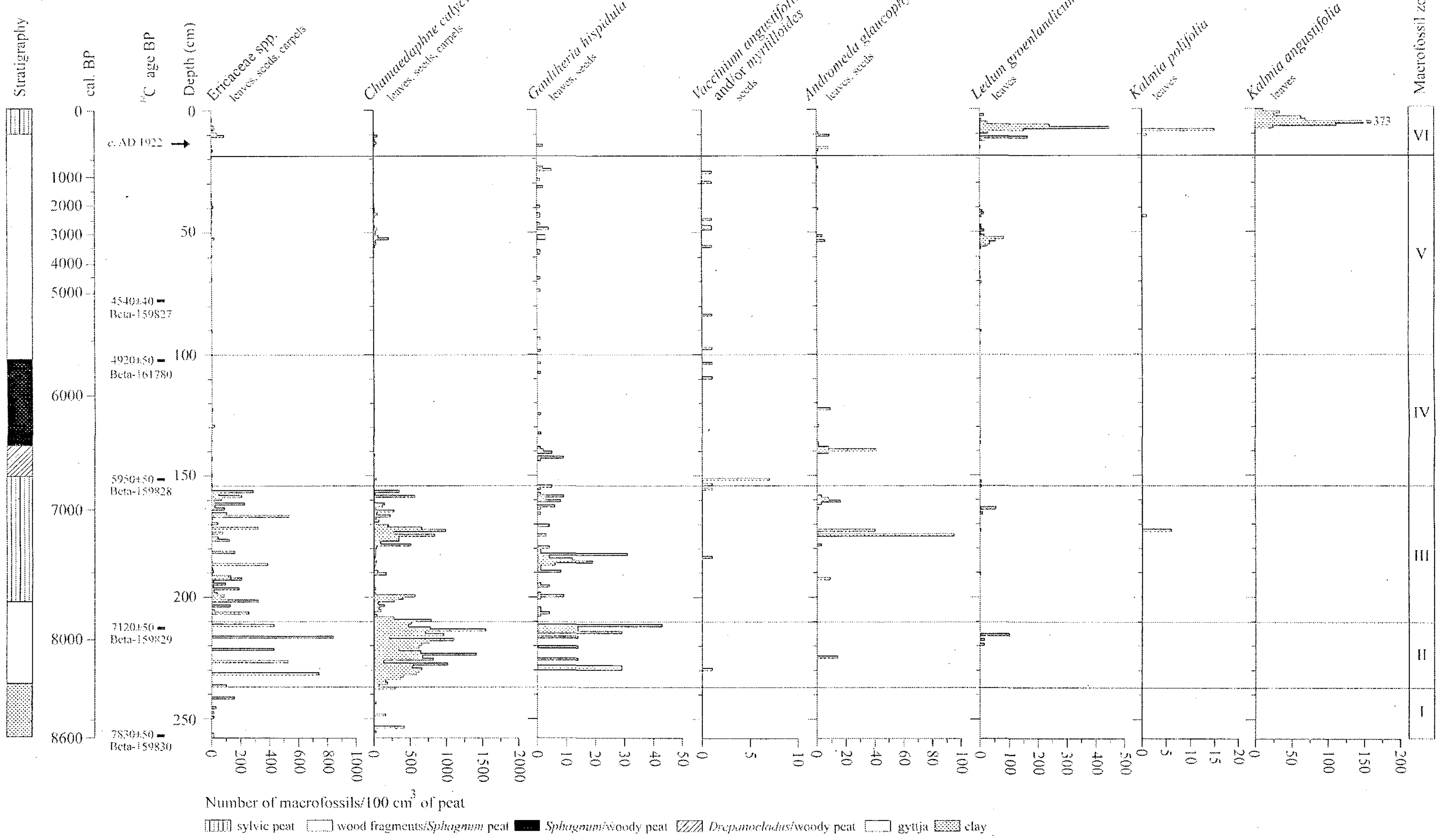
ANNEXES

Annexe 1 Diagrammes macrofossiles complets des sites d'étude

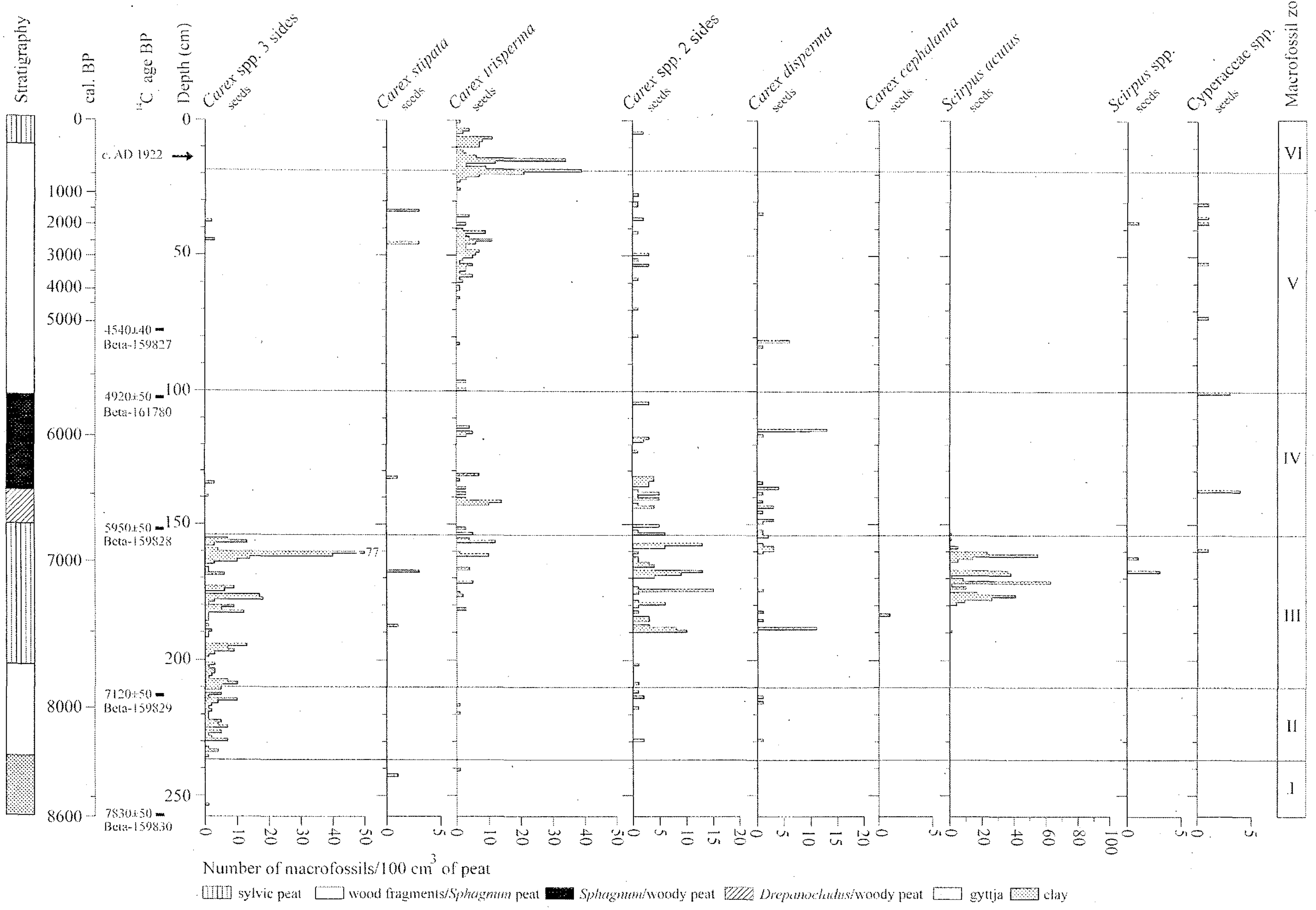
A) ÎLETS CHARCOAL, INSECTS, TREES AND SHRUBS



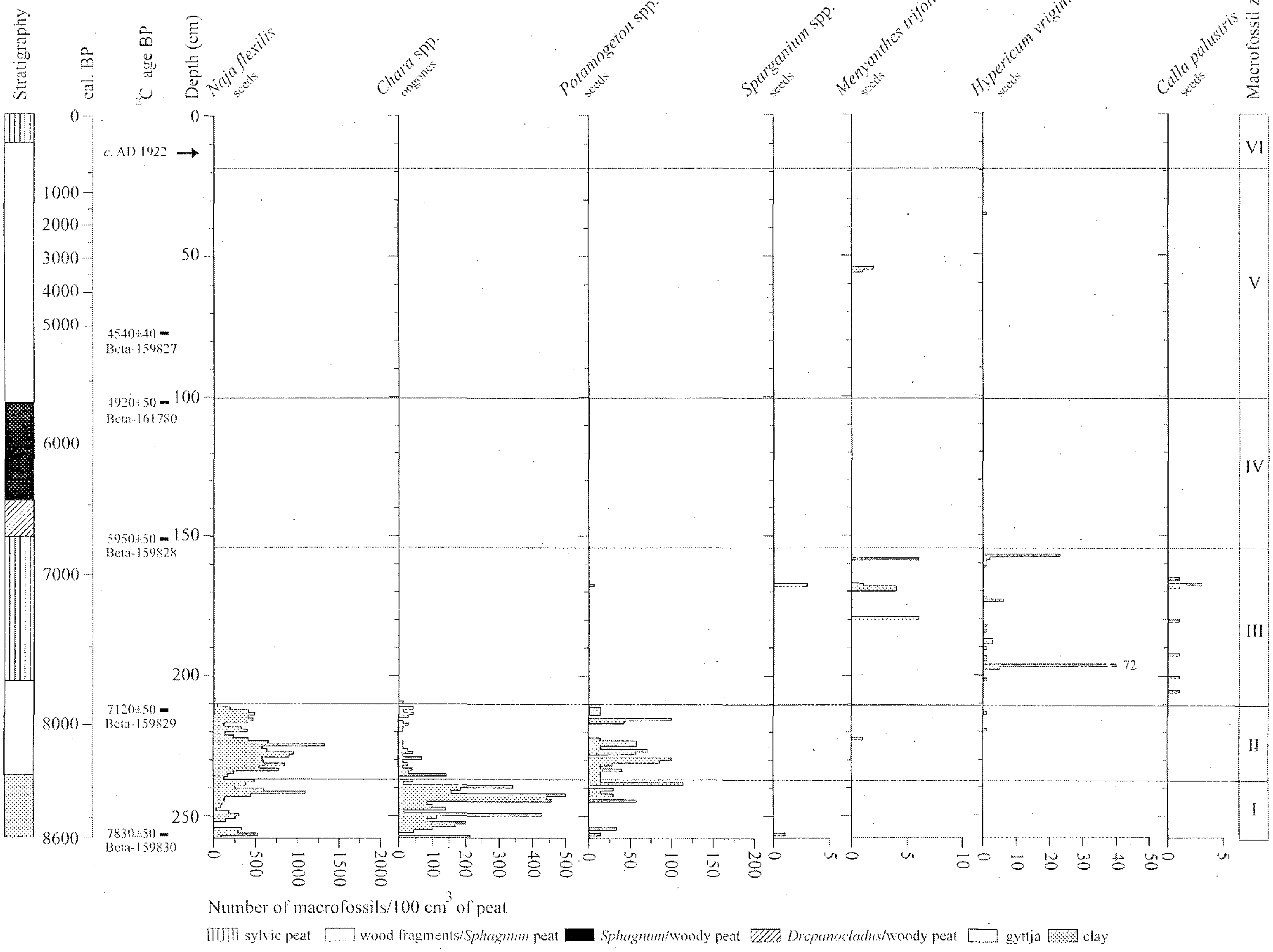


B) ÎLETS ERICACEAE

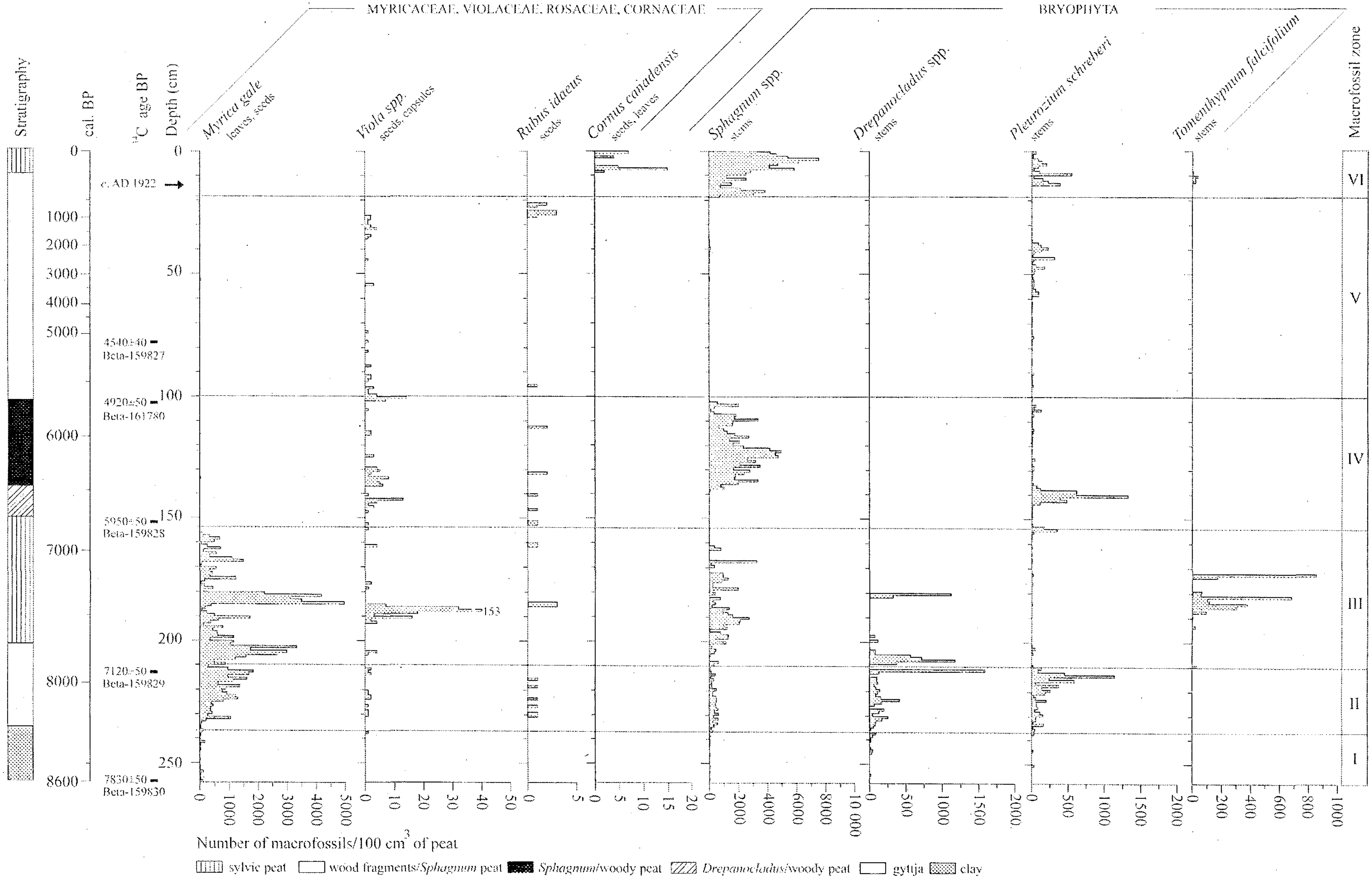
C) îLETS CYPERACEAE



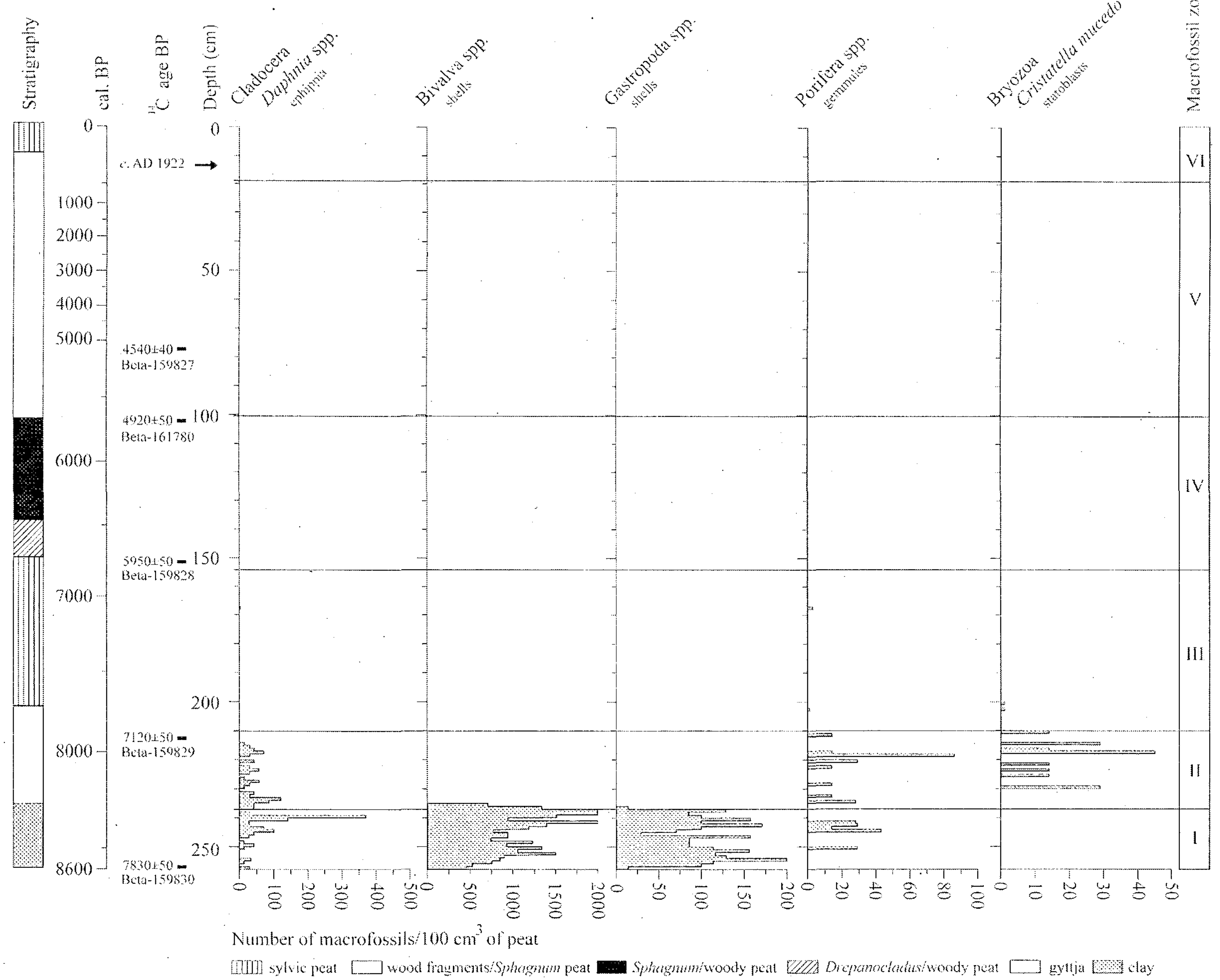
D) ÎLETS AQUATIC VASCULAR PLANTS AND ALGAE



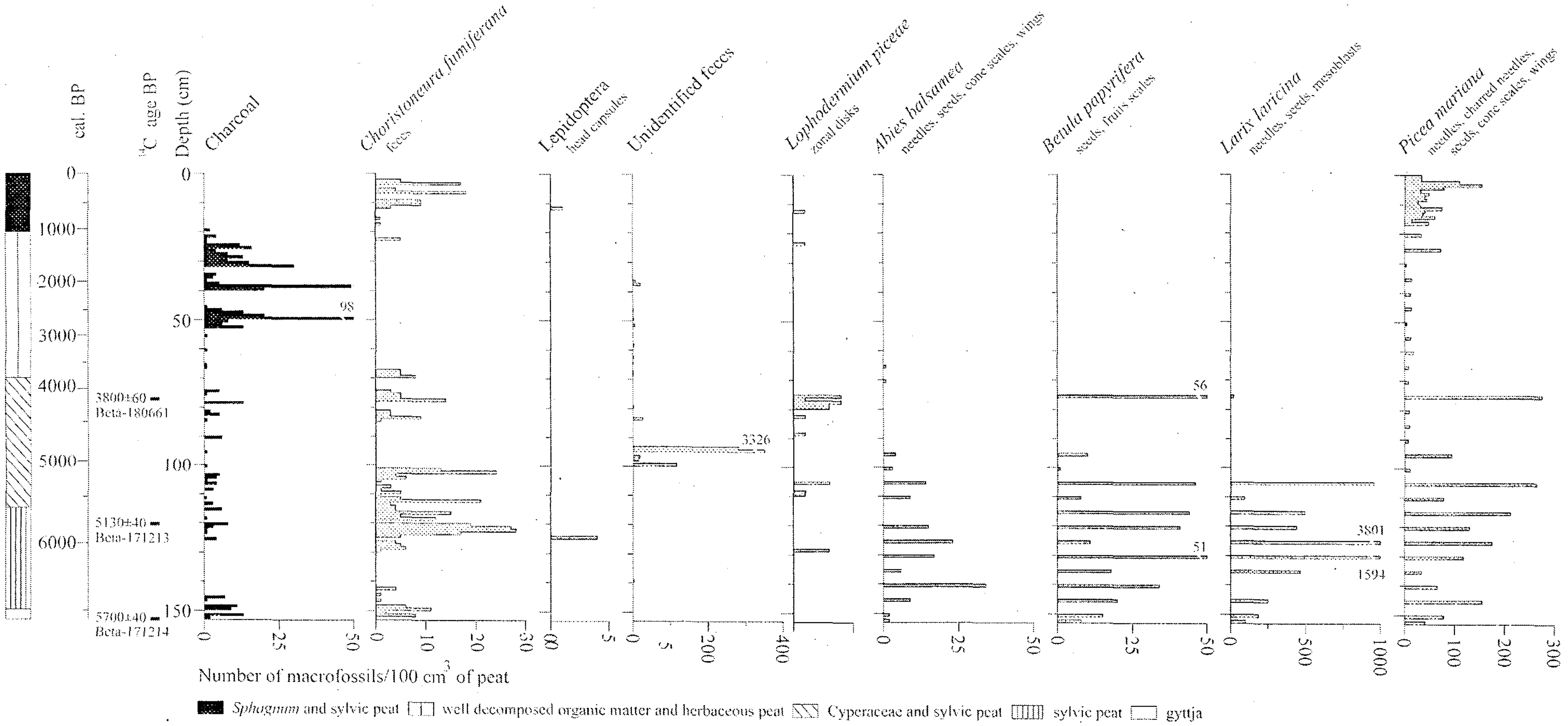
E) ÎLETS MYRICACEAE, VIOLACEAE, ROSACEAE, CORNACEAE AND BRYOPHYTA



F) îLETS OTHER TAXA



G) NEX CHARCOAL, INSECTS AND TREES



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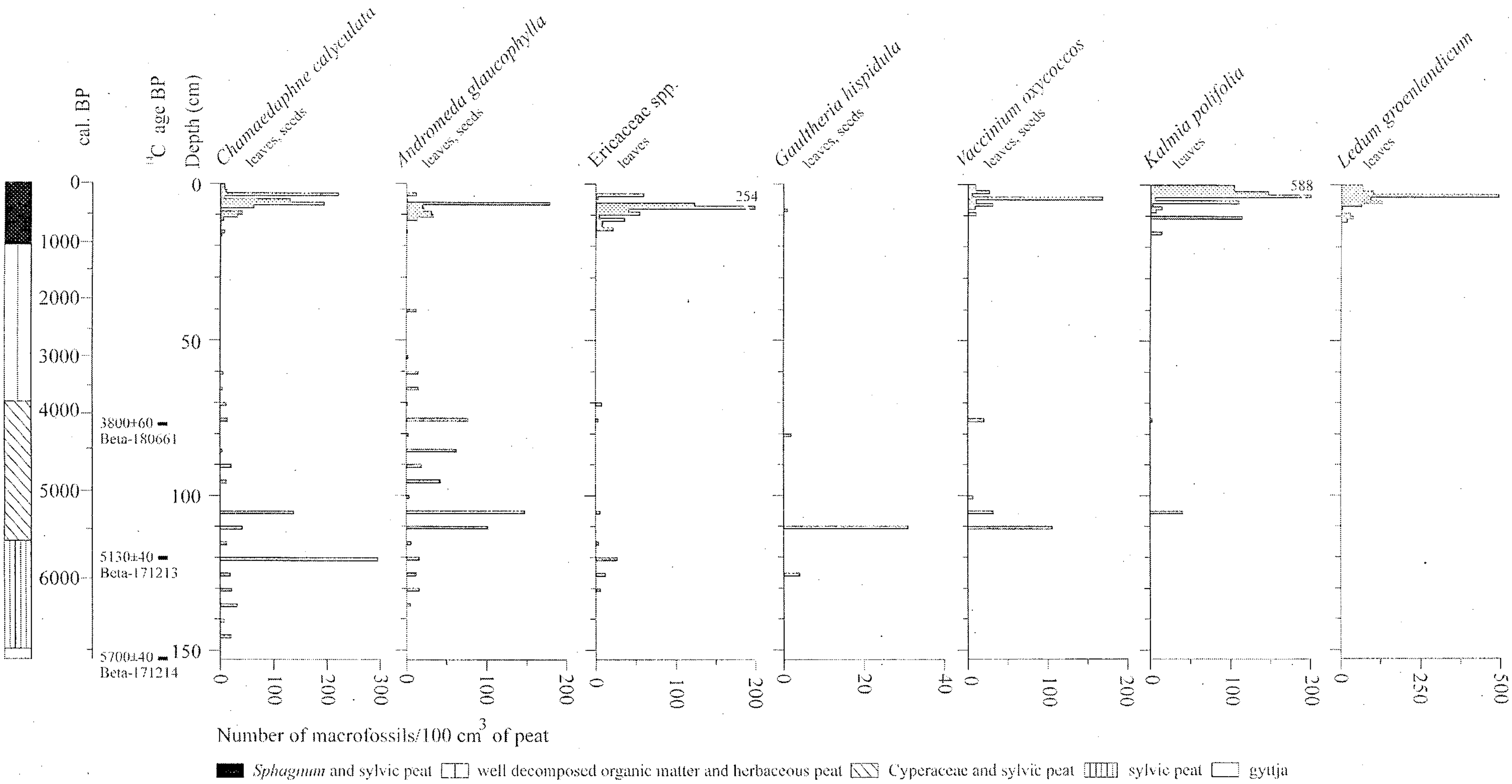
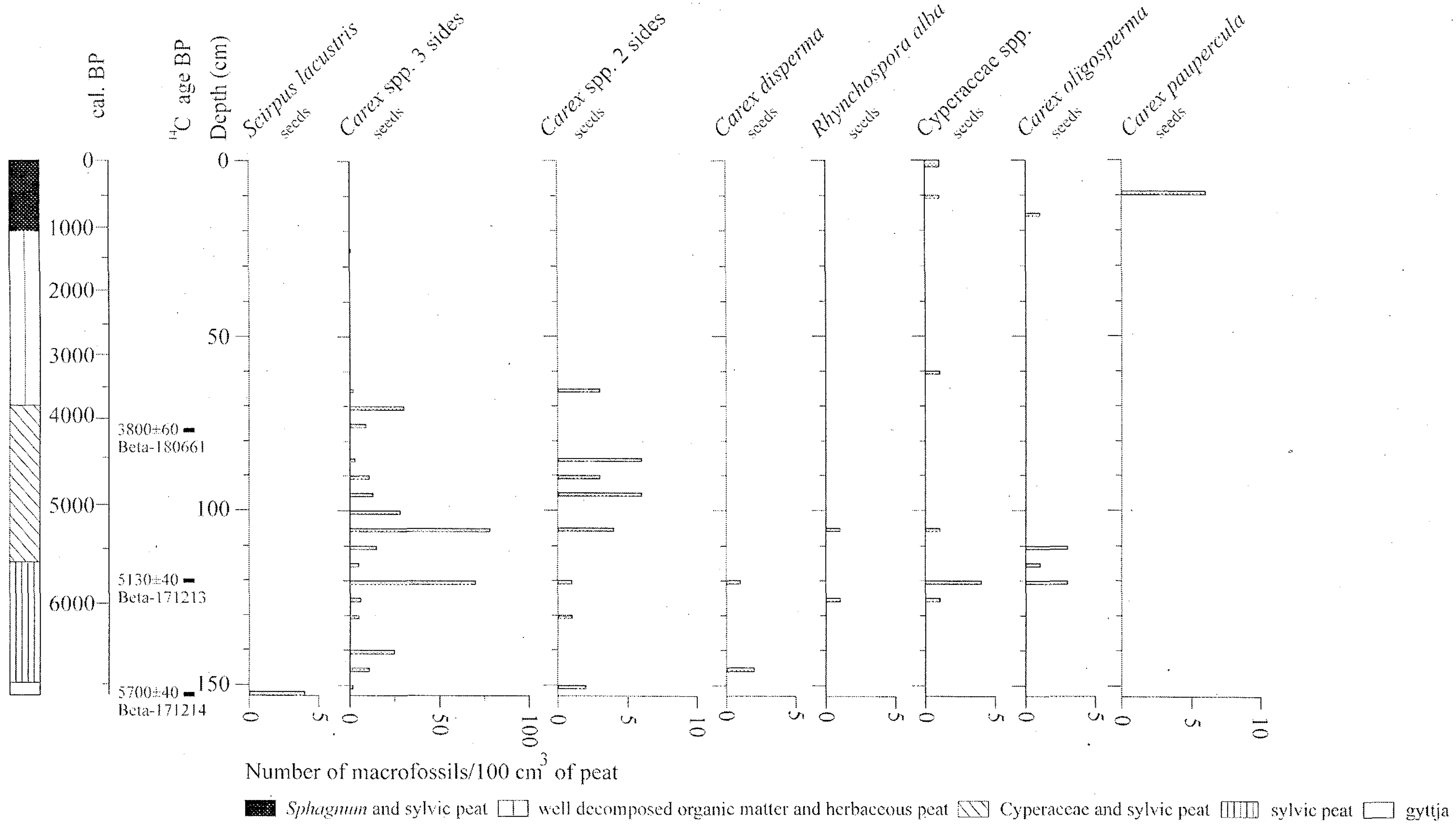
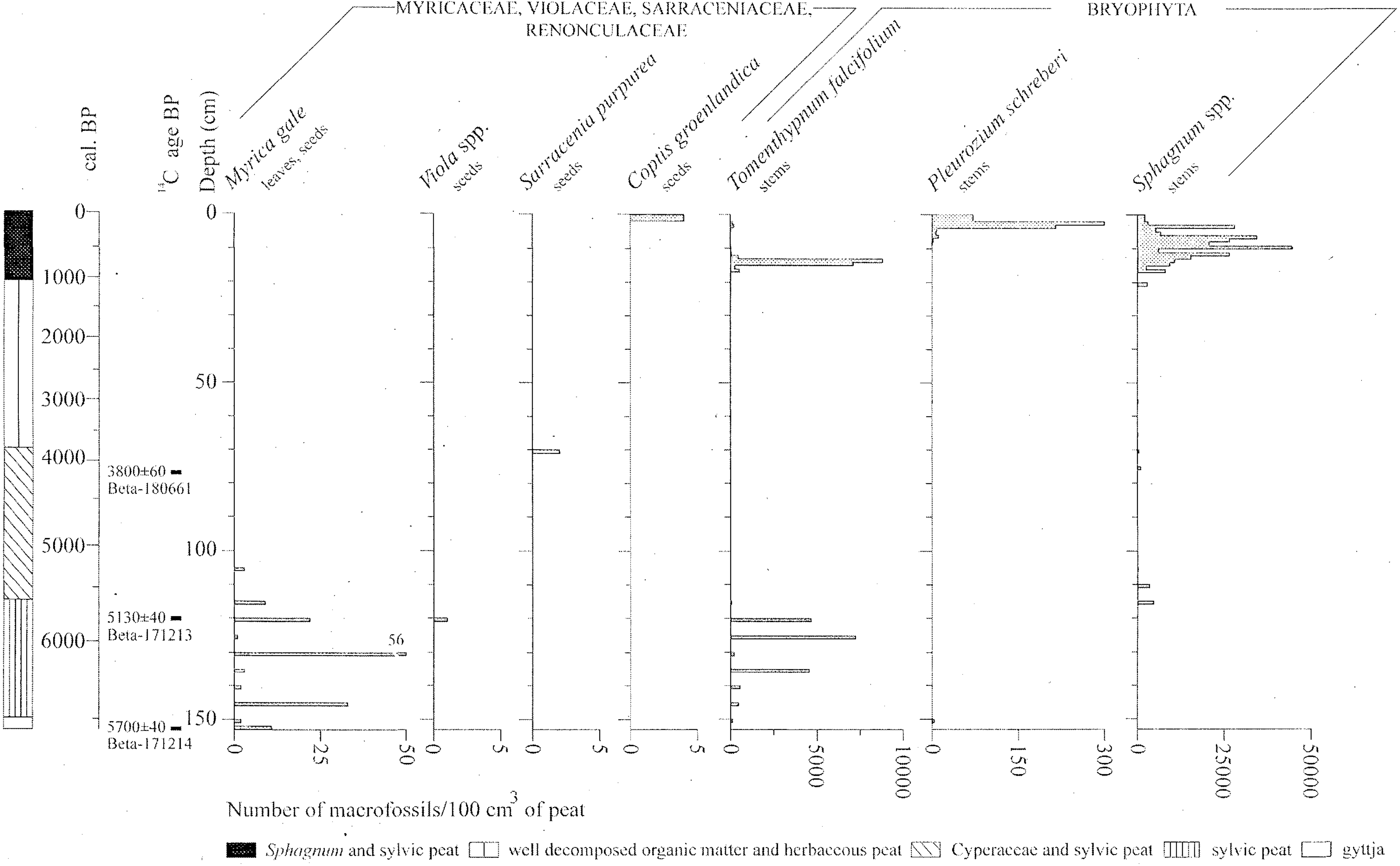


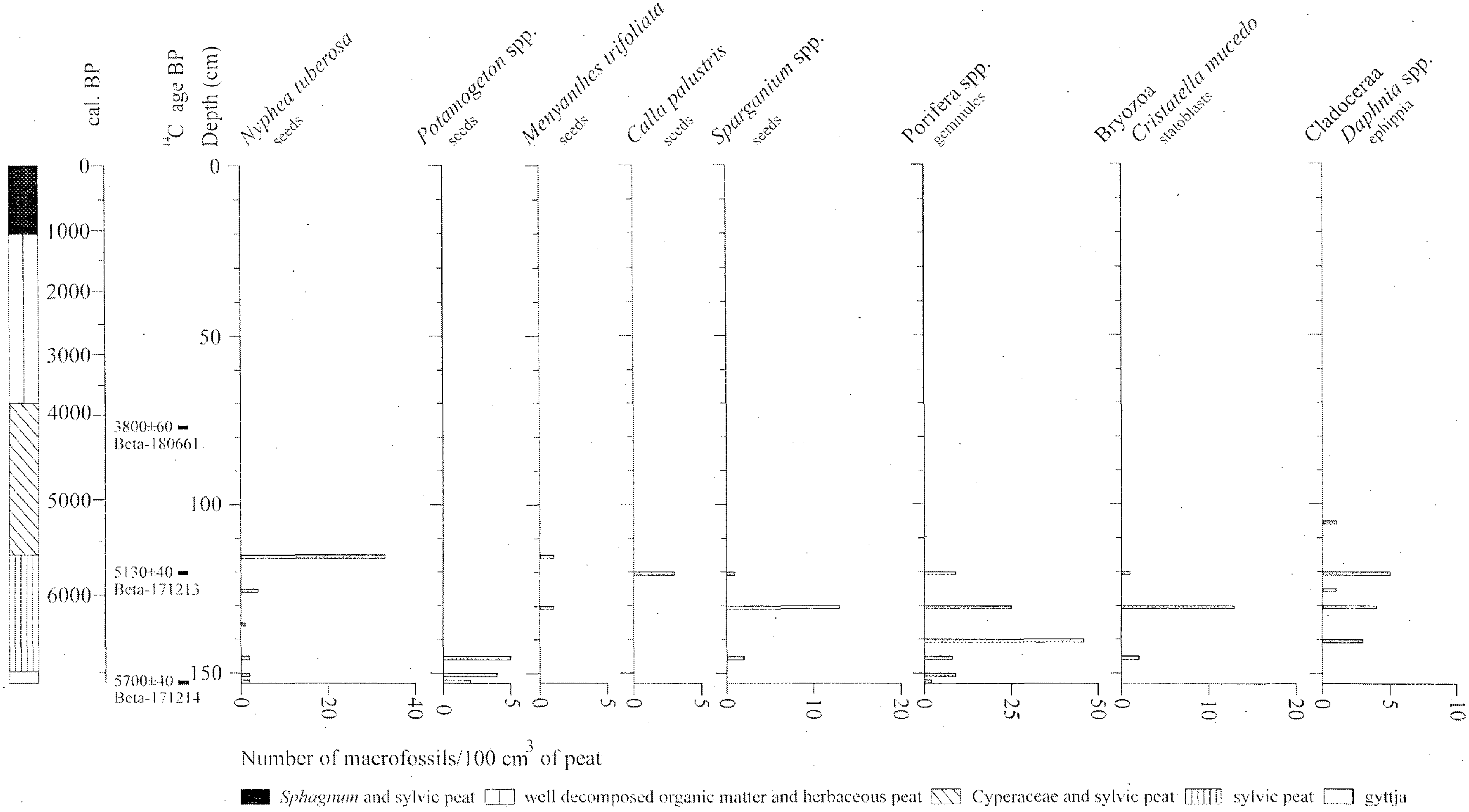
I) NEX CYPERACEAE



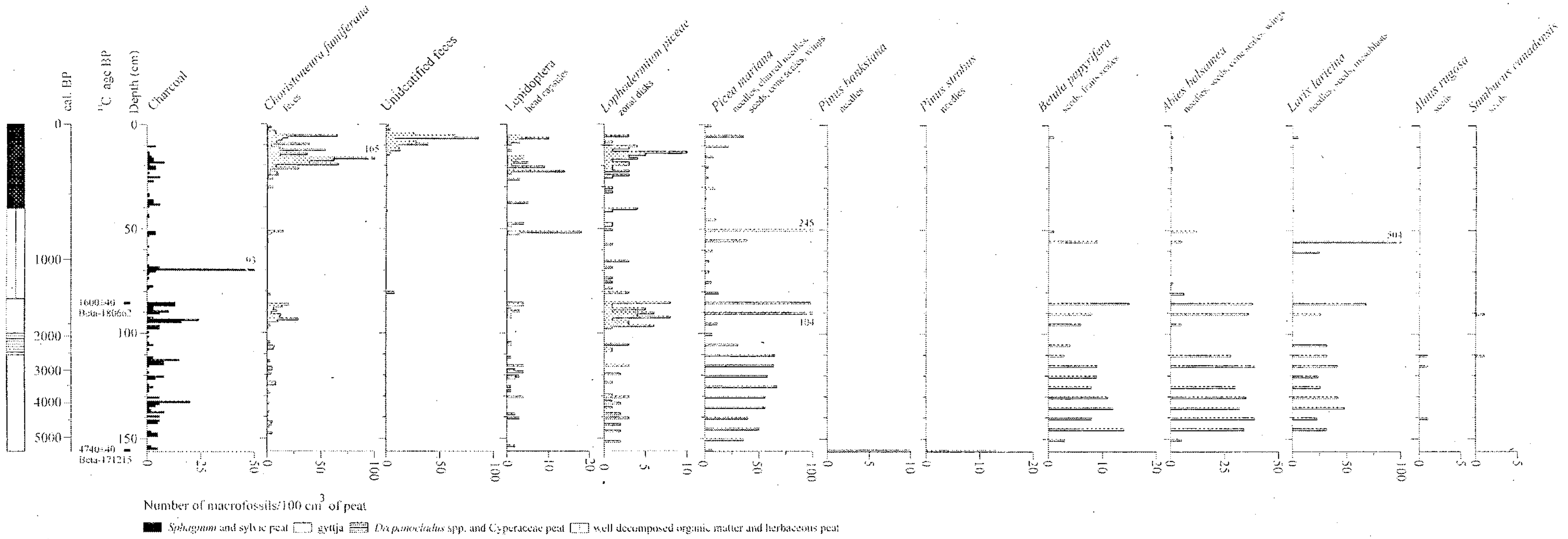
J) NEX MYRICACEAE, VIOLACEAE, SARRACENIACEAE, RENONCULACEAE AND BRYOPHYTA



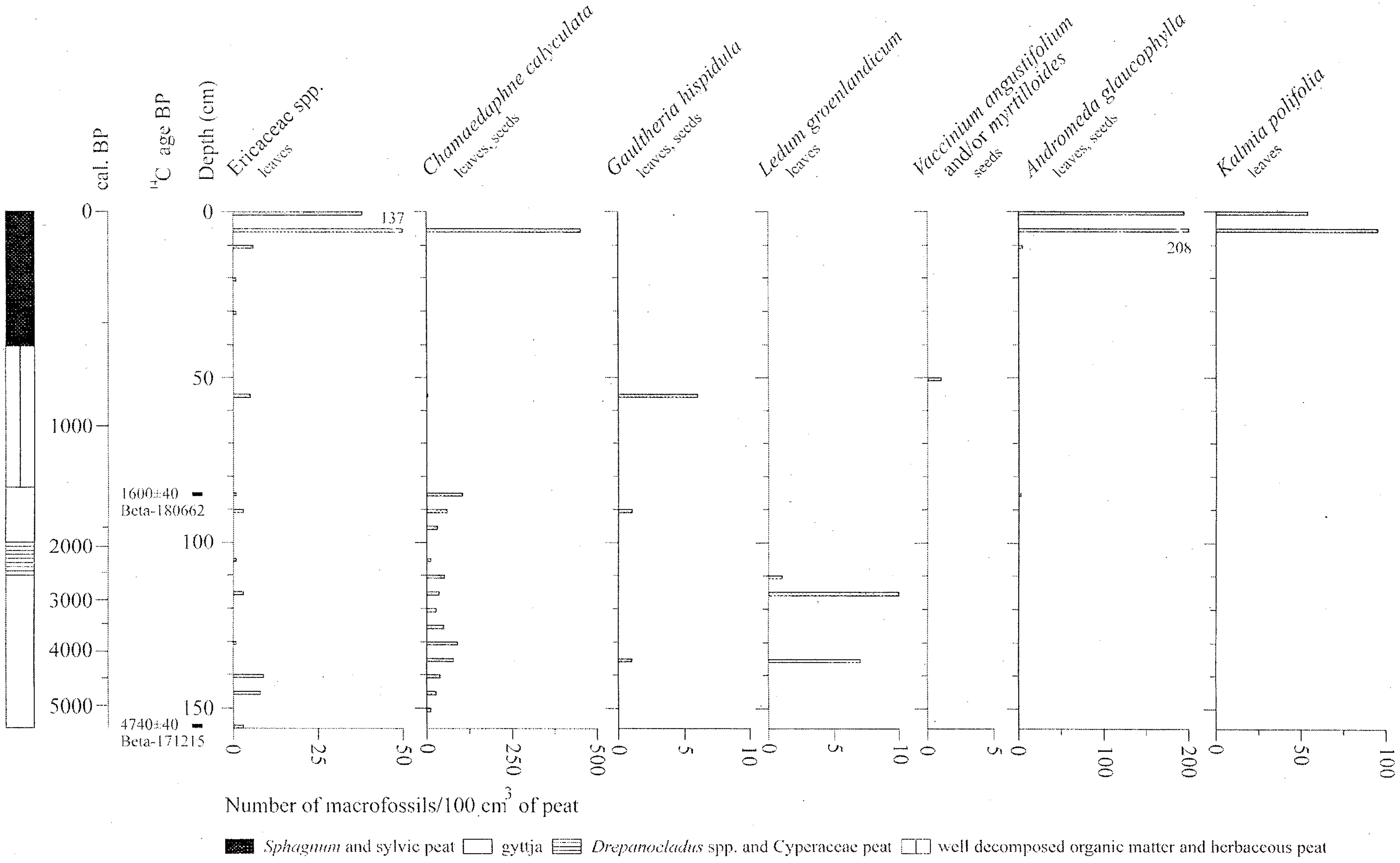
K) NEX AQUATIC VASCULAR PLANTS, ALGAE AND OTHER TAXA



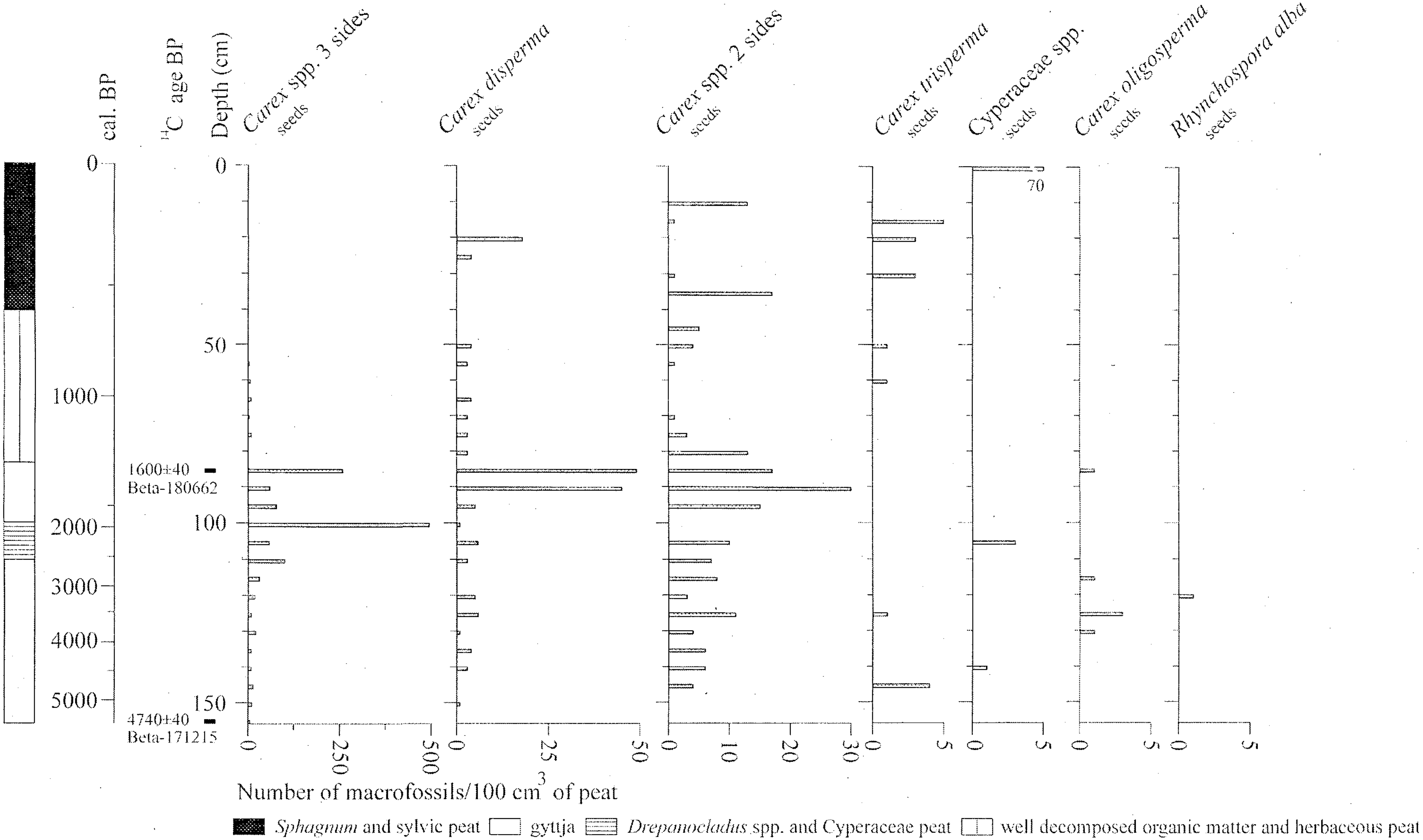
L) VALIN CHARCOAL, INSECTS, TREES AND SHRUBS



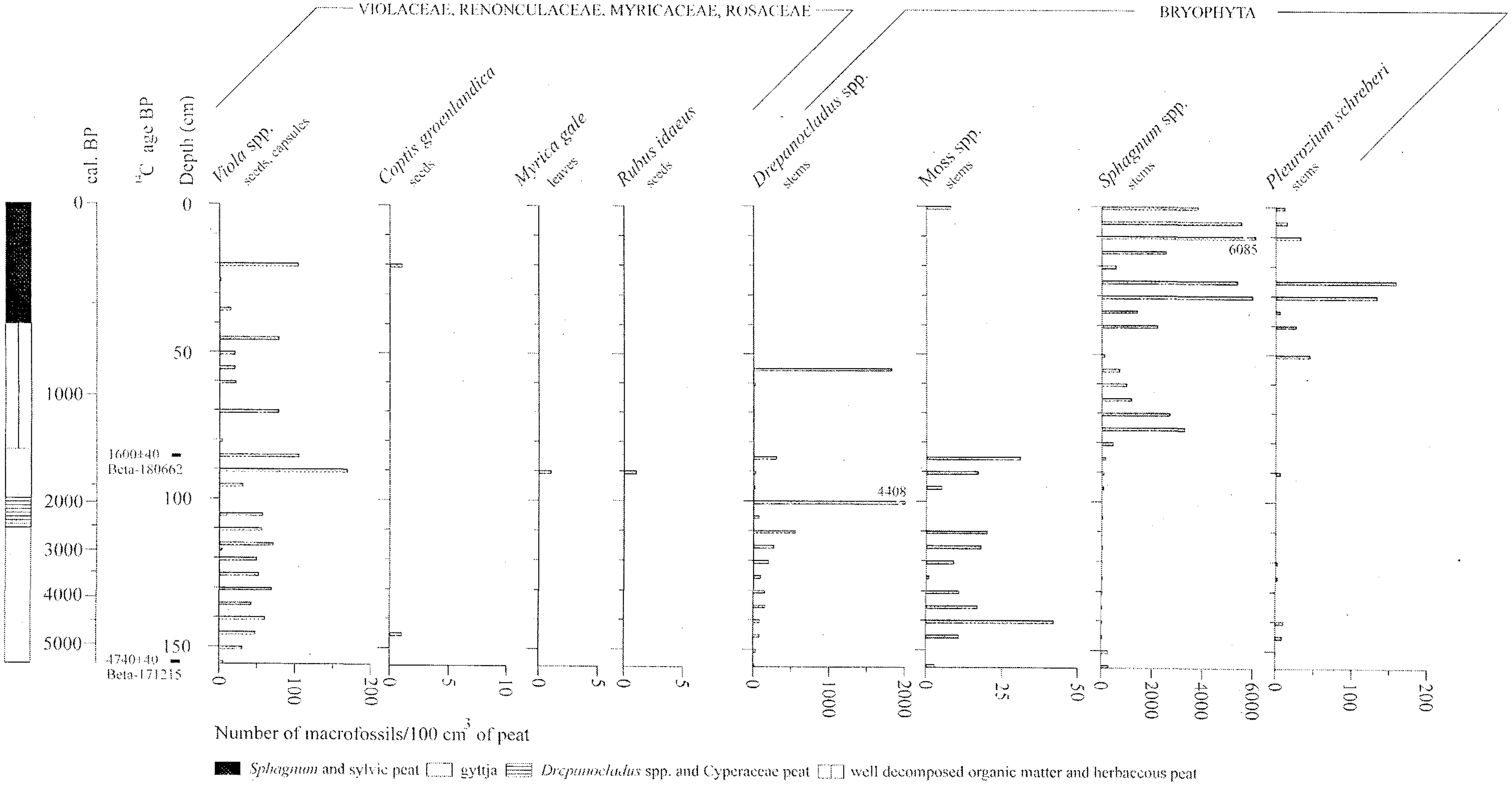
M) VALIN ERICACEAE



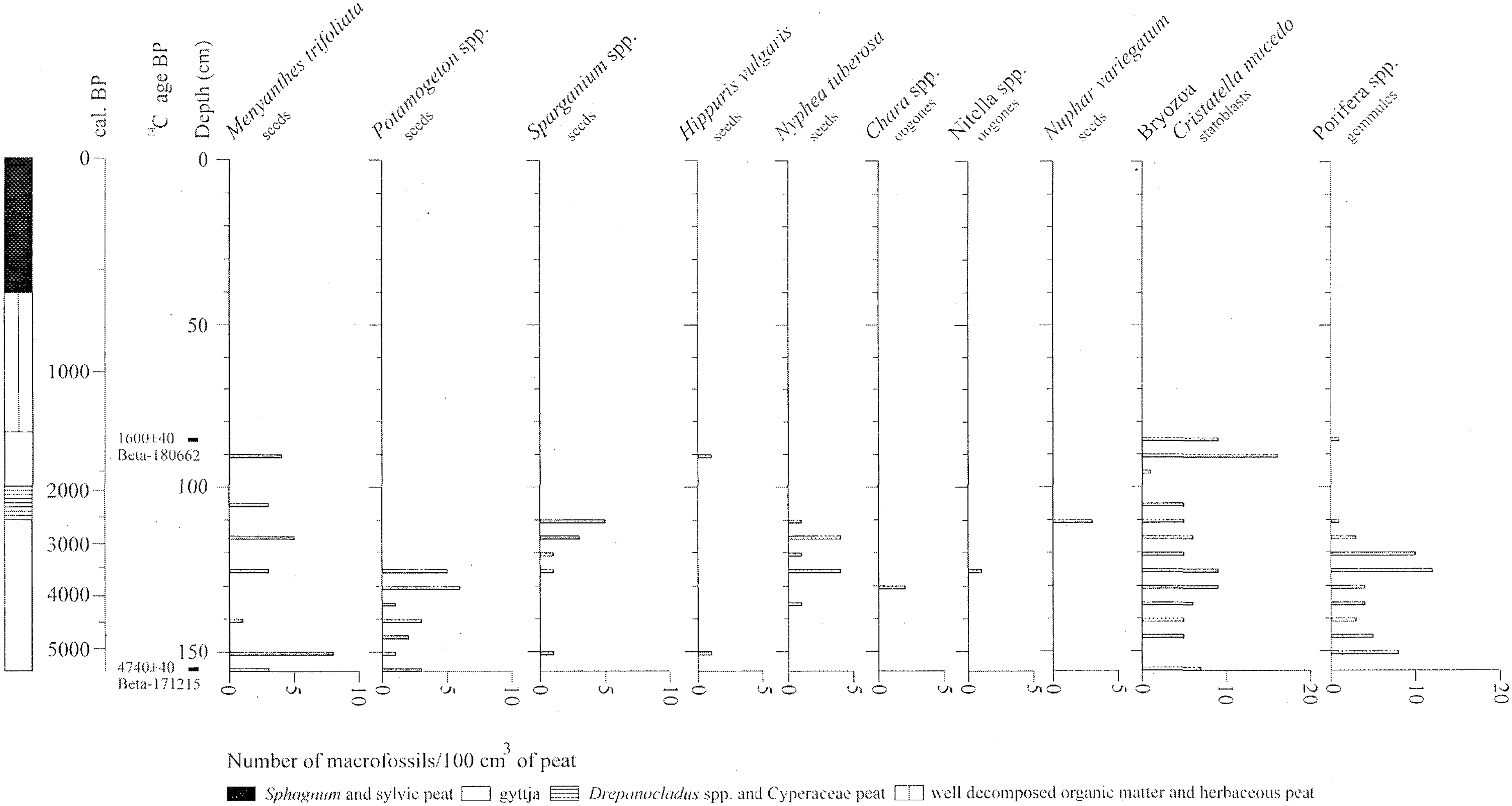
N) VALIN CYPERACEAE



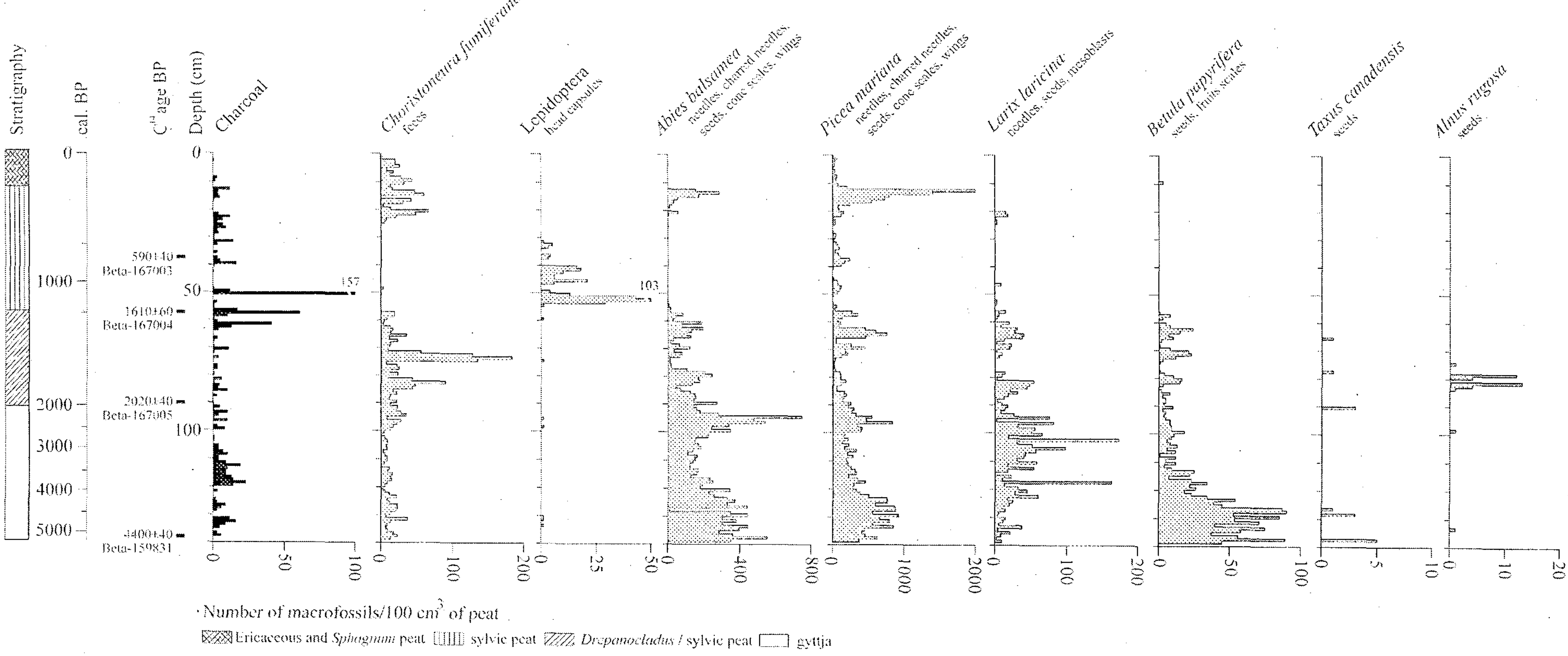
O) VALIN VIOLACEAE, RENONCULACEAE, MYRICACEAE, ROSACEAE AND BRYOPHYTA



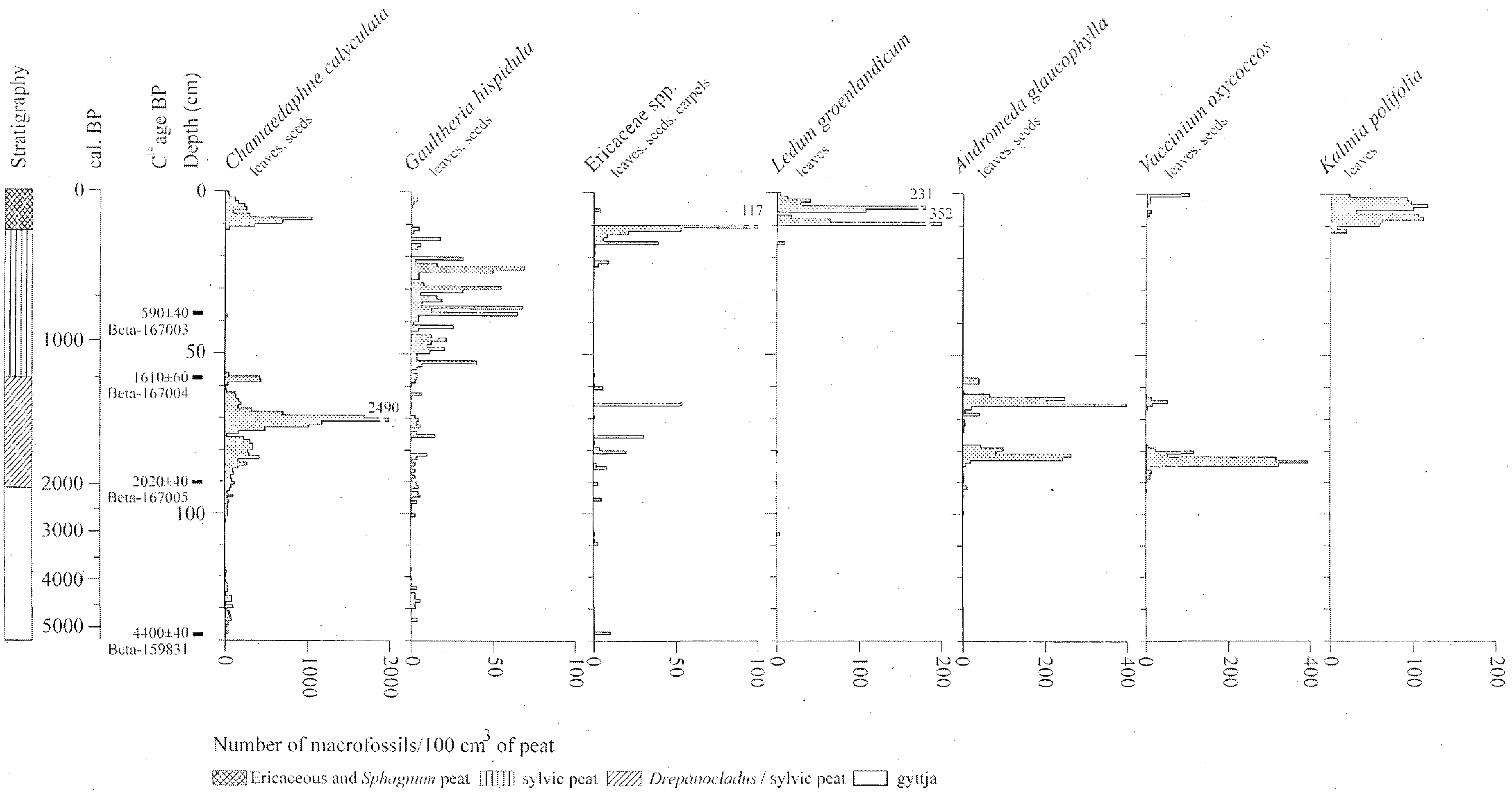
P) VALIN AQUATIC VASCULAR PLANTS, ALGAE AND OTHER TAXA



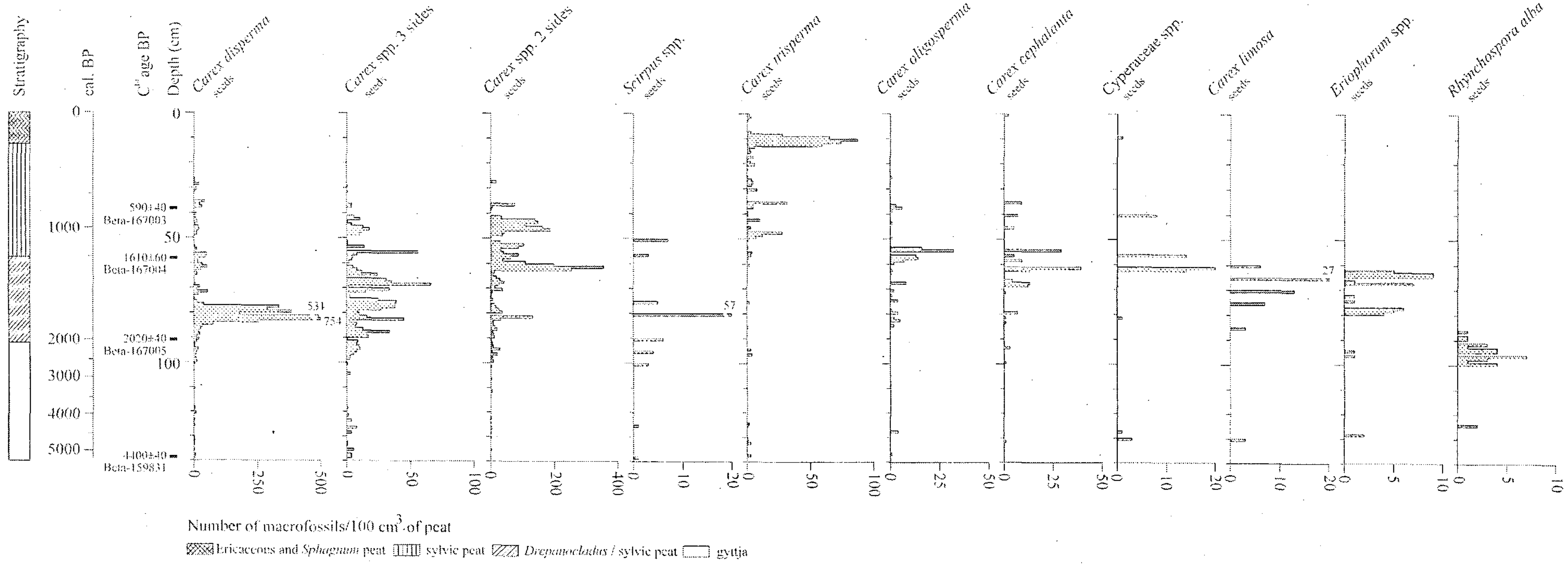
Q) PLT1 TREES AND SHRUBS



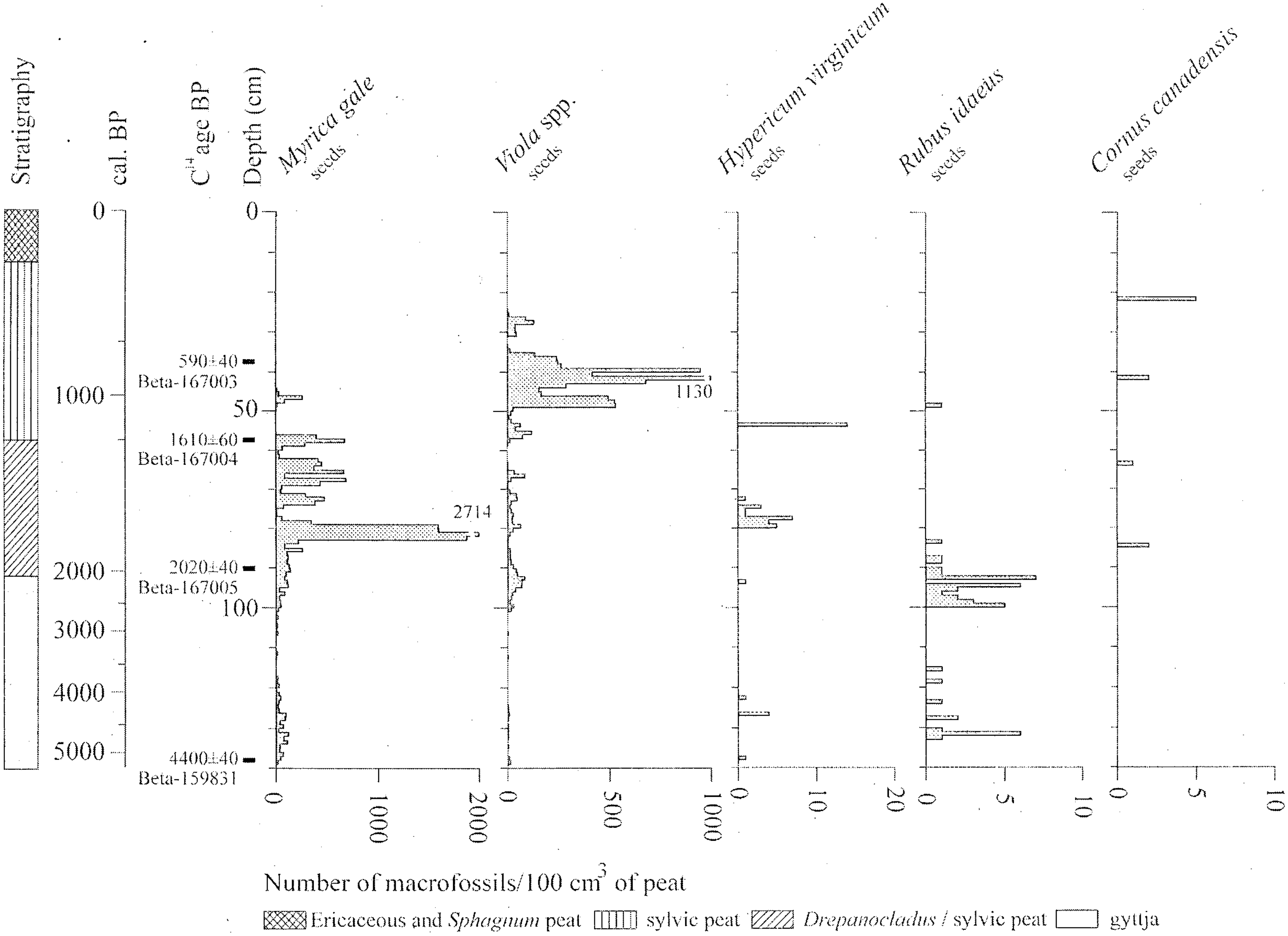
R) PLT 1 ERICACEAE



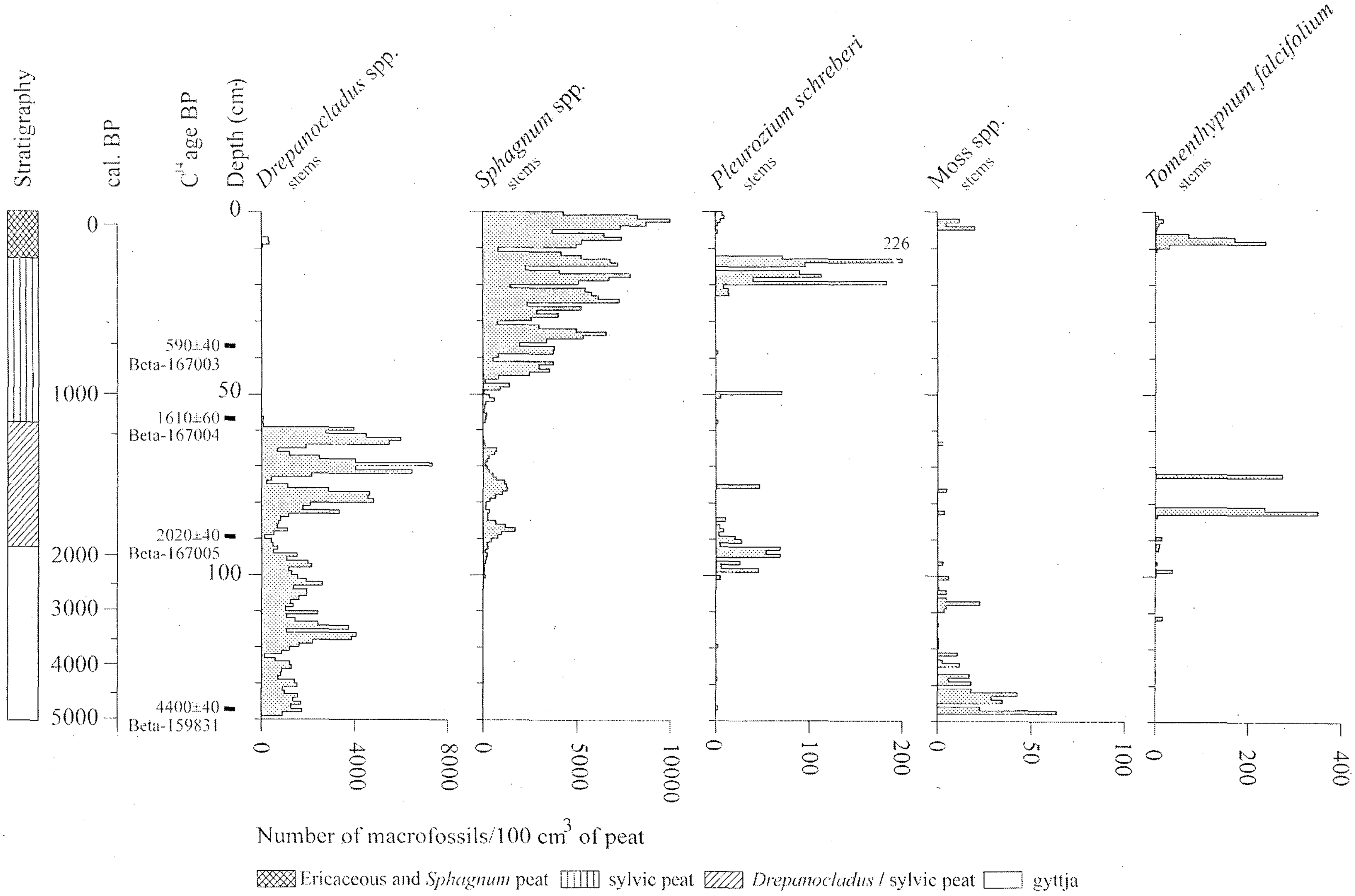
S) PLT1 CYPERACEAE



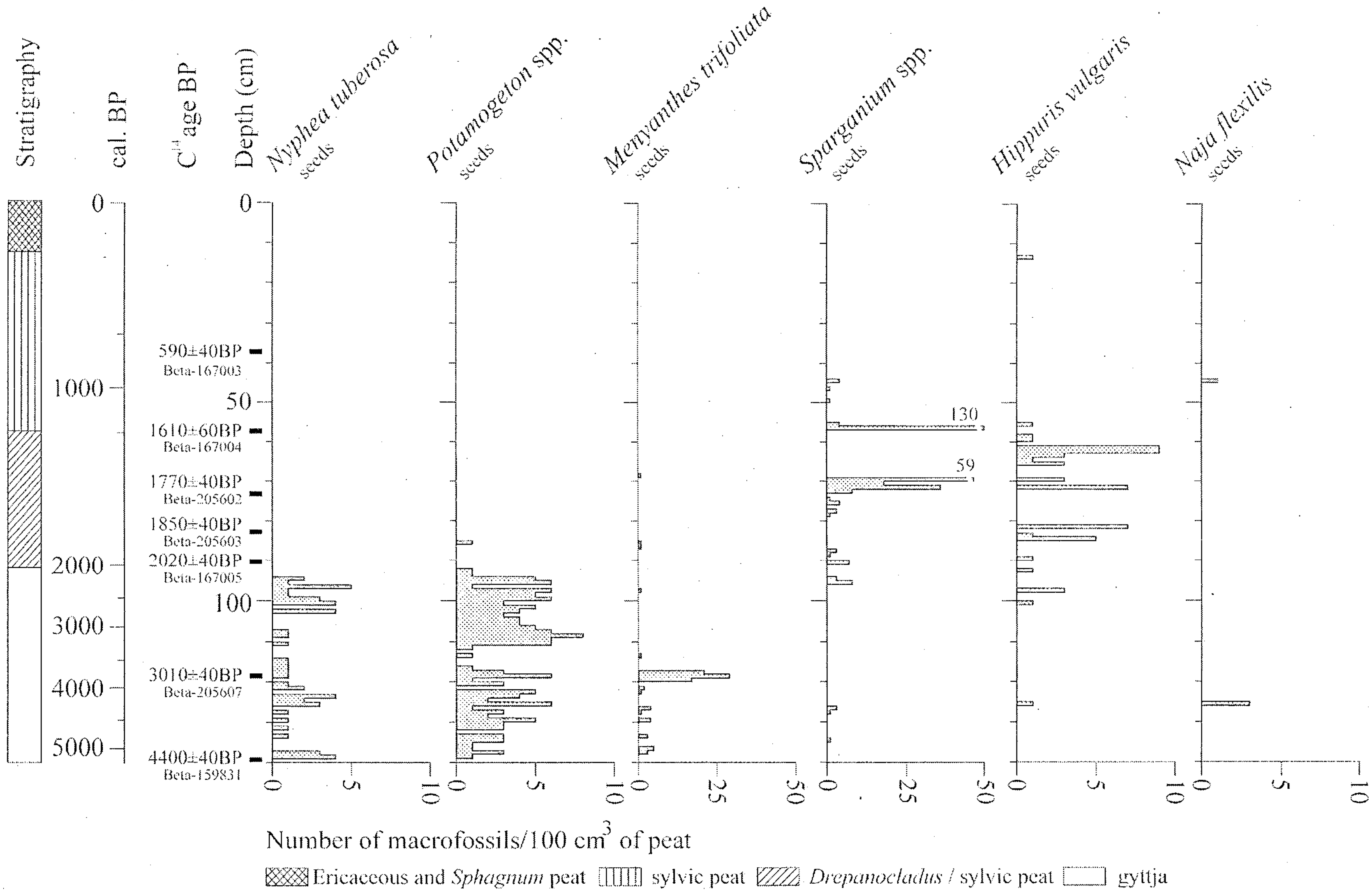
T) PLT1 MYRICACEAE, VIOLACEAE, HYPERICACEAE, ROSACEAE, CORNACEAE



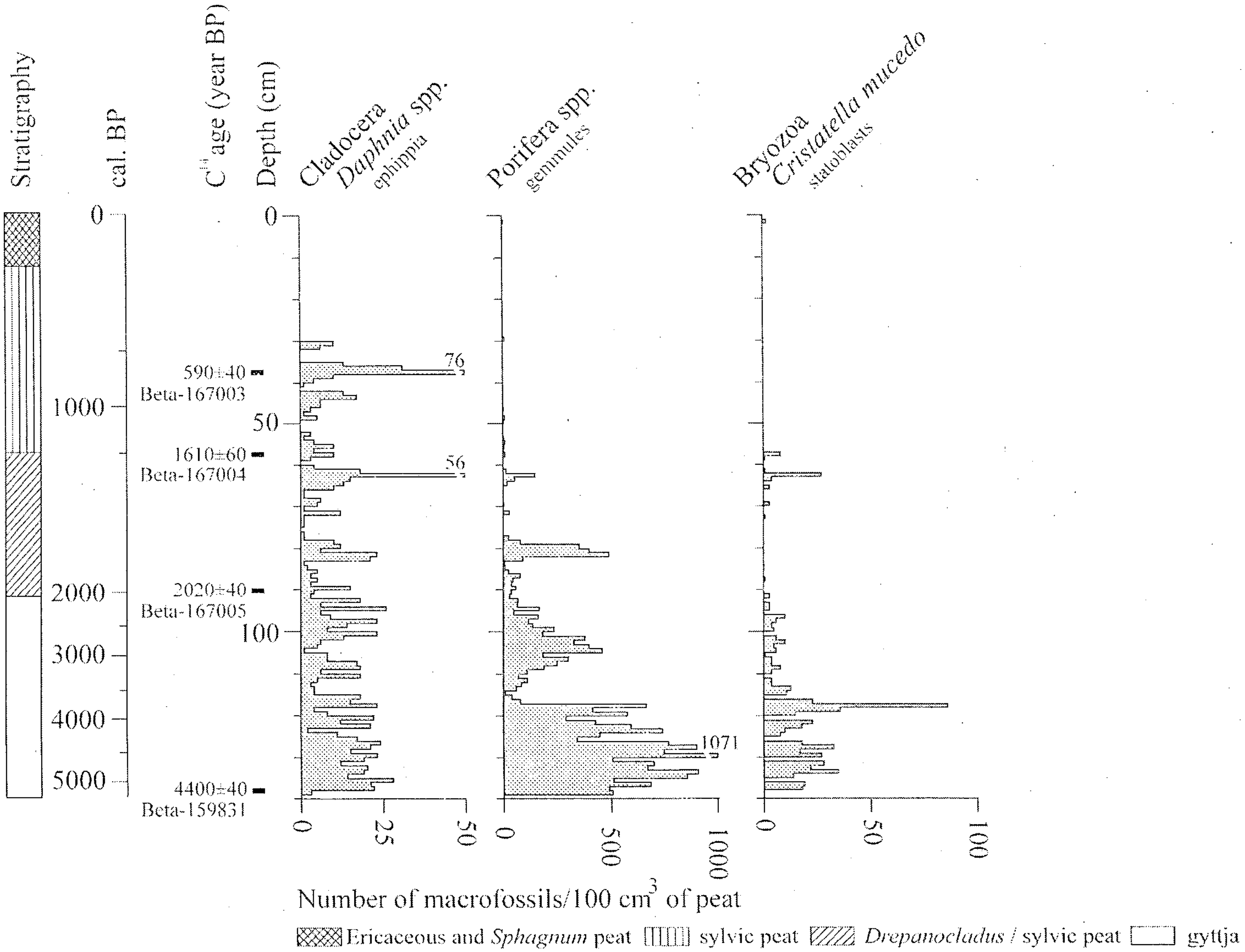
U) PLT1 BRYOPHYTA



V) PLT1 AQUATIC PLANTS



W) PLT1 OTHER TAXA



X) PLT forest humus